Contributions Toward a Monograph of Neotropical Jatropha: Phenetic and Phylogenetic Analyses

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CONTRIBUTIONS TOWARD A MONOGRAPH OF NEOTROPICAL *JATROPHA*: PHENETIC AND PHYLOGENETIC ANALYSES[1]

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ABSTRACT

Phenetic analysis of the New World *Jatropha* L. species generally supports the 1979 classification of the genus by Dehgan and Webster. The distinctness of subgenera *Curcas* (Adans.) Pax and *Jatropha*, the intermediate position of section *Polymorphae* Pax between sections of both subgenera, and the close relationship of sections *Mozinna* (Ortega) Pax and *Loureira* (Cav.) Muell. ex Pax are indicated. Phylogenetic analysis provided evidence of monophyly for subgenus *Jatropha*, sections *Jatropha* and *Mozinna*, and probable paraphyly in subgenus *Curcas* and several sections and subsections. The cladistic analyses described herein produced multiple parsimonious topologies. The circumscriptions of the subgenera and some sections and subsections are significantly clarified. The status of heretofore dubiously placed or recently described species is also elucidated. Although geographical data were not included in the phylogenetic analyses, a distinct correlation between evolutionary trends in morphological features, postulated infrageneric delimitations, and geography of the genus became evident. Evidence is presented to support the antiquity of the genus and its present distribution, which resulted from a Gondwanaland breakup and subsequent overland dispersal across the African and American continents. Adaptive gradual mosaic evolution as a series of successive speciational steps, primarily involving morphological features, in concert with migration to areas of increasing aridity and cold appears to be the norm for the genus.

Adanson (1763) was the first to note that *Jatropha* has proceeded along two evolutionary lines when he recognized the two genera *Jatropha* and *Curcas*, based on Linnaeus's *Species Plantarum* (1763). Although Adanson's generic delimitation proved incompatible with that of later taxonomists (Pohl, 1827; Baillon, 1858; Mueller Argoviensis 1874; Pax, 1910), its basic premise was retained through consolidation and reduction of the two genera to subgenera and/or sections. The gamopetalous nature of the corolla in *Curcas* and its distinctness in *Jatropha* had generally been used as justification for recognition of these groups. McVaugh (1945) was the first to discard the two groups and pointed out the danger of constructing a classification based on a single corolla character. He proposed four "homogeneous" sections for the American species. Dehgan & Webster (1979) accepted and incorporated, with minor modifications, three of McVaugh's four sections into their revised system and recognized them as distinct sections of

the subgenus *Jatropha*. Section *Mozinna* (Ortega) Pax was regarded as more or less equivalent to the subgenus *Curcas* (Adans.) Pax of Dehgan & Webster (1979), which itself now includes four sections. This classification was supported primaily by gross morphology of reproductive structures. A brief review of Dehgan and Webster's classification seems appropriate for better understanding of the results of this study and is presented below.

Two subgenera (*Curcas* and *Jatropha*), ten sections, and ten subsections were recognized to accommodate the Old and New World species. The subgenera were distinguished by growth habit, calyx aestivation, corolla coherence or connation, plant sexuality (monoecious or dioecious), stamen number and arrangement, seed shape, and presence or absence of a caruncle. It was postulated that *J. curcas* L. [sect. *Curcas* (Adans.) Griseb., subg. *Curcas* (Adans.) Pax], retains the most plesiomorphic, or "primitive," features of any species in the genus, notably its palmately lobed leaves,

arborescent growth habit, possession of a discrete coflorescence (a distinct basal-lateral branch of the main-florescence), and occasional hermaphroditic flowers, among other characteristics, including several anatomical features that it shares with members of both subgenera. Evolution from it or a similar ancestral taxon involved changes in growth habit, including loss of arborescence coupled with the acquisition of either a facultative annual growth habit, exemplified by *J. gossypiifolia* L. (sect. *Jatropha*, subg. *Jatropha*), or a rhizomatous subshrub habit, shown by some species of section *Mozinna* (Ortega) Pax, (subg. *Curcas*). These changes were accompanied by a series of reductions in reproductive structures of both subgenera. The evolutionary trends of the inflorescence apparently followed two distinct pathways. On the one hand, modification and ramifications of coflorescences and paracladia (inflorescence branches) resulted in the formation of a highly symmetrical compound dichasium, via section *Polymorphae* Pax, in section *Peltatae* (Pax) Dehgan & Webster (both strictly American) or the coflorescence was reduced to a single pistillate flower in the African section *Collenucia* (Chiov.) Chiov. On the other hand, inflorescences became markedly reduced to a few or solitary flowers in section *Mozinna*, subgenus *Curcas*, in concert with a gradual shift from monoecy to gynodioecy and dioecy. These modifications were often accompanied by changes in chromosome numbers, from diploidy to tetraploidy, nearly always accompanied by acquisition of rhizomatous growth habit. Evolution of the flowers also proceeded in two very different directions. In subgenus *Jatropha*, reduction and rearrangement of stamens has occurred, from ten to eight and from uniseriate to biseriate, connate to free, with no concomitant change in the number of styles and locules of the ovary, all with three bifurcate styles and 3-locular ovary (with the notable exception of two bifurcate styles of *J. martiusii* (Pohl) Baillon). In contrast, the number and arrangement of stamens in the American taxa of subgenus *Curcas* has remained consistently ten, but the number of locules, seeds, and style branches have been gradually reduced from three (in sects. *Curcas* and *Platyphyllae* Dehgan & Webster), to two (in most members of sect. *Loureira* (Cav.) Mull. Arg. ex Pax), and one (in several species of sect. *Mozinna* (Ortega) Pax). In general, these changes exhibit a morphological continuum from south to north, with the southern taxa possessing the more primitive and the northern species the more advanced features.

Several anatomical and micromorphological features support this classification. Both articulated and nonarticulated laticifers are present in members of the subgenus *Jatropha*, but nonarticulated laticifers are lacking from all taxa in sections *Curcas* and *Platyphyllae*. Idioblastic laticifers and chambered crystalliferous parenchyma are characteristic of taxa in subgenus *Curcas* but completely absent from members of the subgenus *Jatropha* (Dehgan & Craig, 1978). Leaf surface morphology indicates the presence of brachyparacytic stomata in subgenus *Jatropha* and the true paracytic type in subgenus *Curcas*. Epidermal hairs of most taxa in subgenus *Jatropha* are uniseriate-multicellular and smooth, while those of subgenus *Curcas* are unicellular and verrucate (Dehgan, 1980; Olowokudejo, 1993). The number and arrangement of petiolar vascular bundles vary from (11–)9, 7, 5, and 3 in a ring, as free traces, medullated cylinder, or U-shaped free or medullated free traces (Dehgan, 1982).

In hybridization studies, Dehgan (1984) presented evidence that taxa further apart in the revised evolutionary classification were progressively less capable of interbreeding than more closely positioned taxa. Related species were shown to have a high degree of unilateral compatibility but to be separated by preferential fertilization, whereas the more phylogenetically distant taxa were incompatible. *Jatropha curcas* L., which, in agreement with McVaugh (1945) and Wilbur (1954), was considered the most primitive species on morphological and anatomical grounds, proved most compatible with species of sections with presumably closest affinity (e.g., *J. integerrima* Jacq. of sect. *Polymorphae*), and least compatible with taxa of the more advanced sections (e.g., *J. gossypiifolia* of sect. *Jatropha* and *J. dioica* Sessé, of sect. *Mozinna*). It was concluded that in *Jatropha* phylogenetic distance may be reflected by ability of the species to interbreed.

Despite these convincing lines of evidence supporting alignment of the taxa, placement of some species remained somewhat dubious. Scarcity of living plants, incomplete herbarium specimens, and insufficient knowledge of the South American taxa (sects. *Jatropha* and *Peltatae*) were among the reasons for doubtful placement of several species. With the senior author's recent extensive field collections in Brazil and Mexico, reappraisal and/or confirmation of Dehgan & Webster's (1979) revision, using all available information for the neotropical taxa, seemed appropriate. The authors were also interested in examining the present taxonomic delimitation and assessment of relationships through

interpretation of the results of phenetic and cladistic analyses. The intent of this paper is not to present a cladistic classification of the New World taxa; we know that New World jatrophas do not constitute a strictly monophyletic group, and that Old World taxa must be included to create a new cladistic classification. Thus, we have used both cladistic and phenetic techniques to examine the current traditional morphology-based classification for corroborative purposes only. With a brief discussion of geography and evolution added, this report is intended as a contribution toward a monographic treatment of the neotropical species in the near future.

A. Ordination and Hierarchical Cluster Analysis

Materials and Methods

Principal component ordination and hierarchical cluster analysis of living and herbarium specimens of 93 taxa (subsequently reduced to 77 based on later assessments of synonymy) representing all New World species, and 32 characters (see Appendix for vouchers, Table 1 for characters) were performed using F. J. Rohlf's NTSYS-pc multivariate statistical program package (version 1.4). The data matrix of 77 taxa by 32 characters is shown in Table 2. Although this program provides three-dimensional scattergrams, two- and three-dimensional scattergrams were constructed from PCA factor scores using a computer program written by the second author. Among other features, this program has the distinct advantage of enabling the user to identify individual taxa by their identification number in the data matrix. It also has the ability to "zoom in" on and enlarge selected areas of the PCA scattergram so that the identity of closely spaced taxa in the diagram may be more easily resolved. Data matrices are input to the NTSYS-pc program, which standardizes the raw data ("z-score" method of Sneath & Sokal, 1973), calculates eigenvectors, and projects them onto axes for display. Schutzman's program can read and display the projection output files from NTSYS-pc with only minor modifications.

Results and Discussion

The results of PCA and hierarchical cluster analyses (Figs. 1–4) for the most part confirmed the earlier infrageneric classification of Dehgan & Webster (1979). Factor loadings, signifying the most meaningful characteristics for each principal

component in each of the three PCAs, were calculated and are listed in Table 3A–C. Two discrete groups of OTUs corresponding to subgenera *Jatropha* and *Curcas* were apparent at the outset (Figs. 1 and 4). The centralized, unifying position of section *Polymorphae* had already been predicted and illustrated by Dehgan (1984). The affinity of this section with both subgenera became more apparent when species of *Polymorphae* were included in both data sets and analyzed independently (Figs. 2 and 3). In addition to their past (see the discussion below) and present geographical affiliation (Mesoamerica and West Indies), it was shown earlier (Dehgan, 1984) that *J. integerrima* and *J. curcas* are highly compatible and produce fertile progeny when artificially crossed. In fact, there is considerable phenetic similarity between sections *Curcas* and *Polymorphae*. The presence of 10 connate biseriate stamens, connation and/or imbrications of the petals, and similarity of leaf morphology are but a few of the reasons for such relationship. The affinity of *J. hernandiifolia* Vent., *J. divaricata* Sw. (both West Indian), and *J. gaumeri* Greenm. (endemic to the Yucatan Peninsula), species placed by Dehgan & Webster (1979) in subsection *Hernandiifoliae* Dehgan & Webster of section *Polymorphae*, has also been confirmed by the results of the phenetic analyses presented here. Recognition of a distinct subsection was based on the seven petiolar traces with secondary growth, corymbose inflorescence without a coflorescence, and campanulate pistillate flowers with imbricate petals. However, their placement with species previously grouped under section *Platyphyllae* in the PCA and cluster analyses (Figs. 1–4) was suspected on morphological and geographical grounds and appears quite reasonable. Except for the unique inflorescences of *J. hernandiifolia* and *J. divaricata*, nearly all other features, including white flowers, number and arrangement of stamens, features of the perianth, and entire nonglandular leaves, are very similar among the taxa in this section.

Reasons for probable derivation of species in section *Mozinna* from those of section *Loureira* based on morphological-anatomical features were discussed by Dehgan & Webster (1979) and by Dehgan & Craig (1978) and Dehgan (1980, 1982, 1984). The plausibility of such relationship is further strengthened by the results of both phenetic and cladistic analyses and is examined further below. Affinities of a few other species, such as *J. moranii* Dehgan & Webster (endemic to a small area in Baja California), *J. bullockii* Lott (with 8 biseriate stamens, endemic to higher elevations of

TABLE 1. Characters and character states for ordination and hierarchical cluster analysis.

1. Growth form:	Trees (0), shrubs (1), subshrubs (2). Based on strict botanical definition a tree is assumed to be in excess of 5 meters, a shrub 1–5 meters, and a subshrub less than 1 meter.	
2. Caudiciform habit:	Plants geophytes (1), plants typical (0). Plants with thickened subterranean stems (a subterranean caudex).	
3. Rhizomatous habit:	Plants rhizomatous (1), plants typical (0), Plants with spreading rhizomes.	
4. Plant sex:	Dioecious (1), monoecious (0).	
5. Laticifers:	Articulated and/or nonarticulated (1), idioblastic (0). Some species possess both articulated and nonarticulated laticifers but only some have idioblastic type.	
6. Laticifers:	Nonarticulated (1), articulated (0). Plants may have both articulated and non-articulated laticifers but nonarticulated absent from some.	
7. Leaf outline:	Lanceolate (0), ovate-lanceolate (1), ovate-elliptic (2), cordate-reniform (3), obovate (4). A general outline of whole leaves regardless of lobing.	
8. Leaf base:	Peltate (1), not peltate (0).	
9. Leaf basal glands:	Present (1), absent (0). Basal glands are considered present even if the entire leaf margin is beset with stipitate glands.	
10. Leaf margins:	Toothed (1), entire (0).	
11. Leaf marginal glands:	Ciliate-glandular (1), eglandular (0). Margins may be toothed or entire and may or may not have glands.	
12. Leaf sinus depth:	Parted (1), not parted (0). Leaves may be shallowly lobed but not necessarily parted.	
13. Leaf lobe numbers:	Unlobed (0), 3- (3); 5- (5); 7- (7); 9-lobed (9). Infrequent occurrences of lobed leaves in plants with typically unlobed leaves have been ignored.	
14. Leaf veins:	Palmate (1), pinnate (0).	
15. Petioles:	Long (1), subsessile (0).	
16. Petiolar traces:	3 (3), 5 (5), 7 (7), 9 (9), 11 (11).	
17. Stipules:	Absent or fugacious (0), foliar (1), glandular-ciliate (2), filiform (3).	
18. Hairs:	Absent (0), unicellular (1), uniseriate-multicellular (2).	
19. Coflorescences:	Present (1), absent (0).	
20. Flower shape:	Campanulate (0), rotate (1), tubular or urceolate (2).	
21. Flower color:	White (1), other (0). This refers to absolute white flowers as opposed to yellowish or greenish white, and other colors.	
22. Petals of ♀ flowers:	Distinct (0), imbricate (1), connate (2).	
23. Petals of ♂ flowers:	Distinct (0), imbricate (1), connate (2). Frequently there is no correspondence between condition of the petals in the male and female flowers. The corolla may be distinct in the female but connate in the male.	
24. Stamen arrangement:	Monadelphous (1), diadelphous (0).	
25. Stamen number:	8 (1), 10 (0). Occasional odd stamen numbers have been ignored.	
26. Stamen fusion:	Free (1), connate (0). Stamens have been considered connate even if only the central group is connate but the outer is free.	
27. Style fusion:	Free (1), connate (0).	
28. Calyx of ♀ flowers:	Foliaceous (1), not foliaceous (0). This refers only to the unusually large, leaf-like sepals.	
29. Calyx lobe margins:	Glandular (1), entire (0).	
30. Fruit dehiscence:	Violently dehiscent (1), tardily dehiscent (0). Fruit may explode upon maturity or remain intact for a considerable length of time.	
31. Fruit locule number:	1 (1), 2 (2), 3 (3).	
32. Seed:	Carunculate (1), ecarunculate (0).	

a small area in Jalisco, Mexico), and *J. purpurea* Rose (narrow endemic in western Mexico), are also discussed below. Other than these few changes the basic delineation of Dehgan & Webster's (1979) infrageneric classification remains intact, but the necessity to create new monotypic sections for such species as *J. martiusii* will also be further elucidated.

B. CLADISTIC ANALYSIS

MATERIALS AND METHODS

Cladistic analyses were performed on the data set of 77 evolutionary units (EUs) and 31 characters using Hennig86 (James Farris, Department of Ecology and Evolution, State University of New York, Stony Brook, 1988) version 1.5. The char-

TABLE 2. Matrix of character states for 77 *Jatropha* species used in the phenetic analysis.

Characters

Taxon	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
alamanii	0	0	0	1	1	1	3	0	0	0	0	0	5	0	1	07	0	0	0	2	1	2	0	0	0	0	0	1	0	0	3	0
andrieuxii	1	0	0	1	0	0	3	0	0	1	0	0	7	0	1	09	3	1	1	0	1	2	0	0	0	0	0	0	0	0	3	0
angustifolia	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	07	0	0	0	1	0	1	1	0	0	0	0	0	0	1	3	1
augustii	1	0	0	0	1	1	3	1	1	0	1	0	5	0	1	07	3	0	0	1	0	0	0	1	1	0	0	0	0	1	3	1
bartlettii	0	0	0	1	0	0	3	0	0	1	0	0	5	0	1	09	3	1	1	0	1	0	1	0	0	0	0	1	1	0	3	0
bullockii	1	0	0	0	0	0	3	0	0	0	0	0	3	0	1	05	0	0	0	2	1	2	0	0	1	0	0	0	0	1	3	1
canescens	1	0	0	1	1	1	2	0	0	0	0	0	0	0	1	05	0	1	0	2	0	2	2	0	0	0	0	1	0	0	2	0
cardiophylla	2	0	1	1	1	1	3	0	0	0	0	0	0	0	1	05	0	0	0	2	0	2	2	0	0	0	0	0	0	0	1	0
cathartica	2	1	0	0	0	0	3	0	0	0	0	1	7	0	1	09	3	0	0	1	0	0	0	1	1	1	1	0	0	1	3	0
chamelensis	0	0	0	1	1	1	2	0	1	0	0	0	0	0	1	09	0	0	0	2	1	0	2	0	0	0	0	1	0	1	3	0
ciliata	1	0	0	1	1	1	3	0	1	1	1	0	5	0	1	07	0	0	0	2	1	2	2	0	0	0	0	0	0	1	3	0
cinerea	1	0	0	1	1	1	3	0	0	0	0	0	3	0	1	05	0	1	0	2	0	2	2	0	0	0	0	1	0	0	2	0
clavuligera	1	0	0	0	0	1	2	0	1	0	1	1	7	0	1	07	2	2	1	0	0	0	0	0	0	0	1	0	1	1	3	1
cordata	0	0	0	1	1	1	3	0	1	0	1	0	0	1	1	07	2	0	0	2	0	2	2	0	0	0	0	1	1	0	2	0
costaricensis	0	0	0	1	0	0	2	0	0	0	0	0	5	0	1	07	0	1	1	2	1	2	2	1	0	0	0	1	0	0	3	0
cuneata	1	0	0	1	1	1	2	0	0	0	0	0	3	2	0	03	0	0	0	2	1	2	2	0	0	0	0	0	0	0	1	0
curcas	0	0	0	0	0	0	3	0	0	0	0	0	5	0	1	09	0	0	1	0	1	0	2	0	0	0	0	0	0	0	3	0
dioica	2	0	1	1	1	1	2	0	0	0	0	0	3	2	0	03	0	0	0	2	0	2	2	0	0	0	0	0	0	0	1	0
dissecta	2	1	0	0	0	1	3	0	1	0	1	1	5	0	1	07	2	2	1	1	0	0	0	1	1	0	1	0	1	1	3	1
divaricata	0	0	0	0	0	1	2	0	0	0	0	0	0	1	1	07	0	0	0	2	1	0	0	0	0	0	0	0	0	1	3	1
eglandulosa	2	0	0	0	0	1	2	0	0	0	0	0	1	0	0	07	3	2	1	0	0	0	1	1	1	0	0	0	0	1	3	1
elbae	1	0	0	1	1	1	2	0	0	0	0	0	2	0	0	03	0	0	0	2	1	2	2	0	0	0	0	0	0	0	1	0
elliptica	2	1	0	0	0	1	2	0	1	0	1	0	0	1	0	07	2	2	1	0	0	2	0	1	1	0	0	0	1	1	3	1
excisa	1	0	0	0	0	1	2	0	1	0	1	0	5	0	1	07	2	1	1	0	0	0	0	0	0	0	1	0	1	1	3	1
flavovirens	1	0	0	0	0	1	2	0	1	0	1	1	3	0	1	07	2	2	1	0	0	0	0	0	1	0	1	0	1	1	3	1
fremontioides	2	0	0	0	1	1	2	0	0	0	0	0	3	0	0	05	0	1	0	2	0	2	0	0	0	0	0	0	0	1	3	1
galvanii	0	0	0	1	1	1	3	0	0	0	0	0	0	0	1	07	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2	0
gaumeri	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	07	0	0	0	2	1	2	2	1	1	0	1	0	0	1	3	1
giffordiana	1	0	0	1	1	1	3	0	0	0	0	0	0	0	1	05	0	1	0	2	0	2	2	0	0	0	0	1	0	0	3	0
gossypiifolia	1	0	0	0	0	1	3	0	1	0	1	0	5	0	1	07	2	2	1	0	0	0	0	1	0	0	1	0	0	1	3	1
grossidentata	1	0	0	0	0	1	2	0	0	1	0	0	5	0	1	07	0	0	0	1	0	0	0	1	1	1	1	0	0	1	3	1
guaranitica	2	1	0	0	0	1	3	0	1	0	1	0	3	0	1	07	2	2	1	0	0	0	0	0	1	0	1	0	1	1	3	1
hernandiifolia	0	0	0	0	0	0	2	1	0	0	0	0	3	0	1	07	0	0	0	2	1	1	2	0	0	0	0	0	0	1	3	1
hieronymii	0	0	0	0	0	1	3	0	0	1	0	0	5	0	1	07	2	0	0	1	0	0	0	1	1	1	1	0	0	1	3	1
hintonii	0	0	0	0	0	0	3	0	0	0	0	0	3	0	1	09	0	1	1	0	1	0	1	0	0	0	0	0	0	0	3	1
humboldtiana	1	0	0	0	0	1	3	1	1	0	1	0	0	0	1	07	2	0	0	1	0	0	0	1	1	1	0	0	0	1	3	1
integerrima	1	0	0	0	0	0	2	0	0	0	0	0	3	0	1	07	3	0	0	1	0	1	1	0	0	0	0	0	0	1	3	1
intercedens	1	0	0	0	0	1	2	0	1	0	1	0	3	0	1	07	2	2	1	0	0	0	0	0	1	0	0	0	1	1	3	1
intermedia	2	1	0	0	0	1	2	0	1	0	1	0	0	1	0	07	2	2	1	0	0	0	0	0	1	0	1	0	1	1	3	1
isabellii	2	1	0	0	0	1	2	0	1	0	1	0	0	1	0	07	2	2	1	0	0	0	0	0	0	1	0	1	1	3	1	1
katharinae	1	0	0	0	0	1	3	0	1	0	1	0	3	0	1	07	2	2	1	0	0	0	0	0	1	0	1	0	1	1	3	1
macrantha	2	0	0	0	0	1	3	0	0	0	0	0	3	0	1	07	1	0	0	1	0	0	0	1	0	0	0	0	0	1	3	1
macrocarpa	0	0	0	0	0	1	2	0	0	0	0	0	5	0	1	07	0	0	0	1	0	0	0	0	1	0	1	0	0	1	3	1
macrorhiza	2	1	0	0	0	1	3	0	0	1	0	1	7	0	1	07	3	0	0	1	0	0	0	0	1	0	1	0	0	1	3	1
malacophylla	0	0	0	1	0	0	3	0	0	1	0	0	5	0	1	09	0	1	0	0	1	2	2	1	0	0	0	1	0	0	3	0
martiusii	1	0	0	0	0	1	2	0	0	0	0	1	5	0	1	07	2	0	0	2	0	2	2	0	1	0	1	0	1	1	3	1
mcvaughii	0	0	0	1	0	0	3	0	0	0	0	0	7	0	1	09	0	1	1	0	1	2	2	1	0	0	0	0	0	0	3	0
mollissima	0	0	0	0	0	1	3	0	0	0	0	0	5	0	1	07	2	1	0	1	0	0	0	1	1	1	1	0	1	1	3	1
moranii	1	0	0	0	0	0	2	0	1	0	1	0	5	0	1	07	0	0	0	1	2	2	0	0	0	0	1	1	0	1	3	1
multifida	0	0	0	0	0	1	3	0	0	0	0	1	9	0	!	11	3	0	0	1	0	0	0	1	1	1	1	0	0	0	3	0
mutabilis	1	0	0	0	0	1	2	0	0	0	0	0	0	1	1	07	1	1	0	1	0	0	0	1	1	1	1	0	1	1	3	1
neopauciflora	1	0	0	1	1	1	2	0	0	0	0	0	2	0	0	05	3	0	0	2	0	2	2	0	0	0	0	0	0	0	2	0
nudicaulis	1	0	0	0	0	1	3	1	0	0	0	0	5	0	1	07	2	0	0	1	0	0	0	1	1	1	1	0	0	1	3	1
olivacea	0	0	0	0	1	1	3	0	1	1	1	0	3	0	1	07	3	1	0	2	1	2	2	0	0	0	0	1	0	0	2	0

TABLE 2. Continued.

| Taxon	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
ortegae	0	0	0	1	1	1	2	0	1	0	1	0	0	1	1	05	0	1	0	2	0	2	2	0	0	0	0	0	1	0	3	0
pachypoda	2	1	0	0	0	1	3	0	1	0	1	0	5	0	1	07	2	0	0	1	0	0	0	1	1	1	1	0	1	1	3	1
pauciflora	1	0	0	0	0	0	0	0	0	0	0	0	3	1	1	07	0	0	0	1	0	0	0	0	0	1	0	0	0	1	3	1
peiranoi	2	1	0	0	0	1	3	0	1	0	1	0	5	0	1	07	2	0	1	0	0	2	2	0	0	0	1	0	1	1	3	1
platyphylla	0	0	0	1	0	0	3	1	0	0	0	0	0	0	1	09	0	0	0	2	1	2	2	0	0	0	1	1	0	1	3	0
podagrica	2	0	0	0	0	1	3	1	0	0	0	0	3	0	1	09	2	0	0	1	0	0	0	1	1	1	1	0	0	1	3	1
pohliana	0	0	0	0	0	1	3	0	0	1	1	0	5	0	1	07	2	1	0	1	0	0	0	1	1	1	0	0	1	1	3	1
pseudocurcas	0	0	0	0	0	0	3	0	0	0	0	0	5	0	1	09	0	1	1	0	1	0	0	1	0	0	0	0	0	0	3	0
purpurea	1	0	0	0	0	0	2	0	1	0	1	0	5	0	1	05	2	0	0	2	0	0	1	1	0	0	1	0	1	1	3	1
ribifolia	1	0	0	0	0	1	3	0	1	0	1	0	3	0	1	07	2	2	1	1	0	0	0	1	1	0	0	0	1	1	3	1
ricinifolia	0	0	0	0	0	0	3	0	0	1	0	0	5	0	1	07	3	0	0	1	0	0	0	1	1	1	0	0	1	1	3	1
riojae	1	0	0	1	1	1	2	0	1	0	0	0	0	1	1	05	0	0	0	2	0	2	2	0	0	0	0	0	0	0	3	0
rufescens	0	0	1	1	0	0	3	0	0	0	0	0	0	0	1	09	0	1	0	0	1	0	2	0	0	0	0	1	0	0	3	0
rzedowskii	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	03	0	1	0	2	0	0	0	0	0	0	0	0	0	0	1	0
standleyi	0	0	0	1	1	1	2	0	1	0	0	0	0	0	1	07	0	0	0	2	1	2	2	0	0	0	0	0	0	0	2	0
stevensii	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	05	0	1	1	2	1	2	2	0	0	0	0	0	0	1	3	1
sympetala	0	0	0	1	1	1	1	0	0	0	0	0	0	1	1	07	0	0	0	2	1	2	2	0	0	0	0	0	0	0	2	0
tlalcozotitlanensis	1	0	0	0	1	1	3	0	1	0	1	0	0	1	1	05	0	1	0	2	1	2	2	0	0	0	0	1	0	1	3	1
thyrsantha	1	0	0	0	0	1	3	0	1	0	1	0	3	0	1	07	2	2	1	0	1	1	0	0	1	1	0	0	0	1	3	1
tupifolia	1	0	0	0	0	0	3	0	1	1	0	0	3	0	1	07	3	0	0	1	0	1	1	0	0	0	0	0	0	1	3	1
vernicosa	1	0	0	1	1	1	2	0	1	0	1	0	0	1	1	07	2	0	0	2	0	0	0	0	0	0	1	1	1	0	2	0
weddelliana	1	0	0	0	0	1	2	0	0	0	0	0	5	0	1	07	0	0	0	1	0	0	0	1	1	1	1	0	0	1	3	1
yucatanensis	0	0	0	0	0	0	3	0	0	0	0	0	0	0	1	09	0	0	1	0	1	0	2	1	0	0	0	0	0	0	3	0
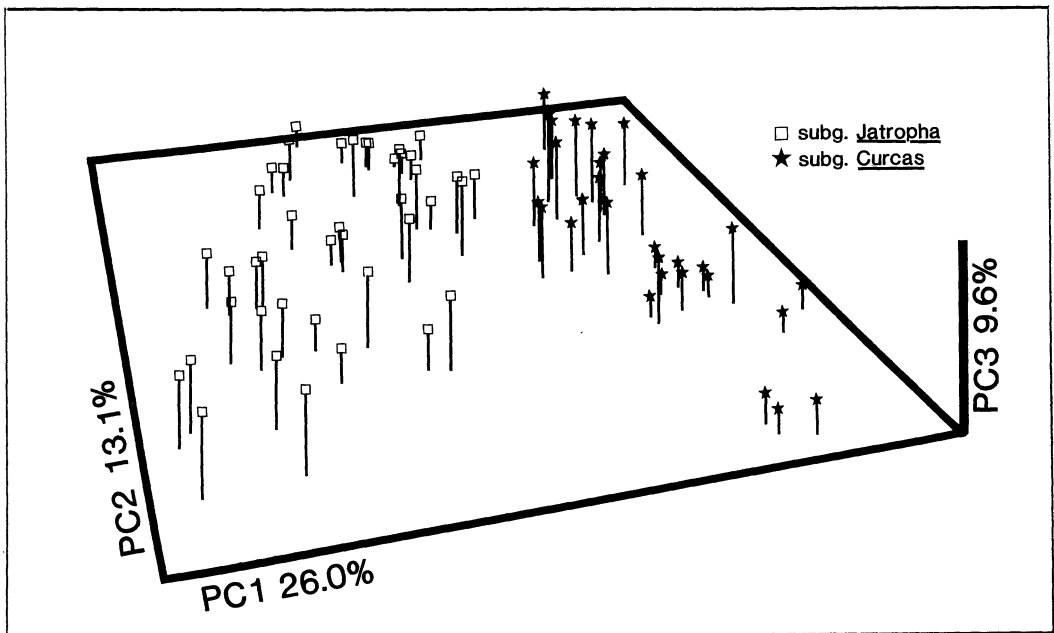
FIGURE 1. PCA of 77 *Jatropha* species from 32 characters, using F. J. Rohlf's NTSYS-pc program. Infrageneric designations are from Dehgan & Webster (1979).

TABLE 3A.   Selected characters* with highest factor loadings (in order of magnitude) for each principal component in analysis of 77 species of *Jatropha*.

PC1		PC2		PC3	
Character number	Factor loading	Character number	Factor loading	Character number	Factor loading
4	−0.278	16	−0.327	19	0.384
5	−0.263	6	0.317	26	−0.351
32	0.259	1	0.307	18	0.327
23	−0.256	15	−0.304	9	0.283
25	0.259	14	0.287	20	−0.257
30	0.252	13	−0.204	11	0.274

* See Table 1.

acters are listed in Table 4, and the data matrix is presented in Table 5. Earlier runs were made using PAUP Version 2.4.1 (David Swofford, Illinois Natural History Survey, 1984) and CLADOS Version 0.9 (Kevin Nixon, Bailey Hortorium, Cornell University, 1988). However, these programs both proved unsatisfactory because of limitations on number of taxa or on character coding.

Three sets of analyses were performed, the first using only *Aleurites* G. Forster as an outgroup, the second using only *Joannesia* Vell., and the third with both genera selected as outgroups. Selection of these outgroups was based on (1) the presumed close affinity of *Joannesia* with *Jatropha*

in tribe *Joannesiae* (Muell. Arg.) Pax (Webster, 1975, 1994, this issue) and (2) the fact that we consider *Aleurites* to be closely related to *Jatropha* on morphological grounds. We know of no prior discussion of possible sister taxa to *Jatropha*. *Cnidoscolus* Pohl had already been ruled out as a possible sister group (McVaugh, 1944; Miller & Webster, 1962).

Character polarities were not explicitly designated (nonadditive option of Hennig86), but the selection of *Aleurites* and *Joannesia* as outgroups effectively polarized the characters (Maddison et al., 1984; Watrous & Wheeler, 1981). Within each outgroup selection, two algorithms were used
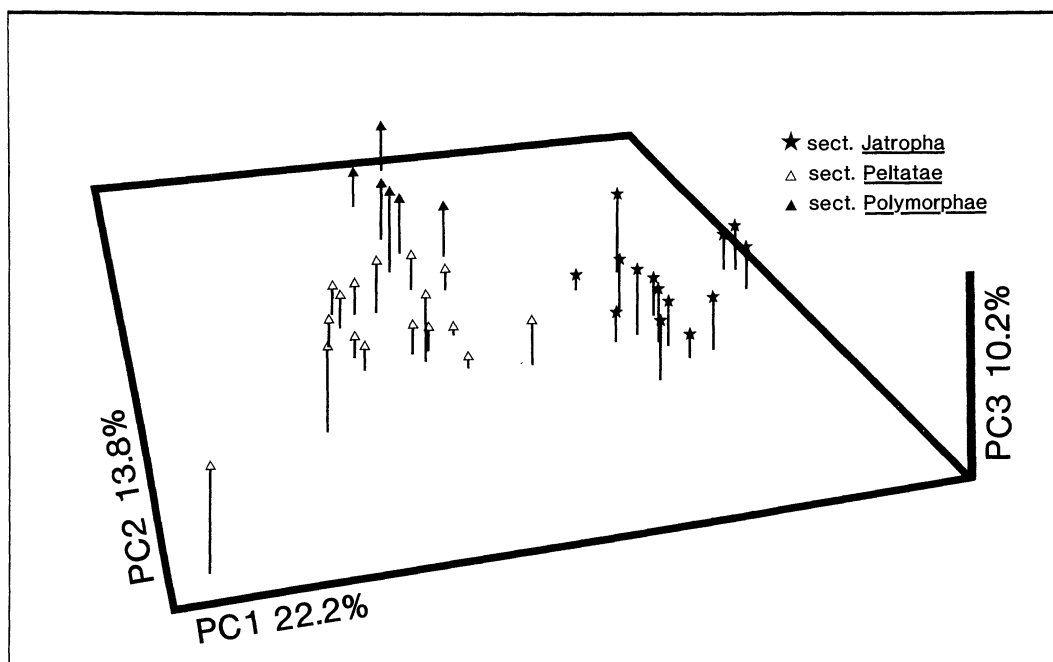

FIGURE 2.   PCA of species in *Jatropha* subg. *Jatropha* (including species of sect. *Polymorphae*) from 32 characters, using F. J. Rohlf's NTSYS-pc program. Infrageneric designations are from Dehgan & Webster (1979).

TABLE 3B. Selected characters* with highest factor loadings (in order of magnitude) for each principal component in analysis of 39 species of subgenus *Curcas* with four species of section *Polymorphae*.

PC1		PC2		PC3	
Character number	Factor loading	Character number	Factor loading	Character number	Factor loading
5	−0.337	32	−0.408	9	0.428
6	−0.333	30	0.373	11	0.415
16	0.329	4	0.328	27	0.286
31	0.296	7	0.295	30	0.273
20	−0.279	28	0.273	15	0.260
14	0.272	26	−0.203	19	−0.243

* Characters 2 and 12 were invariant (see Table 1).

to produce cladograms. The first of these is mentioned by Platnick (1989) in his recent comparison of phylogenetic analysis programs, but is not discussed in the program documentation itself. The data matrix is read in with "xread." Subsequently the "treed" option, usually used to supply a user tree, is summoned without an input tree and passed to the branch-breaking algorithm, "bb," which performs extensive branch rearrangement to find more parsimonious trees. This causes the branch-breaker to start with a completely unresolved "bush" (one polytomy consisting of all the EUs). In the second algorithm, the "mhennig*" option is used to supply the initial tree to the branch-breaker, which then attempts to find parsimonious trees. Also, a representative cladogram from each of the PAUP and CLADOS analyses was input by the "treed" option to Hennig86 and subjected to the "m*; bb;" and "tr; bb;" command sequences to ascertain whether Hennig86 could find more parsimonious cladograms by starting with output trees from another program.

RESULTS AND DISCUSSION

The CLADOS, PAUP, and Hennig86 data sets consisted of different numbers of characters (46 binary in CLADOS, 31 multistate in Hennig86 and
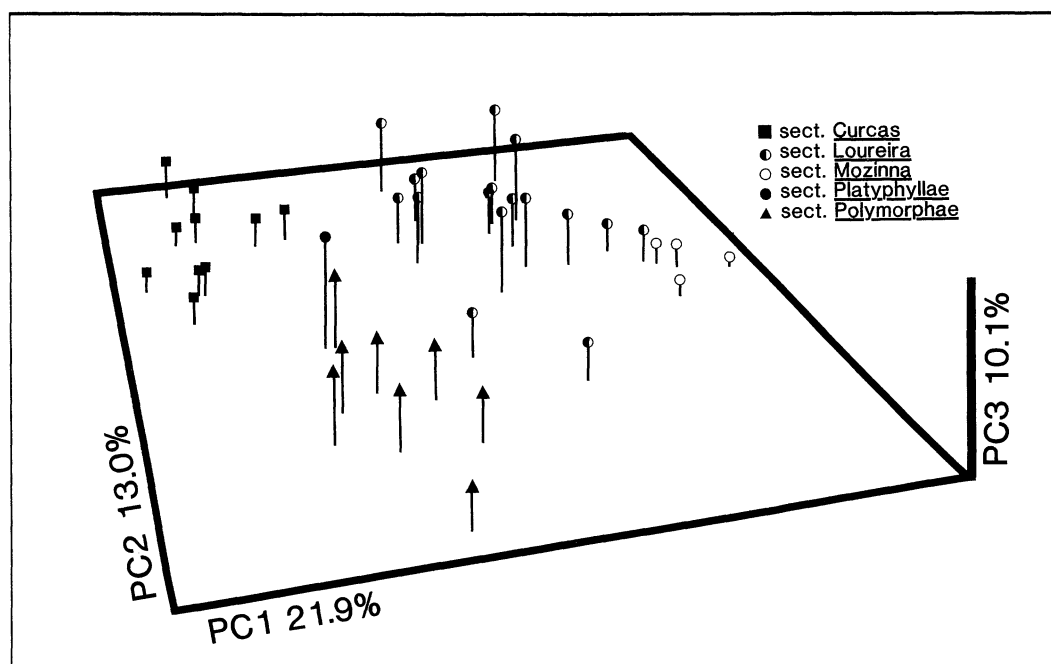

FIGURE 3. PCA of species of *Jatropha* subg. *Curcas* and species of section *Polymorphae* from 32 characters, using F. J. Rohlf's NTSYS-pc program. Infrageneric designations are from Dehgan & Webster (1979).

TABLE 3C. Selected characters* with highest factor loadings (in order of magnitude) for each principal component in analysis of 34 species of subgenus *Jatropha* with four species of section *Polymorphae*.

PC1		PC2		PC3	
Character number	Factor loading	Character number	Factor loading	Character number	Factor loading
19	0.356	7	0.368	12	0.364
18	0.327	25	0.309	23	0.344
9	0.309	6	0.286	24	−0.312
11	0.305	16	0.258	22	0.284
20	−0.298	23	−0.254	8	−0.275
29	0.268	17	0.240	13	0.253

* Characters 3, 4, and 28 were invariant (see Table 1).

PAUP), and taxa (79 in CLADOS and Hennig86, subsets of 4 to 19 taxa in PAUP). Since the consistency index (CI) is highly negatively correlated to the number of taxa and characters in a study, as has been discussed by Archie (1989), we could not compare cladograms by the number of steps or by the CI. Farris himself (1989) admitted that the consistency index (Kluge & Farris, 1969) needed improvement. In order to compare parsimonious cladograms of CLADOS and PAUP to those of Hennig86, we used the "treed" option in Hennig86 to bring one each of the most parsimonious CLADOS and PAUP trees into the program. The "xsteps I" option was then used to calculate the length of

TABLE 4. Characters and character states for cladistic analysis (31 characters numbered 0–30 using the convention of the Hennig86 program).

|	
0. Growth habit:	Plants geophytes (1), plants typical (0).
1. Growth habit:	Plants rhizomatous (1), plants typical (0).
2. Plant sex:	Dioecious (1), monoecious (0).
3. Laticifers:	Articulated and/or nonarticulated (1), idioblastic (0).
4. Laticifers:	Nonarticulated (1), articulated (0).
5. Leaf base:	Peltate (1), not peltate (0).
6. Leaf basal glands:	Present (1), absent (0).
7. Leaf margins:	Toothed (1), entire (0).
8. Leaf marginal glands:	Ciliate-glandular (1), eglandular (0).
9. Leaf sinus depth:	Parted (1), not parted (0).
10. Leaf lobe numbers:	Unlobed (0), 3- (3); 5- (5); 7- (7); 9-lobed (9).
11. Leaf veins:	Palmate (1), pinnate (0).
12. Petioles:	Long (1), subsessile (0).
13. Petiolar traces:	3 (3), 5 (5), 7 (7), 9 (9), 11 (1).
14. Hairs:	Absent (0), unicellular (1), uniseriate-multicellular (2).
15. Coflorescences:	Present (1), absent (0).
16. Flower shape:	Campanulate (0), rotate (1), tubular or urceolate (2).
17. Flower color:	White (1), other (0).
18. Petals of female flowers:	Distinct (0), imbricate (1), connate (2).
19. Petals of male flowers:	Distinct (0), imbricate (1), connate (2).
20. Stamen arrangement:	Monadelphous (1), diadelphous (0).
21. Stamen number:	8 (1), 10 (0).
22. Stamen fusion:	Free (1), connate (0).
23. Style fusion:	Free (1), connate (0).
24. Calyx lobes of female flowers:	Foliaceous (1), not foliaceous (0).
25. Calyx lobe margins:	Glandular (1), entire (0).
26. Fruit dehiscence:	Violently dehiscent (1), tardily dehiscent (0).
27. Fruit locules:	1 (1), 2 (2), 3 (3).
28. Seed:	Carunculate (1), ecarunculate (0).
29. Calyx lobes:	Valvate (1), not valvate (0).
30. Petiolar basal glands:	Present (1), absent (0).
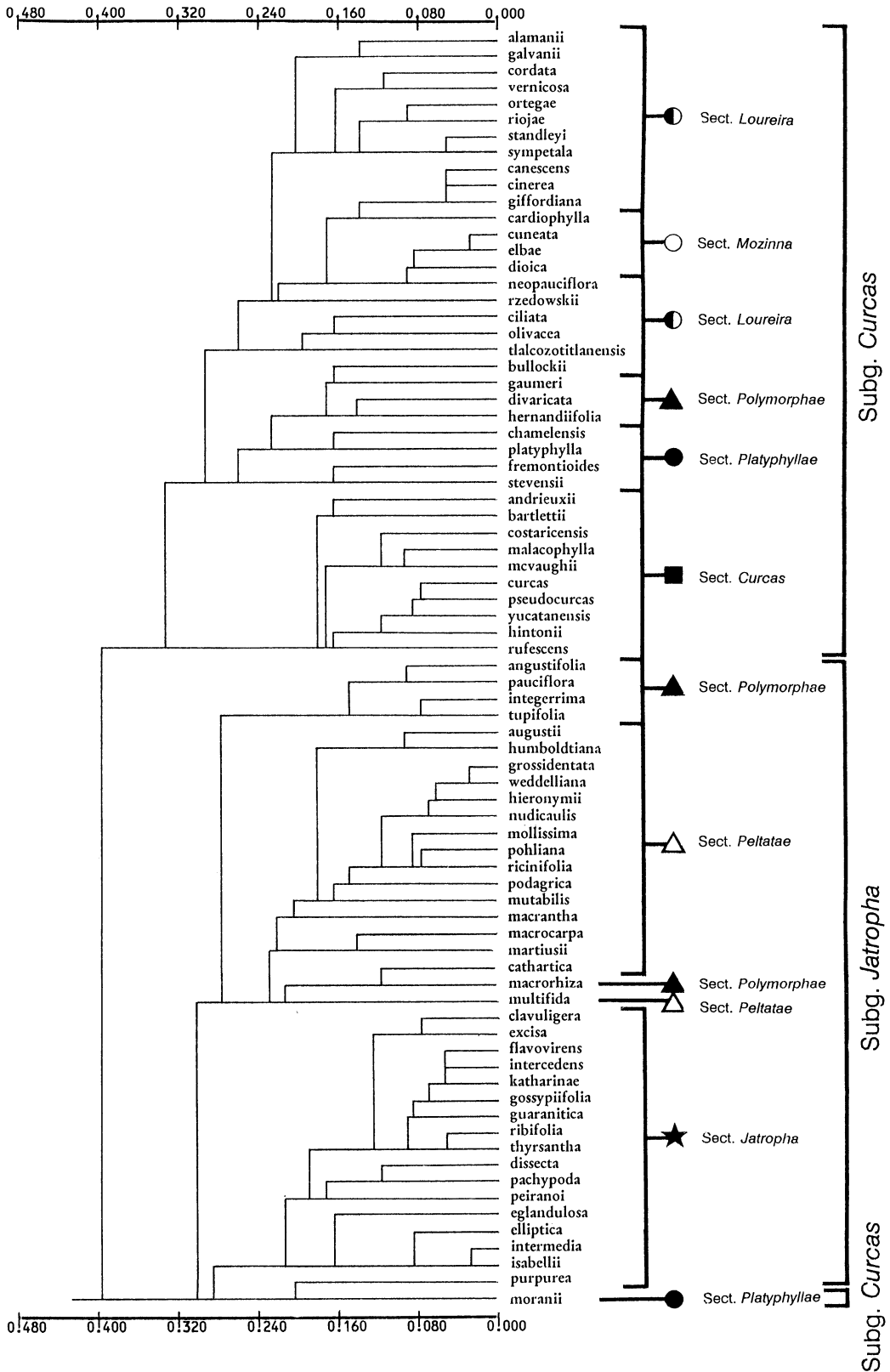
FIGURE 4.   Phenogram of 77 Neotropical *Jatropha* species from 32 characters, using F. J. Rohlf's NTSYS-pc program. Infrageneric designations are from Dehgan & Webster (1979).

TABLE 5.   Matrix of character states for 77 *Jatropha* species and two outgroups used in the Hennig86 program. Missing states are indicated by "?."

```
                                        Characters
                  0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3
Taxon             0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0

joannesia         0 0 0 0 ? 0 0 0 0 1 9 1 0 ? 1 0 0 1 0 0 0 1 0 1 0 1 1 3 1 0 1
aleurites         0 0 0 0 ? 0 0 1 0 0 5 0 0 ? ? 0 1 1 0 0 0 2 0 1 0 1 2 3 1 1 1
alamanii          0 0 1 1 0 0 0 0 0 0 5 0 0 7 0 1 2 1 2 0 0 0 0 0 1 1 1 3 1 0 0
andrieuxii        0 0 1 0 1 0 0 1 0 0 7 0 0 9 1 0 0 1 2 0 0 0 0 0 0 1 1 3 1 0 0
angustifolia      0 0 0 0 1 0 0 0 0 0 1 1 0 7 0 1 1 1 1 1 0 0 0 0 0 1 0 3 0 0 0
augustii          0 0 0 1 0 1 1 0 1 0 5 0 0 7 0 1 1 1 0 0 1 1 0 0 0 1 0 3 0 0 0
bartlettii        0 0 1 0 1 0 0 1 0 0 5 0 0 9 1 0 0 0 0 1 0 0 0 0 1 0 1 3 1 0 0
bullockii         0 0 0 0 1 0 0 0 0 0 3 0 0 5 0 1 2 0 2 0 0 1 0 0 0 1 0 3 0 0 0
canescens         0 0 1 1 0 0 0 0 0 0 1 0 0 5 1 1 2 1 2 2 0 0 0 0 1 1 1 2 1 0 0
cardiophylla      0 1 1 1 0 0 0 0 0 0 1 0 0 5 0 1 2 1 2 2 0 0 0 0 1 1 1 1 0 0
cathartica        1 0 0 0 1 0 0 0 0 1 7 0 0 9 0 1 1 1 0 0 1 1 1 1 0 1 0 3 0 0 0
chamelensis       0 0 1 1 0 0 1 0 0 0 1 0 0 9 0 1 2 0 0 2 0 0 0 0 1 1 0 3 1 0 0
ciliata           0 0 1 1 0 0 1 1 1 0 5 0 0 7 0 1 2 0 2 2 0 0 0 0 1 0 3 1 0 0
cinerea           0 0 1 1 0 0 0 0 0 0 3 0 0 5 1 1 2 1 2 2 0 0 0 0 1 1 1 2 1 0 0
clavuligera       0 0 0 0 0 0 1 0 1 1 7 0 0 7 2 0 0 1 0 0 0 0 1 0 0 0 3 0 0 0
cordata           0 0 1 1 0 0 1 0 1 0 1 1 0 7 0 1 2 1 2 2 0 0 0 0 1 0 1 2 1 0 0
costaricensis     0 0 1 0 1 0 0 0 0 0 5 0 0 7 1 0 2 0 2 2 1 0 0 0 1 1 1 3 1 0 0
cuneata           0 0 1 1 0 0 0 0 0 0 3 2 1 3 0 1 2 0 2 2 0 0 0 0 0 1 1 1 1 0 0
curcas            0 0 0 0 1 0 0 0 0 0 5 0 0 9 0 0 0 0 0 2 0 0 0 0 0 1 1 3 1 0 0
dioica            0 1 1 1 0 0 0 0 0 0 3 2 1 3 0 1 2 1 2 2 0 0 0 0 0 1 1 1 1 0 0
dissecta          1 0 0 0 0 0 1 0 1 1 5 0 0 7 2 0 1 1 0 0 1 1 0 1 0 0 0 3 0 0 0
divaricata        0 0 0 0 0 0 0 0 0 0 1 1 0 7 0 1 2 0 0 0 0 0 0 0 0 1 0 3 0 0 0
eglandulosa       0 0 0 0 0 0 0 0 0 0 1 1 1 7 2 0 0 1 0 0 1 1 1 0 0 1 0 3 0 0 0
elbae             0 0 1 1 0 0 0 0 0 0 1 2 1 3 0 1 2 0 2 2 0 0 0 0 0 1 1 1 1 0 0
elliptica         1 0 0 0 0 0 1 0 1 0 1 1 1 7 2 0 0 1 2 0 1 1 0 0 0 0 0 3 0 0 0
excisa            0 0 0 0 0 0 1 0 1 0 5 0 0 7 1 0 0 1 0 0 0 0 1 0 0 0 0 3 0 0 0
flavovirens       0 0 0 0 0 0 1 0 1 1 3 0 0 7 2 0 0 1 0 0 0 1 0 1 0 0 0 3 0 0 0
fremontioides     0 0 0 1 0 0 0 0 0 0 3 0 1 5 1 1 2 1 2 0 0 0 0 0 0 1 0 3 0 0 0
galvanii          0 0 1 1 0 0 0 0 0 0 1 0 0 7 0 1 0 1 0 0 0 0 0 0 1 0 1 2 1 0 0
gaumeri           0 0 0 0 1 0 0 0 0 0 1 0 0 7 0 1 2 0 2 2 1 1 0 1 0 1 0 3 0 0 0
giffordiana       0 0 1 1 0 0 0 0 0 0 1 0 0 5 1 1 2 1 2 2 0 0 0 0 1 1 1 3 1 0 0
gossypiifolia     0 0 0 0 0 0 1 0 1 0 5 0 0 7 2 0 0 1 0 0 0 1 0 0 0 0 0 3 0 0 0
grossidentata     0 0 0 0 0 0 0 1 0 0 5 0 0 7 0 1 1 1 0 0 1 1 1 1 0 1 0 3 0 0 0
guaranitica       1 0 0 0 0 0 1 0 1 0 3 0 0 7 2 0 0 1 0 0 0 1 0 1 0 0 0 3 0 0 0
hernandiifolia    0 0 0 1 1 0 0 0 0 3 0 0 7 0 1 2 0 1 2 0 0 0 0 0 1 0 3 0 0 0
hieronymii        0 0 0 0 0 0 1 0 0 5 0 0 7 0 1 1 1 0 0 1 1 1 1 0 1 0 3 0 0 0
hintonii          0 0 0 0 1 0 0 0 0 0 3 0 0 9 1 0 0 0 1 0 0 0 0 0 1 1 3 0 0 0
humboldtiana      0 0 0 0 1 1 0 1 0 1 0 1 0 0 7 0 1 1 1 0 0 1 1 1 0 0 1 0 3 0 0 0
integerrima       0 0 0 0 1 0 0 0 0 0 3 0 0 7 0 1 1 1 1 1 0 0 0 0 0 1 0 3 0 0 0
intercedens       0 0 0 0 0 0 1 0 1 0 3 0 0 7 2 0 0 1 0 0 0 1 0 0 0 0 0 3 0 0 0
intermedia        1 0 0 0 0 0 1 0 1 0 1 1 1 7 2 0 0 1 0 0 0 1 0 1 0 0 0 3 0 0 0
isabellii         1 0 0 0 0 0 1 0 1 0 1 1 1 7 2 0 0 1 0 0 0 0 0 0 1 0 0 3 0 0 0
katharinae        0 0 0 0 0 0 1 0 1 0 3 0 0 7 2 0 0 1 0 0 0 1 0 1 0 0 0 3 0 0 0
macrantha         0 0 0 0 0 0 0 0 0 0 3 0 0 7 0 1 1 1 0 0 1 0 0 0 0 1 0 1 0 0 0
macrocarpa        0 0 0 0 0 0 0 0 0 1 5 0 0 7 0 1 1 1 0 0 1 0 1 0 1 0 1 3 0 0 0
macrorhiza        1 0 0 0 0 0 1 0 1 0 1 7 0 0 7 0 1 1 1 0 0 1 0 1 0 1 0 1 0 3 0 0 0
malacophylla      0 0 1 0 1 0 0 1 0 0 5 0 0 9 1 1 0 0 2 2 1 0 0 0 1 1 1 3 1 0 0
martiusii         0 0 0 0 0 0 0 0 0 1 5 0 0 7 0 1 2 1 2 2 0 1 0 1 0 0 0 3 0 0 0
mcvaughii         0 0 1 0 1 0 0 0 0 0 7 0 0 9 1 0 0 0 2 2 1 0 0 0 0 1 1 3 1 0 0
mollissima        0 0 0 0 0 0 0 0 0 0 5 0 0 7 1 1 1 1 0 0 1 1 1 1 0 0 0 3 0 0 0
moranii           0 0 0 0 1 0 1 0 1 0 5 0 0 7 0 1 0 0 2 2 0 0 0 1 1 1 0 3 0 0 0
multifida         0 0 0 0 0 0 0 0 0 1 9 0 0 1 0 1 1 1 0 0 1 1 1 1 0 1 1 3 1 0 0
mutabilis         0 0 0 0 0 0 0 0 0 0 1 1 0 7 1 1 1 1 0 0 1 1 1 1 0 0 0 3 0 0 0
neopauciflora     0 0 1 1 0 0 0 0 0 0 1 2 1 5 0 1 2 1 2 2 0 0 0 0 0 1 1 2 1 0 0
```
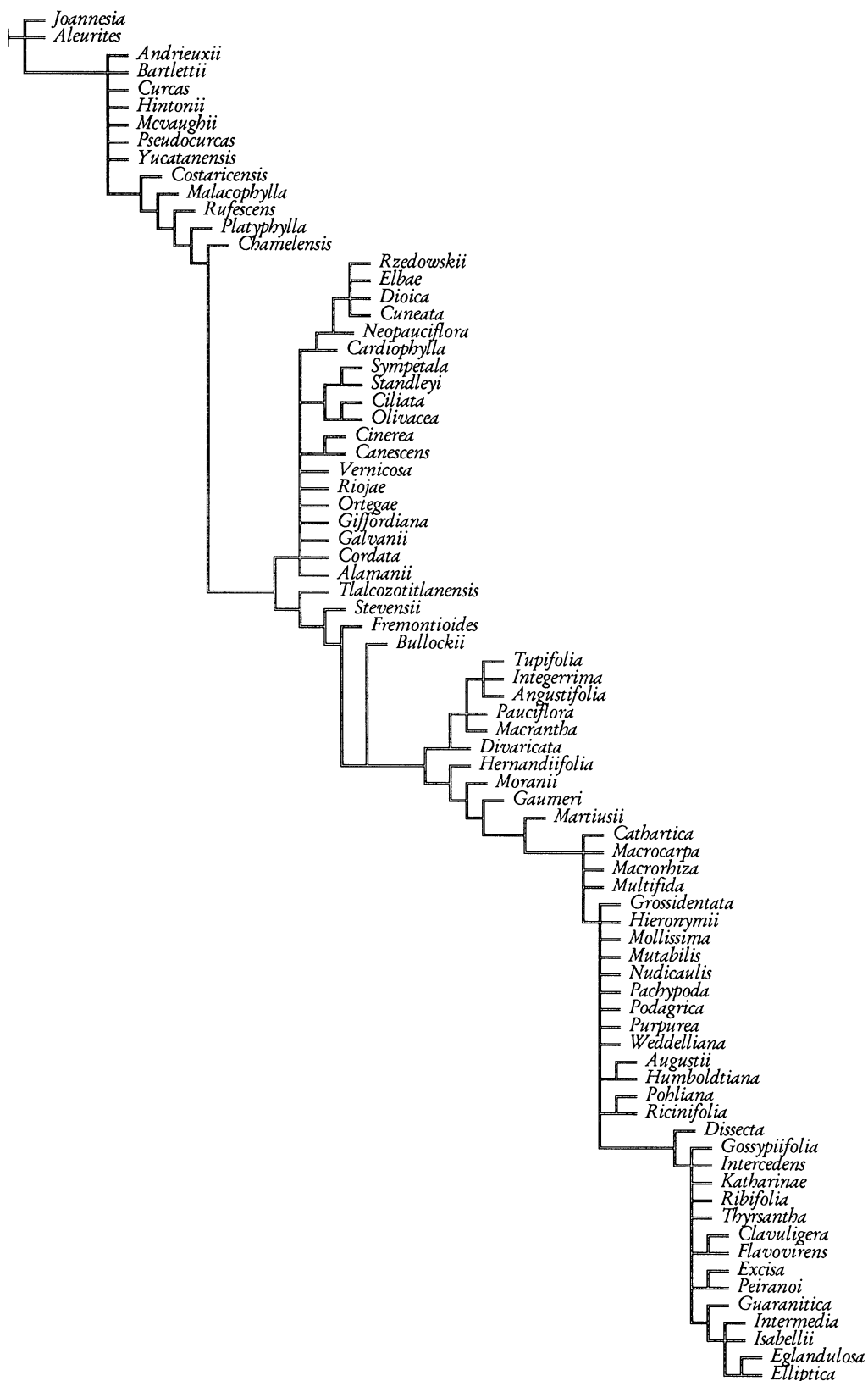
TABLE 5. Continued.

Taxon	Characters 00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
nudicaulis	0	0	0	0	0	1	0	0	0	0	5	0	0	7	0	1	1	1	0	0	1	1	1	1	0	1	0	3	0	0	0
olivacea	0	0	0	1	0	0	1	1	1	0	3	0	0	7	1	1	2	0	2	2	0	0	0	0	1	1	1	2	1	0	0
ortegae	0	0	1	1	0	0	1	0	1	0	1	1	0	5	1	1	2	1	2	2	0	0	0	0	0	0	1	3	1	0	0
pachypoda	1	0	0	0	0	0	1	0	1	0	5	0	0	7	0	1	1	1	0	0	1	1	1	1	0	0	0	3	0	0	0
pauciflora	0	0	0	0	1	0	0	0	0	0	3	1	0	7	0	1	1	1	0	0	0	0	1	0	0	1	0	3	0	0	0
peiranoi	1	0	0	0	0	0	1	0	1	0	5	0	0	7	0	0	0	1	2	2	0	0	0	1	0	0	0	3	0	0	0
platyphylla	0	0	1	0	1	1	0	0	0	0	1	0	0	9	0	1	2	0	2	2	0	0	0	1	1	1	0	3	1	0	0
podagrica	0	0	0	0	0	1	0	0	0	0	3	0	0	9	0	1	1	1	0	0	1	1	1	1	0	1	0	3	0	0	0
pohliana	0	0	0	0	0	0	0	1	1	0	5	0	0	7	1	1	1	1	0	0	1	1	1	0	0	0	0	3	0	0	0
pseudocurcas	0	0	0	0	1	0	0	0	0	0	5	0	0	9	1	0	0	0	0	0	1	0	0	0	0	1	1	3	1	0	0
purpurea	0	0	0	0	1	0	1	0	1	0	5	0	0	5	0	1	2	1	0	1	1	0	0	1	0	0	0	3	0	0	0
ribifolia	0	0	0	0	0	0	1	0	1	0	3	0	0	7	2	0	1	1	0	0	1	1	0	0	0	0	0	3	0	0	0
ricinifolia	0	0	0	0	1	0	0	1	0	0	5	0	0	7	0	1	1	1	0	0	1	1	1	0	0	0	0	3	0	0	0
riojae	0	0	1	1	0	0	1	0	0	0	1	1	0	5	0	1	2	1	2	2	0	0	0	0	0	1	1	3	1	0	0
rufescens	0	1	1	0	1	0	0	0	0	0	1	0	0	9	1	1	0	0	0	2	0	0	0	0	1	1	1	3	1	0	0
rzedowskii	0	0	1	1	0	0	0	0	0	0	1	1	1	3	1	1	2	1	0	0	0	0	0	0	0	1	1	1	1	0	0
standleyi	0	0	1	1	0	0	1	0	0	0	1	1	0	7	0	1	2	0	2	2	0	0	0	0	0	1	1	2	1	0	0
stevensii	0	0	0	1	0	0	0	0	0	0	1	0	0	5	1	0	2	0	2	2	0	0	0	0	0	1	0	3	0	0	0
sympetala	0	0	1	1	0	0	0	0	0	0	1	1	0	7	0	1	2	0	2	2	0	0	0	0	0	1	1	2	1	0	0
tlalcozotitlanensis	0	0	0	1	0	0	1	0	1	0	1	1	0	5	1	1	2	0	2	2	0	0	0	0	1	1	0	3	0	0	0
thyrsantha	0	0	0	0	0	0	1	0	1	0	3	0	0	7	2	0	0	0	0	0	1	1	0	0	0	0	0	3	0	0	0
tupifolia	0	0	0	0	1	0	1	1	0	0	3	0	0	7	0	1	1	1	1	1	0	0	0	0	0	1	0	3	0	0	0
vernicosa	0	0	1	1	0	0	1	0	1	0	1	1	0	7	0	1	2	1	0	0	0	0	0	1	1	0	1	2	1	0	0
weddelliana	0	0	0	0	0	0	0	0	0	0	5	0	0	7	0	1	1	1	0	0	1	1	1	1	0	1	0	3	0	0	0
yucatanensis	0	0	0	1	0	0	0	0	0	0	1	0	0	9	0	0	0	0	0	2	1	0	0	0	0	1	1	3	1	0	0

the trees relative to the Hennig86 data set. The shortest CLADOS and PAUP trees evaluated to 263 and 269 steps, respectively. The Hennig86 program, however, produced in excess of 100 equally parsimonious trees, all 230 steps long, when a data set with two outgroups was used. The trees from all data sets with one outgroup had a greater number of steps. The cladogram in Figure 5 was selected by calculating character weights ("xsteps w" command) and applying them to all 100+ cladograms. The program arrives at weights based upon the CI and retention index (RI) of the cladograms considered. The lengths of the cladograms were recalculated using weighted characters ("xsteps l" command). The shortest one is illustrated in Figure 5. The trees were calculated using all available unweighted data, but the one selected gives more credence to characters showing less homoplasy, without resorting to a successive approximations approach, such as that suggested by Carpenter (1988). Even prior to Archie's (1989) criticism of the consistency index, Farris had already abandoned it in his 1988 release of Hennig86 in favor of two new indices: the Retention Index (RI) and the Rescaled Consistency Index (RC). These are constructed to behave as true indices, possessing values between 0 and 1 (Farris, 1989). The most parsimonious cladograms from Hennig86 all had RC = 0.19 and RI = 0.72. Stated simply, RC displays a high degree of homoplasy in the data set; while the high value for RI shows that these cladograms exhibit a relatively low degree of homoplasy as compared to the total amount possible for the data set.

The strict (Nelson) consensus cladogram (Fig. 5) output by Hennig86 is remarkably similar to Dehgan & Webster's (1979) evolutionary model, which utilized morphological similarities and dif-

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FIGURE 5. Nelson (strict) consensus tree for 77 *Jatropha* species and two outgroups (*Joannesia* and *Aleurites*) derived from analysis of 31 unweighted and unordered morphological characters (cf. Table 4), using Farris's Hennig86 program.

Joannesia
Aleurites
Andrieuxii
Bartlettii
Curcas
Hintonii
Mcvaughii
Pseudocurcas
Yucatanensis
Costaricensis
Malacophylla
Rufescens
Platyphylla
Chamelensis
Rzedowskii
Elbae
Dioica
Cuneata
Neopauciflora
Cardiophylla
Sympetala
Standleyi
Ciliata
Olivacea
Cinerea
Canescens
Vernicosa
Riojae
Ortegae
Giffordiana
Galvanii
Cordata
Alamanii
Tlalcozotitlanensis
Stevensii
Fremontioides
Bullockii
Tupifolia
Integerrima
Angustifolia
Pauciflora
Macrantha
Divaricata
Hernandiifolia
Moranii
Gaumeri
Martiusii
Cathartica
Macrocarpa
Macrorhiza
Multifida
Grossidentata
Hieronymii
Mollissima
Mutabilis
Nudicaulis
Pachypoda
Podagrica
Purpurea
Weddelliana
Augustii
Humboldtiana
Pohliana
Ricinifolia
Dissecta
Gossypiifolia
Intercedens
Katharinae
Ribifolia
Thyrsantha
Clavuligera
Flavovirens
Excisa
Peiranoi
Guaranitica
Intermedia
Isabellii
Eglandulosa
Elliptica

ferences in concert with the principles of evolutionary reduction series. The classification of Dehgan & Webster (1979) is consistent with a convex interpretation of the most parsimonious Hennig86 cladogram. Use of convex groups in systematics, though debatable, has been advocated by many, including Ashlock (1971), Cronquist (1987), Meacham & Duncan (1987), and others. Although delimitations of the sections and subsections are subject to individual interpretation and some minor realignment of taxa within groups is advisable, the fundamental infrageneric relationships remain mostly intact. Subgenus *Jatropha* as a whole is shown to be monophyletic, whereas subgenus *Curcas* and some of its species groups are paraphyletic.

The strict (Nelson) consensus tree (Fig. 5) clearly indicates the relationship between the two subgenera. In particular, early derivation and basal position of subgenus *Curcas* closely corresponds to the previously suggested arrangement. The consensus cladogram (Fig. 5) would support reduction of sections *Platyphyllae* and *Mozinna* to subsections of the more heterogeneous section *Loureira*. *Mozinna*, which initially included only three species, was recognized as a distinct section based on unilocular fruit with a single seed, rhizomatous growth habit, and tetraploid (in *J. cuneata* Wiggins & Rollins and *J. dioica*) or unusually large (in *J. cardiophylla* (Torr.) Muell. Arg.) chromosomes. Recent discovery of two new species (*J. elbae* J. Jiménez Ramírez and *J. rzedowskii* J. Jiménez Ramírez) and inclusion of *J. neoplauciflora* Pax (placed in subsect. *Neopauciflorae* Pax of sect. *Loureira* by Dehgan & Webster, 1979), all three with bilocular fruit but with several characteristics similar to those of the three original species, make recognition of the group at sectional level more debatable. Analogous to *Mozinna*, section *Loureira* includes species with bi- and trilocular fruit. In subsection *Canescentes* Pax ex Dehgan & Webster, for example, *J. canescens* (Benth.) Muell. Arg. and *J. cinerea* (Ortega) Muell. Arg. are bilocular, while *J. giffordiana* Dehgan & Webster is mostly trilocular. Although higher locule number in some exceptional cases may be the result of reversal (as in *J. neopauciflora*), in nearly all other cases it is ancestral.

The suggested changes in subgenus *Jatropha* include transfer of *J. moranii*, which was initially placed in section *Platyphyllae* (Dehgan & Webster, 1978) to section *Polymorphae*. This species differs from most members of *Polymorphae* by its glandular leaf margins and possession of foliar sepals in the female flowers. *Jatropha macrorhiza* Benth. (endemic to southern Arizona in the Sonoran Desert), which was recognized as distinct subsection *Macrorhizae* in *Polymorphae*, would be transferred to section *Peltatae*, together with *J. cathartica* Terán & Berland, *J. macrocarpa* Griseb., and *J. multifida* L., with which it shares several characters, all of which would be accommodated in subsection *Multifidae* Pax. *Jatropha macrantha* Muell. Arg. is accurately placed in section *Polymorphae*. *Jatropha purpurea*, *J. martiusii* (a narrow endemic in Bahia, Brazil), and *J. bullockii* have previously been enigmatic. However, the results of cladistic analysis clearly show their phylogenetic position. *Jatropha bullockii* is indicated to be a sister taxon to the clade containing subgenus *Jatropha* with several autapomorphies and also is phenetically distinct. It is the only non-caudiciform Mexican species with eight stamens, trilocular fruit, and carunculate seeds but very small tubular flowers. *Jatropha martiusii* occupies a transitional position between sections *Polymorphae* and *Peltatae*. It shares certain features of both sections, but in fact does not fit properly into either one. It is the only known South American species with distinctly tubular flowers and trilocular fruit but only two (as opposed to three) style branches. No other species in the genus is known to consistently possess a combination of tubular flowers, two style branches, and three locular fruits. *Jatropha purpurea* is morphologically intermediate between sections *Peltatae* and *Jatropha*. It shares extrafloral glands, ten biseriate stamens, and tubular flowers with *J. cordata* (Ortega) Muell. Arg. (sect. *Loureira*), but has red flowers, trilocular fruit, and carunculate seeds similar to those of section *Jatropha*. Two new sections should be erected to accommodate *J. martiusii* and *J. purpurea*. Accordingly, section *Jatropha* would include three subsections: *J. gossypiifolia* and its related taxa, *J. purpurea*, and *J. isabellii* Muell. Arg. and its related caudiciform South American species.

C. COMPARISONS BETWEEN AND RAMIFICATIONS OF PHENETIC AND CLADISTIC ANALYSES

There exists a general concordance between groupings suggested by phenetic and cladistic analyses. Where discrepancies exist, these may be mostly attributed to the inability of phenetic analyses to distinguish homoplastic from patristic similarity. Since the *Jatropha* data set exhibited a large degree of homoplasy, some differences between the two were anticipated. In fact, fewer discrepancies were noted than expected. There was general agreement between the two methodologies

with regard to establishment of subgenera, sections, and most subsections. Moreover, correspondence of the results of cladistic and phenetic studies to Dehgan & Webster's (1979) intuitive classification confirms that intimate knowledge of living (as opposed to preserved) organisms is often essential for establishment of phylogenetic relationships. The nearly identical intuitive and numerical results in *Jatropha* are not a coincidence, but rather are the result of recurrent observation of growth and flowering of plants in the wild and in cultivation. The large numbers of evolutionary changes that have resulted in recognizable morphological discontinuities were reflected in the traditional classification, and for the most part, supported by the numerical analyses presented here.

D. RELATIONSHIPS BETWEEN PHYTOGEOGRAPHY, EVOLUTION, AND THE RESULTS OF NUMERICAL ANALYSES

We are fully cognizant of the shortcomings of performing phenetic and phylogenetic analyses of only the American taxa. To have a better understanding of the entire genus it is imperative that African and Indian species also be included in the study. Accordingly, we have not used this opportunity to construct a new classification of the genus. This would have been largely unnecessary because of the close similarity between these results and those of the previous classification of Dehgan & Webster (1979). Moreover, it is highly unlikely that inclusion of the Old World taxa would profoundly change the results and discussions presented here. Analogous to the neotropical species, complex evolutionary history of the African taxa is illustrated in the recent works of Hemming & Radcliffe-Smith (1987), in which 25 Somalian species are placed in six sections and five subsections (all in sect. *Spinosae* Pax). The limitation of this study to the neotropical species precludes inclusion of the Old World species at this time. However, the large number of neotropical taxa in *Jatropha*, their widespread geography in concert with narrow endemism of a vast majority of the taxa, known cases of natural hybridization, and probability of extinctions, all profoundly influence the results of numerical studies and will be discussed in the monograph of the genus. Suffice it to say that the adaptive radiation in Mexico and South America that Dehgan & Webster (1979) have addressed is also reflected in the consensus tree. Several other evolutionary concepts that were put forth in earlier works (Dehgan, 1980, 1982, 1984; Dehgan & Craig, 1978; Dehgan & Webster, 1978, 1979)

have been confirmed. Of particular interest is the evolutionary progression of infrageneric groups.

As evidenced by the cladistic analyses, species of section *Curcas* originated first. Primitiveness of the section, and of *J. curcas* in particular, was noted by McVaugh (1945) and Wilbur (1954), who maintained that the genus must have originated in Mexico because *J. curcas*, the most primitive species, and several closely related taxa occur there. The primitiveness of this taxon was justified by Dehgan & Webster (1979) on morphological grounds and is supported by the results of the present study. The large number and extreme diversity of taxa of subgenus *Curcas* in Mexico may be explained by recent introduction of a taxon similar to *J. curcas* to an ecogeographically dissimilar habitat, followed by progressive mosaic evolution and mosaic selection (Stebbins, 1984). Geological and climatic disturbances in Mexico (Toledo, 1981; Graham, 1987, 1989b) have probably resulted in both elimination of many taxa related to those in South America and relatively rapid mosaic speciation, which resulted in the largest concentration of *Jatropha* species of any region.

In general, speciation of *Jatropha* in the Neotropics has been most rapid in three seasonally dry regions: grassland-savanna (cerrado), thorn forest-scrub, and caatingas vegetation. In South America, species of sections *Jatropha* and *Peltatae* are found in drier areas of northern Argentina, Brazil, Paraguay, Bolivia, Peru, and Colombia, but are completely lacking from the moist Amazon region. Although a vast majority of the species in sections *Curcas*, *Loureira*, and *Mozinna* are Mexican endemics, all other sections are also represented in Mesoamerica, from Costa Rica, Guatemala, Mexico, Baja California, northward to southern Arizona and Texas. Of the comparatively few West Indian species, at least four are endemic to Cuba and one to Jamaica. Since nearly all jatrophas are to a greater or lesser extent dry-adapted succulents, their absence from the wetter regions of South America is understandable. Webster (1994) has suggested that the Euphorbiaceae probably arose in West Gondwanaland, with Africa harboring the greatest diversity of the primitive taxa in the five subfamilies. Dehgan (1980 et seq.) and Dehgan & Craig (1978) enumerated the primitive features of *Jatropha* and suggested its possible ancestral position to the Euphorbiaceae. This view is further supported by Gilbert and others in this issue. As such, jatrophas probably originated and evolved in drier regions of Gondwanaland and never developed the ability to adapt to wet tropical forests (cf. Retallack & Dilcher, 1981).

Despite pantropical distribution of *Jatropha*, a vast majority of its species are endemic and often restricted to small regions. Other than *J. gossypiifolia*, which is reported to be eaten and disseminated by pigeons (Standley, 1923), no cases of long-distance dispersal have been reported, and the present distribution of the genus appears to be the result of progressive overland dispersal. With the exception of a few taxa that have become spontaneous or subspontaneous with the help of humans, no truly disjunct species have been reported within or between the continents of Africa, America, and the subcontinent of India. Their complete absence from all oceanic islands (except *J. divaricata* and *J. hernandiifolia* in Jamaica) is a further indication of their inability to disperse by birds or ocean currents. The large number of narrowly endemic species is indicative of natural habitat disturbance, as has reportedly occurred in Central and South America (Graham, 1989a), and hence agrees with the refugium theory (Prance, 1982). Interestingly, several other genera in the Euphorbiaceae with dehiscent fruit and carunculate seeds, such as *Aleurites* in Asia, *Hevea* Aubl., *Joannesia*, *Cnidoscolus*, *Manihot* Miller, and others in America, and *Grossera* Pax, *Crotonogyne* Muell. Arg., and others in Africa, although widespread within the confines of a single continent, are not dispersable by interoceanic means. Therefore, it is reasonable to assume that disjunct presence of jatrophas in three widely separated regions is a good indication of its antiquity, and hence, its primitiveness.

Reductions and modifications have occurred in conjunction with migration from south to north in Mesoamerica and north to south in South America and are generally associated with increasing aridity and cold. Grant (1963: 566–568) has suggested that speciation may be inextricably involved in some cases of phyletic evolution, where a progression takes place as a series of successive speciational steps. Adaptive gradual speciation (Stebbins, 1984) in *Jatropha* is exhibited in growth habit (from arborescent to rhizomatous or tuberous-caudiciform), inflorescences (terminal compound dichasium with a distinct coflorescence to lateral or terminal solitary flowers), number of stamens (10 to 8) and their arrangement (uni- or biseriate, monadelphous or free), reductions in ovary locule numbers (from 3 to 2 and 1) which, with the notable exception of *J. martiusii* (with 2 styles but 3 locules), is invariably accompanied by reduction from 3- to 2- to 1-bifid, free or connate styles, and plant sexuality (from monoecy to gynodioecy to dioecy). Progressive diversifying selection, as a result of

migration and ensuing geographical isolation, was probably followed by a shorter or longer period of directional selection, finally culminating in stabilizing selection at the maximum level of fitness possible for the gene pool (Dobzhansky, 1970; Stebbins, 1974). Since overland migration often involves shifts in environmental and edaphic conditions, a population may respond by evolving in a new direction or by becoming extinct (Stebbins, 1974).

Gradual shifts in response to aridity and/or cold are illustrated in the species of subgenus *Curcas*. Species of southern Mexico are usually monoecious semi-evergreen trees with large to very large leaves, massive terminal inflorescences, female flowers with three bifid stigmas, trilocular fruit, and diploid chromosome numbers. In contrast, extreme northern species of section *Mozinna* are much branched, dioecious, deciduous, rhizomatous subshrubs with short shoots and small to very small leaves, lateral few (♂) or solitary (♀) inflorescences, female flowers with a single bifid stigma, unilocular fruit, and polyploid chromosome numbers. Thus, species of *Jatropha* have endured gradual mosaic evolutionary changes, as reflected in their great diversity of adaptive types, which are inextricably correlated with their geographical distribution.

The above observations are reflected in the results of the phylogenetic analyses. An ancestral taxon similar to *J. Curcas* (sect. *Curcas*) seems to have been the source from which species of sections *Platyphyllae*, *Loureira*, and subsequently *Mozinna* originated in Mesoamerica. Furthermore, section *Curcas* or a taxon with similar features also gave rise to species of section *Polymorphae*, leading the way to evolution of taxa in section *Peltatae*. Section *Jatropha* is shown to have evolved from some portion of section *Peltatae*. Several taxa described after Dehgan & Webster's (1979) publication appear to have been appropriately placed in the phylogenetic scheme. In short, the earlier classification recognized grade taxa based on symplesiomorphic features. Only some minor adjustments to previously recognized phylogenetic groupings will have to be made in the forthcoming monograph of the genus. It is fascinating that while the classification of Dehgan & Webster (1979) is based on phenetic studies, the authors have presented a phylogenetic diagram remarkably similar to the results of cladistic analyses presented herein.

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APPENDIX. Specimens representative of the *Jatropha* species examined.

Species and authority	Herbarium	Collector and number	Country
J. alamanii Muell. Arg.	MICH	King 1397	Mexico
J. andrieuxii Muell. Arg.	CAS	Salas 1175	Mexico
J. angustifolia Griseb.	NY	Jennings 147	Cuba
J. augustii Pax & Hoffm.	CAL	Belshaw 3056	Peru
J. bartlettii Wilbur	MICH*	R. L. & C. R. Wilbur 1472	Mexico
J. bullockii E. Lott	MICH	McVaugh 26284	Mexico
J. canescens (Benth.) Muell. Arg.	KEW*	Hinds 1841	Mexico
J. cardiophylla (Torr.) Muell. Arg.	DAV	Dehgan & Webster B74.023	US—Arizona
J. cathartica Terán & Berland	BM	Fryxell 2943	US—Texas
J. chamelensis L. A. Pérez-Jiménez	ENCB, MICH	Rzedowski & McVaugh 1400	Mexico
J. ciliata Sessé	CAS, ENCB, F, GH, M, MIN, MO, NY, UC, US, BM	Pringle 6348	Mexico
J. cinerea (Ortega) Muell. Arg.	RSA, GH, NY	Gentry 7050	Mexico
J. clavuligera Muell. Arg.	GM, GH**, NY**	G. Mandon 1073	Bolivia
J. cordata (Ortega) Muell. Arg.	MICH	McVaugh 22107	Mexico
J. costaricensis Webster & Poveda	DAV*	G. L. Webster & L. J. Poveda 22160	Costa Rica
J. cuneata Wiggins & Rollins	DAV, MICH, NY	Webster & Lynch 17008	Mexico
J. curcas L.	FLAS	Dehgan B86.050	Mexico
J. dioica Sessé	DAV	Dehgan B67.279	Mexico
J. dissecta (Chod. & Hassl.) Pax	GH*, KEW**	Hassler 4333	Paraguay
J. divaricata Swartz	BM	Webster & Wilson 5073	Jamaica
J. eglandulosa Pax	BM*	Hassler 8233	Paraguay
J. elbae J. Jiménez Ramírez	FLAS	Soto 254	Mexico
J. elliptica (Pohl) Muell. Arg.	BM, KEW, MO	Steinbach 6708	Brazil
J. excisa Griseb.	KEW, BM	Venturi 7991	Argentina
J. flavovirens Pax & Hoffm.	KEW*, BM**	Hassler 2489	Paraguay
J. fremontioides Standley	NY**	Fisher 35498	Mexico
J. galvanii J. Jiménez Ramírez	FLAS	Contreras & Jiménez s.n.	Mexico
J. gaumeri Greenman	US, TEX, MICH	Lundell & Lundell 7502	Mexico
J. giffordiana Dehgan & Webster	DAV*	Dehgan B74.019	Mexico
J. gossypiifolia L.	FLAS	Dehgan & Webster BD86.300	Brazil
J. grossidentata Pax and Hoffm.	LPB	Beck 6442	Bolivia
J. guaranitica Speg.	UC*	Hassler 10104	Paraguay
J. hernandiifolia Vent.	KEW	Fuertes 359	Dominican Republic
J. hieronymii O. Ktze.	LPB	Beck 4970	Bolivia
J. hintonii Wilbur	BM*	Hinton 4300	Mexico
J. humboldtiana McVaugh	GH	Weberbauer 6211	Peru
J. integerrima Jacq.	MO, NY, F, GH	Combs 99	Cuba
J. intercedens Pax	MICH*, BM**, B**	Fiebrig 5393, Fiebrig 2158	Bolivia
J. intermedia (Chodat & Hassler) Pax	MICH*	Hassler 3795	Paraguay
J. isabellii Muell. Arg.	BM*	Hassler 4338, 5930	Paraguay
J. katharinae Pax	BM**	E. Hassler 9078	Paraguay
J. macrantha Muell. Arg.	KEW	Sauderman 3983	Peru
J. macrocarpa Griseb.	BM, KEW	Venturi 5472	Argentina
J. macrorhiza Benth.	DAV	Dehgan B74.076	US—Arizona
J. malacophylla Standley	US*	Gentry 1449	Mexico

APPENDIX. Continued.

Species and authority	Herbarium	Collector and number	Country
J. martiusii (Pohl) Baillon	FLAS, DAV	Dehgan & Webster BD86.346	Brazil
J. mcvaughii Dehgan & Webster	DAV	Dehgan B74.206	Mexico
J. mollissima (Pohl) Baillon	FLAS	Dehgan & Webster BD86.318	Brazil
J. moranii Dehgan & Webster	DAV*	Howell 10606	Mexico
J. multifida L.	MO, KEW	Valeur 684	Dominican Republic
J. mutabilis (Pohl) Baillon	FLAS	Dehgan & Webster 312	Brazil
J. neopauciflora Pax	TEX, NY, GH, DAV	Webster et al. 17319	Mexico
J. nudicaulis Benth.	MO	Dodson & Dodson 12941	Colombia
J. olivacea Muell. Arg.	US	Pringle 6348	Mexico
J. ortegae Standley	MIN*	Ortega 6455	Mexico
J. pachypoda Pax	M*	Fiebrig 3042	Bolivia
J. pauciflora Griseb.	NY	Ekman 16169	Cuba
J. peiranoi Lourt. & O'Donn.	MO	O'Donell & Meyer 5308	Argentina
J. platyphylla Muell. Arg.	DAV	Webster & Lynch 17032	Mexico
J. podagrica Hook.	MICH	Breedlove 11810	Mexico
J. pohliana Muell. Arg.	M	Luetzelburg 26802	Brazil
J. pseudocurcas Muell. Arg.	DAV	Webster et al. 11746	Mexico
J. purpurea Rose	BM*	Palmer 785	Mexico
J. ribifolia (Pohl) Baillon	KEW*	Gardner 2303	Brazil
J. ricinifolia Pax	UC	Venturi 2350	Argentina
J. riojae Miranda	F**	Miranda 2111	Mexico
J. rufescens Brandegee	UC*	Purpus 4049	Mexico
J. rzedowskii J. Jiménez Ramírez	FLAS**	Jiménez s.n.	Mexico
J. standleyi Steyermark	MICH	Matuda 2260	Mexico
J. stevensii G. L. Webster	MO	Stevens 22902	Nicaragua
J. sympetala Blake & Standley	BM, ENCB, GH, MICH, TEX, UC, NY	McVaugh 15637	Mexico
J. thyrsantha Pax & Hoffm.	MICH	Troll 455	Bolivia
J. tlalcozotitlanensis J. Jiménez Ramírez	FLAS	Lozano 38	Mexico
J. tupifolia Griseb.	DAV, GH	Webster et al. 198	Cuba
J. vernicosa Brandegee	UC**, GH	Brandegee s.n.	Mexico
J. weddelliana Baillon	CEN	Allem 669	Brazil
J. yucatanensis Briq.	CAS	Thorn & Lathrop 40462	Mexico

* Type.
** Isotype.