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Investigation and documentation of hybridization between *Parkinsonia aculeata* and *Cercidium praecox* (*Leguminosae: Caesalpinioideae*)

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Key words: *Leguminosae*, *Parkinsonia aculeata*, *Cercidium praecox*, *Parkinsonia × carterae*. – Hybridization, morphometric analysis, cytology, weeds.

Abstract: Morphometric, cytogenetic, geographical and ecological evidence for hybridization between *Parkinsonia aculeata* and *Cercidium praecox* is presented. Morphometric investigation using the character count procedure and cytogenetic observations confirm hybrid status. All diagnostic morphometric characters were intermediate in the hybrid. Both parents ($2n = 28$) show regular tetrad formation and pollen fertility greater than 94%. Hybrids have a chromosome number of $2n = 28$ or $2n = 30$, and display meiotic abnormalities including lagging chromosomes and micronucleus formation; less than 21% of hybrid pollen was fertile. Ecological and geographical information suggests that hybridization is occurring at increasing frequency due to the expanding range of *P. aculeata* associated with cultivation as an ornamental, coupled with ecological disturbance and weediness, and the cultivation of *C. praecox* and hybrids as fodder, ornamental and shade trees. Hybrid fertility and phenological observations, in conjunction with F-weighted principal component analysis, suggest that the progeny of F_1 hybrids are established. The hybrid is formally described as *P. × carterae*.

Parkinsonia L. and *Cercidium* TULASNE together comprise ten species of small trees and spreading shrubs found mainly in subtropical and tropical arid habitats; the greatest number of species are found in the Sonoran Desert of Mexico and the southern USA. (CARTER 1974a, HAWKINS 1996). It has been suggested that natural hybridization occurs between four pairs of species which are found in this region: *C. microphyllum* (TORREY) ROSE & JOHNSTON and *C. praecox* (RUIZ & PAVÓN) HARMS; *C. microphyllum* and *C. floridum* BENTH. ex GRAY; *P. aculeata* L. and *C. microphyllum*; *P. aculeata* and *C. praecox* (CARTER 1974a, b; CARTER & REM 1974; JONES 1978; DIMMIT 1987). Both *P. aculeata* and *C. praecox* have ranges which extend well beyond the Sonoran Desert and southern USA. *Parkinsonia aculeata* has an almost pan-tropical distribution following introduction as a ornamental, hedging, fodder and shade tree (STEWART & al. 1992). The establishment of

extensive naturalised weedy populations has made the demarcation of the natural distribution of the species difficult (ISELY 1975, McVAUGH 1987, WOODS 1992). *Cercidium praecox* has a disjunct distribution spanning the arid regions of tropical and subtropical North, and South America (CARTER 1974a; BURKHART & CARTER 1976).

The original suggestion that natural hybridization occurs between *P. aculeata* and *C. praecox* was based on examination of three specimens (CARTER & REM 1974). In 1971 in Sonora, Mexico, CARTER, HASTINGS and TURNER collected a flowering specimen (CARTER 5575) of a tree which exhibited characteristics of both *C. praecox* and *P. aculeata*; these traits were matched in two collections (HINTON 6040; HINTON 9968) from Guerrero, Mexico specimens (CARTER & REM 1974). Both *C. praecox* and *P. aculeata* were observed in the immediate vicinity of the Sonoran specimen and are known to occur in Guerrero. The possibility that these collections might be of hybrids between *P. aculeata* and *C. praecox*, led CARTER & REM (1974) to include the putative hybrids in a survey of pollen stainability in *Parkinsonia* and *Cercidium* and to compare morphological characteristics of *P. aculeata*, *C. praecox* and the putative hybrid. Two of the putative hybrids showed pollen fertility of 20–21%, as compared to the parent species which showed pollen fertility of 95% or more; variation in pollen size in the putative hybrid was also much greater than in the putative parents. The morphological study included two specimens of putative hybrid origin, one of *C. praecox* and one of *P. aculeata*. The two hybrid specimens were intermediate or showed parental values for eleven morphometric characters and six qualitative characters (CARTER & REM 1974).

Criteria for the identification of hybrids have been reviewed by WAGNER (1969), GOTTLIEB (1972), STACE (1975, 1989), ROSEN (1979) and RUSHTON (1993). Recreation of the hybrid through controlled crossing, and the observation of chromosome abnormalities or low fertility are strongly suggestive of hybrid origin (WAGNER 1969; STACE 1975); some of the strongest evidence for hybridity comes from cytogenetic studies (STEBBINS 1945). Morphological or molecular characters may also indicate hybrid origin (ANDERSON 1949, WELLS 1980, ADAMS 1982, NELSON 1983, RIESEBERG & BRUNSFELD 1992, WILSON 1992, RIESEBERG & ELLSTRAND 1993, RIESEBERG 1995, McDADE 1995, RIESEBERG & MOREFIELD 1995). Morphological intermediacy has long been considered to provide evidence of hybridity, and often forms the basis of an a priori hypothesis of hybridity (GOTTLIEB 1972). Hybrids may possess some characters of one parent, some of the other, some intermediate and some extreme character states (STACE 1989), and a number of authors have attempted to characterise precisely the patterns of morphometric or cladistic character expression in hybrids (e.g. WELLS 1980, ADAMS 1982, WILSON 1992, McDADE 1995, RIESEBERG & MOREFIELD 1995). Principal component analysis (PCA), principal coordinates analysis (PCO), Wells hybrid distance diagrams, pictorialised scatter diagrams, hybrid indices and canonical variate analysis have all been used to demonstrate morphometric intermediacy in studies of putative hybrids (ANDERSON 1949, WELLS 1980, ADAMS 1982, WILSON 1992). WILSON (1992) demonstrated that the type of intermediacy that distinguishes hybridity from divergence is not multivariate intermediacy, but the coincidence of intermediate character states. He showed that only pictorialised scatter diagrams and the character count procedure could distinguish intermediacy due to hybridization.

Segregation in an F₂ or backcrossed population may also provide evidence of hybridity (GOTTLIEB 1972, STACE 1975); segregation can be demonstrated where a priori groups are recognised using biometrical techniques such as F-weighted PCO (ADAMS 1982). Most morphological cladistic studies use qualitative variation partitioned into two or more character states (THIELE 1993). The observation that the morphological variation shown by hybrid individuals may be difficult to encode as qualitatively varying characters, and the empirical demonstration of unpredictable character expression, suggest that morphological cladistic analyses are not able to universally indicate hybridity (HUMPHRIES 1983; MCDADE 1990, 1992, 1995; RIESEBERG 1995). Geographical and ecological observations can provide circumstantial evidence for hybrid origin. Some of the most useful circumstantial evidence for the identification of hybrids comes from the study of the species present in the vicinity of a putative hybrid (STACE 1989). ANDERSON & HUBRICHT (1938) were amongst the first to discuss the relevance of ecological observations in studies of hybridization and introgression. ANDERSON (1949) noted that disturbance of the habitat and hybridization are often associated, and postulated that ecological disturbance and the human movement of plants brings into contact weedy, domesticated and incipiently domesticated species which otherwise might not show sympatry, whilst creating an ecological niche in which hybrid segregates might become established.

GOTTLIEB (1972) suggested that individual criteria of hybridity may not distinguish between hypotheses of hybridization and alternate hypotheses. He considered the criteria to be a series of questions; the more of them that are answered positively, the higher is the level of confidence in a hypothesis of hybridity. Here we present a combination of evidence from cytogenetic, morphometric, geographical and ecological studies of the putative hybrid *P. aculeata* × *C. praecox*. These studies were made as part of a wider systematic study of *Parkinsonia* and *Cercidium* undertaken by HAWKINS (1996).

Materials and methods

Morphometric studies. Herbarium specimens of six individuals of *P. aculeata*, eight of *C. praecox* and 16 of the putative hybrid *P. aculeata* × *C. praecox* were collected in Mexico and Central America (see Table 1). Seeds from the putative *P. aculeata* × *C. praecox* hybrids (HUGHES 1161 and 1164) were planted in field trials in Comayagua, Honduras in 1990 (HUGHES 1989); herbarium specimens representing these plantings account for five of the putative hybrids included in the morphometric studies. Twenty four morphometric characters (see Table 2) were identified without prior consideration of their ability to distinguish the taxa. Where possible, five measurements for each character were made from each of the 30 accessions. It was not possible to make five measurements for the following character-specimen combinations: characters 13, 14, 15, 16 and 17 for HAWKINS 90, 137, HUGHES 1364, 1365, 1366, 1367 due to absence of flowering; characters 18, 19, 20, 21 for HAWKINS 18, 30, 39, 70, 81, 82, 83, 89, 90, 91, 96, 130, 132, 137, HUGHES 1364, 1365, 1366, 1367, 1415 due to absence of ripe fruit. Five measurements were made from HAWKINS 36, 48, 40, 56, 59, 28, 45, 46 for characters 22, 23 and 24, and two measurements were made from HAWKINS 131; other specimens lacked ripe seeds and were not scored for these characters. Means and standard deviations of the means were calculated for each character for the three taxa. The data was analysed by the character count procedure (WILSON 1992),

Table 1. Collections used in the morphometric investigation of the status of putative hybrids between *Parkinsonia aculeata* and *Cercidium praecox*. Collections were made by JULIE A. HAWKINS (JAH) or COLIN E. HUGHES (CEH); voucher specimens (left column) are lodged at FHO

<i>Parkinsonia aculeata</i> L.		
JAH 33	Tacupa, Michoacan, Mexico	18° 24'N 100° 41'W
JAH 40	Río Florido, Guerrero, Mexico	18° 23'N 100° 43'W
JAH 56	Salina Cruz, Oaxaca, Mexico	16° 20'N 95° 10'W
JAH 59	Lago Tismas, Granada, Nicaragua	12° 10'N 85° 58'W
JAH 90	Rancho El Impossible, Baja California Sur, Mexico	24° 48'N 111° 35'W
JAH 131	Guaymas, Sonora, Mexico	27° 56'N 110° 50'W
<i>Cercidium praecox</i> (RUIZ & PAVÓN) HARMS		
JAH 36	Tacupa, Michoacan, Mexico	18° 24'N 100° 41'W
JAH 41	Río Florido, Guerrero, Mexico	18° 23'N 100° 43'W
JAH 48	Santo Domingo, Guerrero, Mexico	18° 24'N 100° 43'W
JAH 81	La Paz, Baja California Sur, Mexico	24° 15'N 110° 30'W
JAH 89	Rancho El Impossible, Baja California Sur, Mexico	24° 48'N 111° 35'W
JAH 96	Sierra La Giganta, Baja California Sur, Mexico	25° 35'N 111° 35'W
JAH 134	Empalme, Sonora, Mexico	27° 58'N 110° 46'W
JAH 137	Highway between Guaymas and Hermosillo, Sonora, Mexico	—
<i>Parkinsonia aculeata</i> × <i>Cercidium praecox</i>		
JAH 18	Tehuantepec, Oaxaca, Mexico	16° 19'N 95° 09'W
JAH 28	Tacupa, Michoacan, Mexico	18° 24'N 100° 41'W
JAH 30	Tacupa, Michoacan, Mexico	18° 24'N 100° 41'W
JAH 39	Río Florido, Guerrero, Mexico	18° 23'N 100° 43'W
JAH 45	Santo Domingo, Guerrero, Mexico	18° 24'N 100° 43'W
JAH 46	Santo Domingo, Guerrero, Mexico	18° 24'N 100° 43'W
JAH 82	La Paz, Baja California Sur, Mexico	24° 15'N 110° 30'W
JAH 83	La Paz, Baja California Sur, Mexico	24° 15'N 110° 30'W
JAH 91	Rancho El Impossible, Baja California Sur, Mexico	24° 48'N 111° 35'W
JAH 130	Guaymas, Sonora, Mexico	27° 56'N 110° 50'W
JAH 132	Empalme, Sonora, Mexico	27° 56'N 110° 46'W
CEH 1364	La Soledad trial site, Comayagua, Honduras	14° 27'N 87° 41'W
CEH 1365	La Soledad trial site, Comayagua, Honduras	14° 27'N 87° 41'W
CEH 1366	La Soledad trial site, Comayagua, Honduras	14° 27'N 87° 41'W
CEH 1367	La Soledad trial site, Comayagua, Honduras	14° 27'N 87° 41'W
CEH 1415	La Soledad trial site, Comayagua, Honduras	14° 27'N 87° 41'W

except that characters were considered to be diagnostic (twice the standard deviations of the putative parents did not overlap), taxonomically useful (standard deviations did not overlap) or useless (standard deviations overlapped) according to BATEMAN & FARRINGTON (1987). The character state in the hybrids relative to the putative parents was then scored as intermediate, equivocal or extreme. Intermediate hybrid characters were those where the character mean for the putative hybrid fell between one standard deviation interval of the putative parents. Means which fell within the bounds of one standard deviation of either

Table 2. Characters used in the morphometric analysis. Characters were selected without prior consideration of their ability to distinguish the putative parents. Where possible five measurements for each character were made from each of the 30 accessions listed in Table 1

1. Length of primary rachis (mm)	13. Length of banner petal (mm)
2. Length of mucro (mm)	14. Length of banner petal claw (mm)
3. Length of leaflet (mm)	15. Maximum width of banner petal (mm)
4. Width of leaflet (mm)	16. Maximum width of upper petal (mm)
5. Width of pinna (mm)	17. Length of upper petal (mm)
6. Length of pinna (cm)	18. Maximum width of fruit (mm)
7. Number pairs of leaflets per pinna	19. Width of fruit at constriction between seeds (mm)
8. Number of pairs of leaflets per cm on pinna	20. Length of fruit (cm)
9. Number of pairs of pinnae per leaf	21. Number of seeds per fruit
10. Length of inflorescence (cm)	22. Length of seed (mm)
11. Distance between pedicel joint and flower (mm)	23. Width of seed (mm)
12. Distance between pedicel bract and pedicel joint (mm)	24. Thickness of seed (mm)

parent were scored as equivocal. Means which were greater than the upper standard deviation bound of the larger parent or less than the lower standard deviation bound value of the lesser parent were scored as extreme. F-ratio weighted Gower-metric principal coordinates analysis (PCO; GOWER 1966, ADAMS 1982) of Box-Cox transformed data (SOKAL & ROHLF 1981) was carried out. Principal coordinates analysis and data transformation were performed using the R-package (LEGENDRE & VADOUR 1991); MINITAB (1991) was used for one-way analysis of variance calculations.

Cytogenetic studies. For mitotic preparations, 10 to 15 seeds were collected from one individual of *P. aculeata* (CONTRERAS s.n.), one individual of *C. praecox* (HAWKINS 36) and three putative hybrids (HAWKINS 25 and 43, WHITE 2). Seeds were scarified and germinated in the dark at 30 °C. Tips of emergent primary roots (1–3 cm) were pretreated at 18 °C in 2 mM 8-hydroxyquinoline for 5 hours in total darkness, then fixed in Farmer's solution (3:1 absolute ethanol:glacial acetic acid) for a minimum of twenty four hours, rinsed in distilled water, hydrolysed with 1 M HCl at 60 °C for 12 minutes and stained with Feulgen solution (GARCÍA 1988) for one hour in total darkness. Squashes were made with 1% aceto-orcein, and permanent slides were prepared according to the dry ice method of CONGER & FAIRCHILD (1953). Chromosome counts were made from five to seven cells for each of the mitotic preparations. Meiotic observations were made from pollen mother cells (PMCs) from immature anthers dissected from flower buds collected from one individual of *P. aculeata* (TORRES s.n.), one individual of *C. praecox* (CONTRERAS s.n.) and one putative hybrid (CONTRERAS s.n.) and fixed in Farmer's solution. Anthers were cut open and steeped in a drop of 1% acetocarmine solution to release PMCs. A drop of Hoyer's solution (ANDERSON 1954) was added to the acetocarmine-PMC suspension in order to make a temporary mount. The frequencies of meiotic irregularities, including the incidence of micronuclei, were scored for 500 PMCs. The best mitotic and meiotic fields were photographed using a Contax camera.

Pollen studies. Pollen was obtained from flower buds removed from two herbarium specimens of *C. praecox* (HAWKINS 41, TORRES 1547), two of *P. aculeata* (BOEGE 1628, HUGHES 906) and two of their putative hybrid (HAWKINS 25, HUGHES 1514). Pollen was

stained with nitro blue tetrazolium according to HAUSERY and MORRISON (1964). Four hundred and fifty grains from each specimen were scored and percentage staining, as an index of pollen viability, was determined.

Species distributions and ecology. Species distributions were mapped from field collected specimens and from specimens lodged at BM, FHO, JEPS, K, LL, MEXU, TEX, and UC using the botanical database BRAHMS (Botanical Research and Herbarium Management System; ver. 1, FILER 1993) and the compatible mapping programme MUSICA (Multiscale Information and Cartographic Assistant; ver. 1; HAWTHORNE, in prep.). Ecological and associated observations were made in the field, and recorded from specimen labels. In particular, the degree of disturbance of the site and the occurrence of other species or the putative hybrid was recorded.

Results

Morphology. Hybrid and parent morphologies are illustrated in Fig. 1. The characters used to identify *P. aculeata*, *C. praecox* and the putative hybrid are that *Parkinsonia aculeata* has a spinescent primary leaf rachis and spinescent stipules, longer brachyblasts with a distinct axis of growth, longer flattened pinnae, minute leaflets, and fruits which are elliptic in cross section and often strongly constricted between the seeds. *Cercidium praecox* has spinescent determinate shoots, extremely reduced brachyblasts which lack an obvious axis of growth, an indurate primary leaf rachis and flattened fruits with little or no constriction between the seeds. The putative hybrid lacks armature, and appears intermediate in leaf and fruit characters. The morphometric data are summarised in Table 3. When the 24 characters were classified according to the procedure of BATEMAN & FARRINGTON (1987), six diagnostic characters, and four useful characters were identified. The putative hybrid showed intermediacy relative to the parents for all the diagnostic characters and two of the four useful characters. Hybrid values were equivocal for a third useful character and extreme for the fourth. The first two axes of variation of the F-weighted, Box-Cox transformed, Gower-metric principal coordinates analysis are shown in Fig. 2. Percentage variance of eigenvalues for the first two axes are indicated. Parent groups are strongly delimited on the first axis of variation only. The putative hybrids show almost the full range of variation on the first and second axes.

Cytogenetic studies. *Parkinsonia aculeata* and *C. praecox* both have mitotic chromosome numbers of $2n = 28$. Two of the putative hybrids (HAWKINS 25 and 43) have a count of $2n = 30$; a third hybrid (WHITE 2) has a count of $2n = 28$. Figure 3A–D show mitotic preparations of the putative parents and hybrid. Meiosis was normal in *P. aculeata* and *C. praecox* and abnormal in the putative hybrids. Lagging chromosomes were observed (Fig. 3E) and one or two micronuclei were formed in approximately 22% of tetrads (Fig. 3F). *Parkinsonia aculeata* showed pollen viability of 94 to 97%, *C. praecox* 95 to 99% and the putative hybrid 20 to 23%.

Distribution and ecology. Figure 4 shows the distribution, in Mexico, of *P. aculeata*, *C. praecox* and their putative hybrid. Table 4 describes the sites at which the putative hybrid *P. aculeata* × *C. praecox* have been collected. Figure 4 shows that *P. aculeata* is widespread across Mexico, whilst the distribution of *C. praecox* is more restricted, occurring in two disjunct areas, one centred in Sonora and Baja

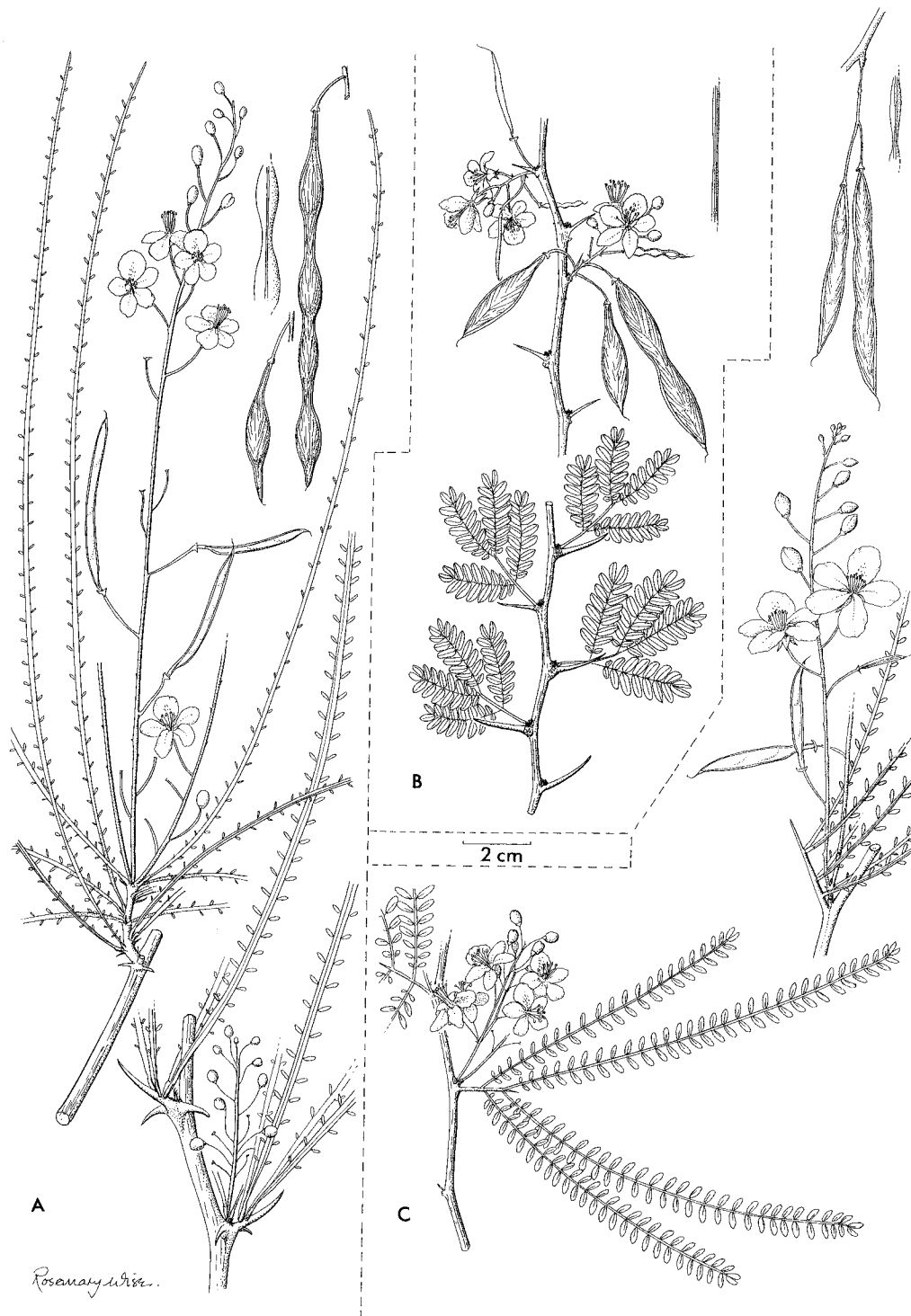


Fig. 1. Morphology of *Parkinsonia aculeata*, *Cercidium praecox* and their putative hybrid. A *P. aculeata* (HAWKINS 7 and 125). B *C. praecox* (HAWKINS 19, 36 and 89). C *P. aculeata* × *C. praecox* (HAWKINS 26, 45 and 46)

Table 3. Mean values (with standard deviations) for *Parkinsonia aculeata*, *Cercidium praecox* and the putative hybrid as collected in the field, calculated for 24 morphometric characters. Standard deviations among species means are shown in parentheses. The taxonomic utility of each character is indicated according to BATEMAN & FARRINGTON (1987): ** diagnostic; * useful; 0 useless. The status of the hybrid mean relative to the parental range of values is also indicated: I intermediate; E equivocal; X extreme

Character	<i>P. aculeata</i> (n = 6)	Putative hybrid (n = 11)	<i>C. praecox</i> (n = 8)	Status of hybrid mean
1	17.32 (4.59)	19.45 (8.12)	13.86 (5.31)	0 / E
2	13.53 (3.60)	3.21 (1.78)	1.05 (0.30)	** / I
3	3.00 (1.20)	5.24 (0.94)	5.89 (1.93)	0 / E
4	0.98 (0.22)	1.72 (0.34)	2.68 (0.98)	* / E
5	1.90 (0.87)	0.58 (0.19)	0.34 (0.05)	* / I
6	27.87 (4.91)	9.52 (4.17)	2.25 (0.51)	** / I
7	39.03 (14.81)	22.92 (8.23)	7.45 (0.95)	** / I
8	2.10 (0.63)	3.13 (0.42)	4.48 (1.04)	* / I
9	1.97 (0.23)	2.58 (0.75)	1.78 (0.62)	0 / X
10	12.70 (3.77)	7.62 (2.09)	1.37 (0.55)	** / I
11	1.96 (0.52)	2.17 (0.59)	2.70 (0.59)	0 / E
12	8.76 (0.66)	7.73 (1.57)	5.47 (0.67)	** / I
13	11.03 (1.47)	13.61 (1.09)	11.51 (1.09)	0 / X
14	4.36 (0.54)	5.92 (0.58)	4.75 (0.33)	0 / X
15	8.39 (0.70)	10.38 (1.06)	8.64 (0.77)	0 / X
16	7.88 (0.42)	9.31 (0.85)	7.81 (0.89)	0 / X
17	11.20 (1.61)	12.60 (1.28)	10.81 (0.61)	0 / E
18	7.77 (0.77)	6.95 (0.59)	7.70 (0.41)	0 / X
19	5.05 (1.54)	6.23 (0.90)	7.15 (0.44)	* / E
20	4.24 (1.41)	4.24 (1.10)	4.03 (0.41)	0 / E
21	2.08 (0.61)	1.60 (0.35)	1.50 (0.20)	0 / E
22	9.72 (1.83)	10.43 (0.82)	7.94 (0.14)	0 / E
23	4.91 (0.56)	4.43 (0.55)	3.97 (0.38)	0 / E
24	3.81 (0.26)	2.00 (0)	1.55 (0.07)	** / I

California in northern Mexico, and the other straddling the states of Guerrero, Michoacan and Oaxaca in south-central Mexico. Putative hybrids have been collected at nine sites, each in an area where *P. aculeata* and *C. praecox* are sympatric. Data collected at putative hybrid sites, or from herbarium specimen notes, show that *P. aculeata* and *C. praecox* were collected or recorded as occurring in the immediate locality of seven of the nine sites at which putative hybrids have been collected, there was no site information for one of the remaining sites, and only *P. aculeata* was recorded at the ninth site (Table 4). Table 4 also shows that all collections of the putative hybrid were made from sites which are disturbed by human activity; hybrids and their parents are cultivated at two of the eight hybrid sites which have been described, and ruderal or weedy at the others. In the case of the Río Florido, Santo Domingo and Tacupa sites, neither the putative

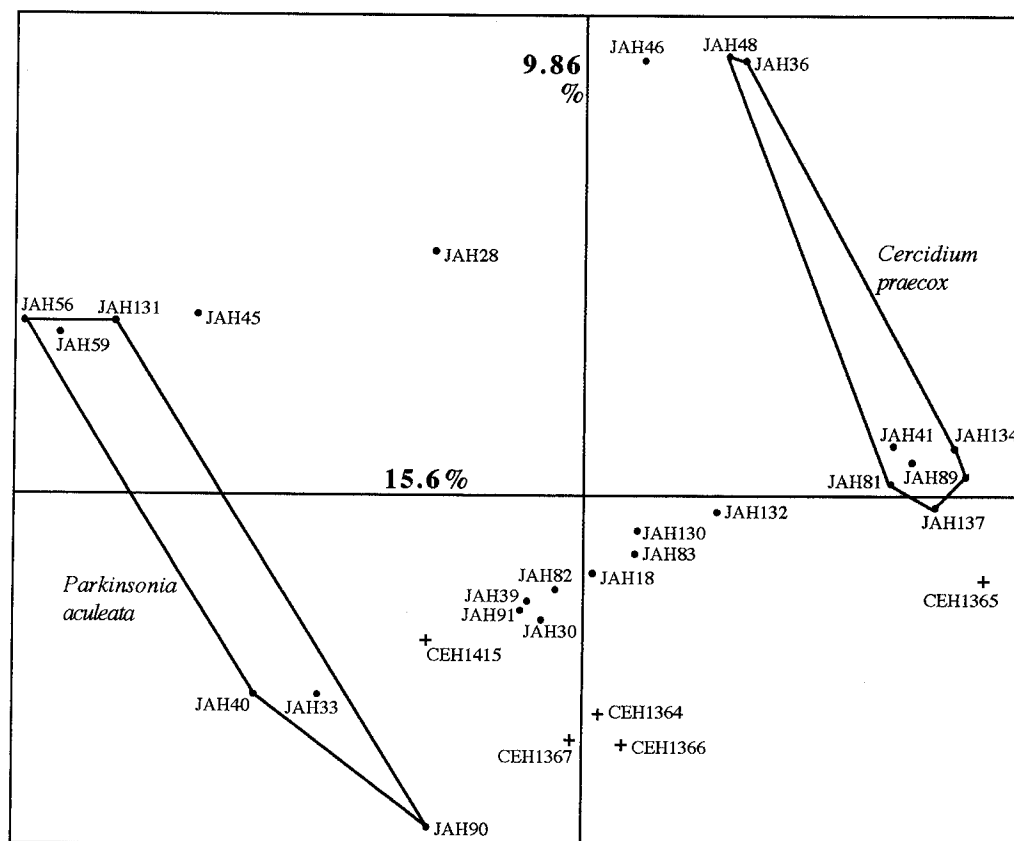


Fig. 2. F-weighted Gower-metric principle coordinates analysis of morphometric data. Points represent collections made by either JULIE A. HAWKINS (JAH) or COLIN E. HUGHES (CEH). Those collections identified in the field as of the parent species are joined or enclosed by lines. Hybrid collections are those which are outside of the lines delimiting parental groups. Collections made from the trial site progeny of putative hybrids are indicated with a cross. The percentage variation represented by the two axes are given

hybrid nor *C. praecox* are found outside cultivation, and *P. aculeata* is restricted to fenceline and irrigation channel sites.

The distributions in Fig. 4 indicate sites from which *P. aculeata* and *C. praecox* have been collected between 1800 and 1993. A number of observations suggest that the natural or original distribution of *P. aculeata* may have been more restricted, and several authors have noted that its natural distribution is difficult to ascertain (ISELY 1975, McVAUGH 1987, WOODS 1992). ISELY (1975) suggested that this is because *P. aculeata* is widely cultivated and may rapidly become established after introduction. The invasiveness of *P. aculeata* is well known in several tropical and sub-tropical countries to which it has been introduced (WILSON & MILLER 1987); for example, since its introduction to Australia in the mid to late nineteenth century, extensive weedy populations have established across the Northern Territories and Western Australia (WILSON & MILLER 1987, WOODS 1992). STEWART & al. (1992) suggested that the range of *P. aculeata* may increase rapidly due to

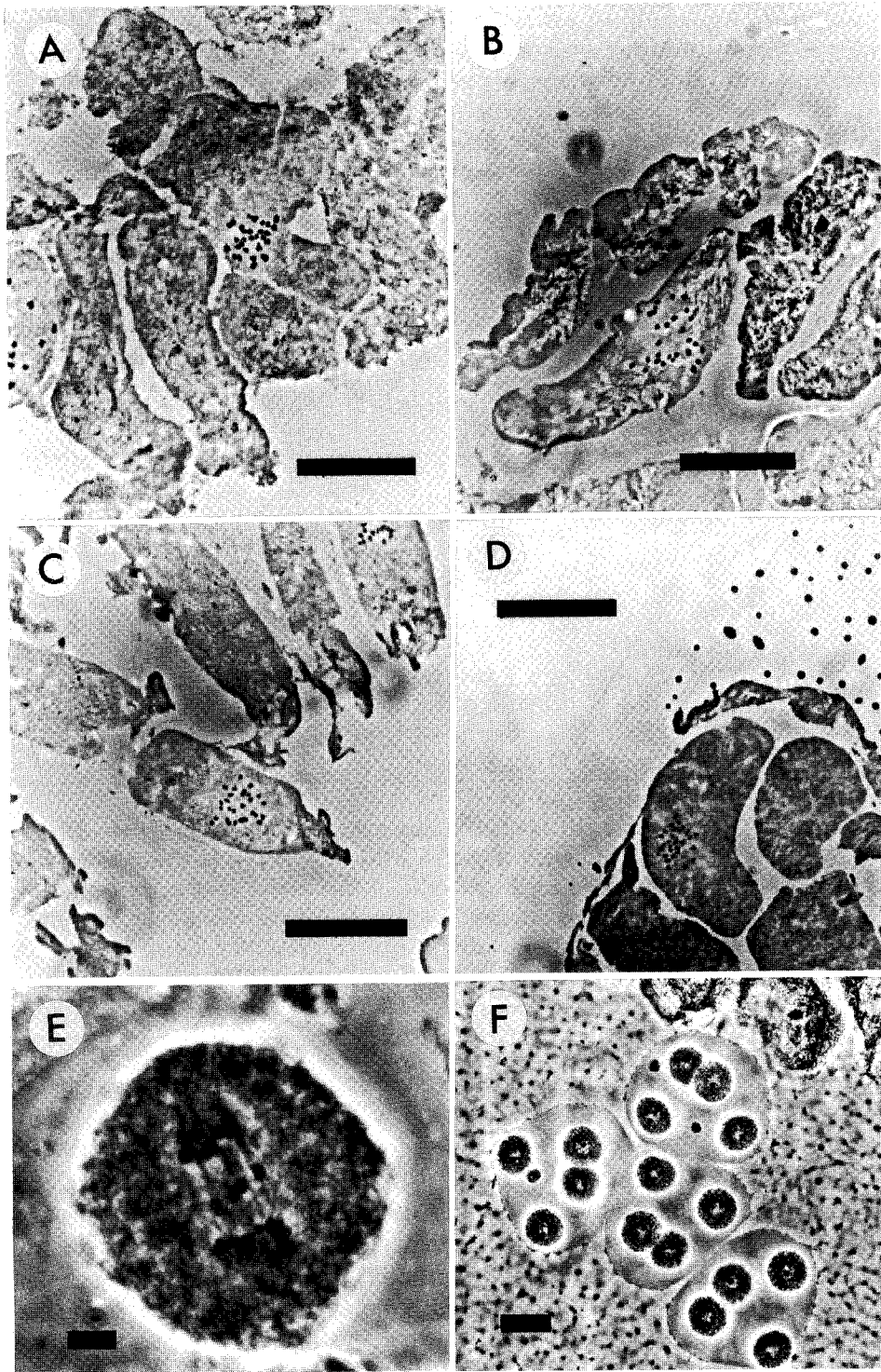


Fig. 3. Mitotic and meiotic preparations. *A* *P. aculeata*, mitosis, $2n=28$. *B* *C. praecox*, mitosis, $2n=28$. *C* *P. aculeata* \times *C. praecox*, mitosis, $2n=28$. *D* *P. aculeata* \times *C. praecox*, mitosis, $2n=30$. *E* *P. aculeata* \times *C. praecox*, meiotic abnormalities; note laggards. *F* *P. aculeata* \times *C. praecox*, meiotic abnormalities; note micronucleus formation. Bars: $20\ \mu\text{m}$

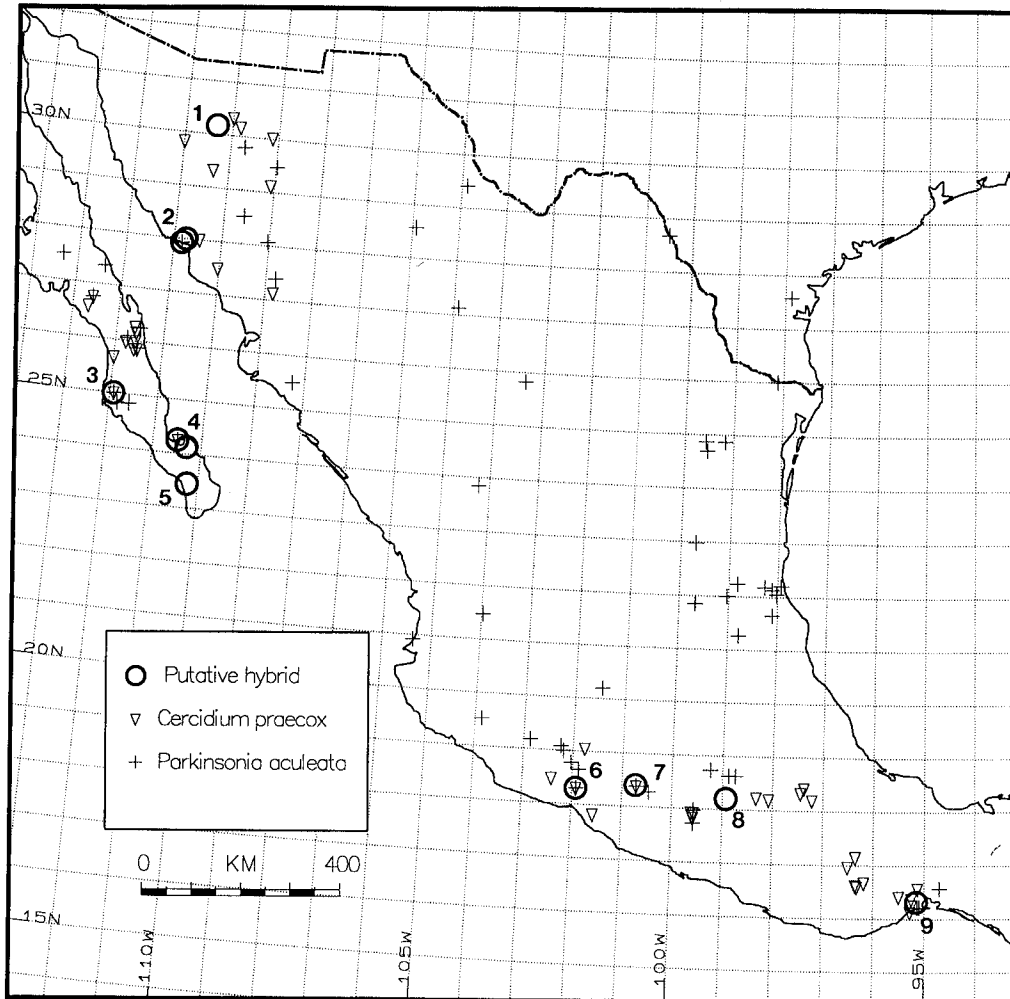


Fig. 4. The distribution, in Mexico, of *Parkinsonia aculeata*, *Cercidium praecox* and their putative hybrid. The nine sites at which the putative hybrid *P. aculeata* × *C. praecox* has been collected are indicated: 1. Los Hoyos, Sonora; 2. Guaymas and La India, Sonora; 3. Rancho El Imposible, Baja California del Sur; 4. La Paz, Baja California del Sur; 5. Todos Santos, Baja California del Sur; 6. Presa El Infiernillo, Michoacan; 7. Tacupa, Michoacan and Río Florido and Santo Domingo, Guerrero; 8. Miltepec, Puebla; 9. Tehuantepec, Oaxaca

effective water dispersal of the indehiscent fruit. This suggestion is supported by observations made during recent field work. The specimens HAWKINS 147, 148, and 149 were collected from the banks of recently-excavated irrigation ditches in Sonora and Sinaloa; these water-ways were observed to be frequently heavily infested with *P. aculeata*. Also, fruits were observed floating in seasonal flood water in lake bed populations of *P. aculeata* (HAWKINS 5 and 57), and pods have been recorded to float for up to two weeks in fresh water. Populations of *P. aculeata* are frequently observed to comprise subpopulations of stands of trees of equal age; one explanation for this structuring of populations might be that each year fruits are

Table 4. Ecological information for sites at which the putative hybrid *Parkinsonia aculeata* × *Cercidium praecox* has been collected. All collections of the putative hybrid indicated are lodged at FHO except for DOMINGUEZ 234, 677 and 901A (MEXU) and CARTER 5575 (K, UC)

Site (and putative hybrids collected)	Site description
1. Los Hoyos, Sonora (CARTER 5575)	Thorn scrub in an agricultural area very near a small village. <i>P. aculeata</i> and <i>C. praecox</i> noted. (CARTER & REM 1974)
2. Guaymas and La India, Sonora (HUGHES 1560, HAWKINS 130, 132 and 133)	HUGHES 1560 and HAWKINS 130: an industrial area adjacent to a disused iron works, on the main road from Guaymas ferry terminal. HAWKINS 132, 133: La India, an agricultural area in the vicinity of Guaymas. <i>Cercidium</i> species and the putative hybrid fence-line trees. <i>P. aculeata</i> and <i>C. praecox</i> noted.
3. Rancho El Imposible, Baja California del Sur (HAWKINS 91)	The two parents and the putative hybrid with intertwined branches by a track in agricultural land.
4. La Paz, Baja California del Sur (DOMINGUEZ 234, 677, HAWKINS 82, 83, 84 and 85)	Dirt roadsides and backyards of houses in the outskirts of La Paz. Both parent species and especially the putative hybrid cultivated or protected as shade and ornamental trees, <i>P. aculeata</i> established as a building-lot weed in other parts of the city.
5. Todos Santos, Baja California del Sur (DOMINGUEZ 901A)	Site information not known.
6. Presa El Infiernillo, Michoacan (HUGHES 1864)	Rocky spoil from dam and power station construction. <i>P. aculeata</i> and <i>C. praecox</i> collected.
7. Tacupa, Guerrero, and Río Florido and Santo Domingo, Michoacan (HINTON 6040 and 9968, HUGHES 1161, 1164 and 1514, HAWKINS 25, 26, 27, 28, 29, 30, 35, 37, 39, 42, 43, 44, 45, 46, 49, 50, 51, 73, 74, 75, 76 and 78)	Three villages where <i>C. praecox</i> and the putative hybrid are cultivated as shade trees and as ornamentals. The putative hybrid is used for fodder for donkeys. <i>P. aculeata</i> is rarely cultivated in the villages, but is often found in their immediate vicinity alongside rivers or irrigation channels. Neither <i>P. aculeata</i> , <i>C. praecox</i> nor the putative hybrid found in the surrounding degraded deciduous dry forest.
8. Miltepec, Puebla (HUGHES 1820)	Ruderal roadside site. <i>P. aculeata</i> noted. <i>C. praecox</i> not seen in immediate vicinity.
9. Tehuantepec, Oaxaca (HAWKINS 18, 21, 53 and 54)	Ruderal roadside site. <i>C. praecox</i> and <i>P. aculeata</i> collected.

deposited at the outermost extent of seasonal floodwaters, so that the site at which seed is deposited each year is dependent on the extent of flooding and wind direction. HUGHES (1989) described the extensive isolated pure stands of *P. aculeata* which occur in Costa Rica, Nicaragua, Guatemala and southern Mexico. All these sites are seasonally flooded former lake bed sites, coastal estuaries or lagoons with deep black vertisols. He proposed that such sites might comprise the natural habitat of *P. aculeata*, and that the extensive occurrence of the species outside of these sites is the result of naturalisation following introduction and cultivation. Only one hybrid site (Tehuantepec) was in close proximity to a putatively natural seasonally flooded site of this type. The cultivation, for shade, ornamental or forage use, of *C. praecox* in areas where it was not found in the local remnant dry forest (e.g. HAWKINS 25) suggests that this species might also have a more restricted natural distribution. Many of the hybrid sites are of relatively recent origin. For example, the Presa El Infiernillo site can be dated with some certainty, as all putative hybrids and their parents occur on the rocky spoil from the dam and power station construction site; construction was completed in 1964, only 31 years before the collection of putative hybrids. Similarly, the Tehuantepec and Guaymas roads have been paved only in the last few decades; the parents and hybrids are found at these sites only on the disturbed ground along the roadside. Several other hybrid sites occur in villages and towns (e.g. La Paz, Tacupa) where one or both parents are cultivated as ornamentals.

Discussion

The demonstration of morphometric intermediacy using the character count procedure supports the hypothesis of hybridity. Principal coordinates analysis is not used for the detection of hybridity, but can reveal the structure of a hybrid swarm (WILSON 1992). Despite the ease with which putative hybrids can be identified in the field (based on absence of determinate spinescent shoots, spinescent primary leaf rachises and spinescent stipules, flower and seed size, length of the pinnae and number of pairs of leaflets per pinnae), and that characters were F-weighted, parental and hybrid groups were not clearly delimited in the principal coordinates analysis of morphometric data. These observations suggest that there is either segregation in an F₂ generation, backcrossing or introgression. The principal coordinates analysis includes progeny of hybrids cultivated in field trials. These progeny are strongly separated on the first axis of variation; the segregation of these F₂ or backcross individuals contributes to lack of distinction between parents and hybrids. Segregation provides additional evidence that hybridization has occurred. Overlapping flowering times between the two parents and the putative hybrid suggest that further hybridization and backcrossing could also be possible. Hybrid flowering in August (HUGHES 1514), when neither parent was in flower, was not accompanied by seed-set, suggesting that seed that is set during overlapping flowering times results from backcrossing.

Cytogenetic abnormalities and low pollen viability support the hypothesis that there is hybridization between *P. aculeata* and *C. praecox*. The chromosome count for *P. aculeata* ($2n = 28$, $n = 14$) presented here agrees with previous counts of $2n = 28$ and $n = 14$ by MIEGE (1962) and ATCHISON (1951). Counts for *C.*

microphyllum ($2n=28$; TURNER & FEARING 1960), *C. floridum* ($2n=28$, $n=14$; TURNER & FEARING 1960; RAVEN & al. 1965), *C. macrum* ($n=14$ TURNER & FEARING 1960), *C. texanum* ($n=14$; TURNER 1956) have been published, but the count of $2n=28$, presented here, is to our knowledge the first for *C. praecox*. The chromosome count of $n=15$, $2n=30$ found in two of the three accessions of the putative hybrid has not been recorded in the *Caesalpinioideae* (GOLDBLATT 1981, 1984, 1985, 1988; GOLDBLATT & JOHNSON 1990, 1991, 1994).

Extra chromosomes may arise through Robertsonian fission (JACKSON 1971; MARKS 1983). Following Robertsonian fission one would expect two pairs of chromosomes to be very much smaller than the rest; in this case all chromosomes are of similar sizes (Fig. 3). The unusual count 30 recorded for two of the three accessions of the putative hybrid might be more convincingly attributed to the presence of B chromosomes. B chromosomes have been reported in *Lotus* L. (*Leguminosae*) where they are associated with interspecific hybridization (SOMAROO & GRANT 1971), though in the absence wider sampling there is no firm evidence that the extra chromosomes are B chromosomes. In the absence of further study, it is the observation of chromosomal abnormalities and not the unusual count which supports the hypothesis that the specimens examined here are of hybrid origin. The pollen fertility data agrees with that of CARTER & REM (1974); low pollen fertility is also characteristic of hybrids with meiotic abnormalities (STACE 1975).

The observation that the numerous disjunct sites of putative hybridization between *P. aculeata* \times *C. praecox* all lie within the sympatric range of the two putative parents lends further support to the hypothesis of hybrid origin, whilst also suggesting that there have been multiple independent origins of the hybrid. Ecological observations are also suggestive of a hybrid origin. ANDERSON (1949) first noted that ecological disturbance and human movement of plants brings together weedy and domesticated species whilst providing ecological niches in which hybrids may establish. Since ANDERSON'S time there have been many well-documented studies of interspecific hybridization following the introduction of one species into the range of a second (reviewed by ABBOTT 1992). The patterns observed in the distribution of *P. aculeata* are typical of a weedy species which may have become established only recently at many hybrid sites, and at some sites it seems that *C. praecox* is also only present as a result of human movement.

The evidence presented here strongly suggests that hybridization between *P. aculeata* and *C. praecox* has accompanied and been facilitated by recent human activities, and that hybridization occurs easily. The hybrid is much more widespread than CARTER & REM (1974) believed, and given the likelihood of increasingly widespread ecological disturbance and continued human movement and cultivation of the parent species, it seems probable that the hybrid will become more common in the future. Indeed, one recent record of the putative hybrid has been made from Ecuador (LEWIS 3761); collection notes indicate that site characteristics closely resemble those of the Mexican sites, with *C. praecox* native and *P. aculeata* introduced and cultivated sporadically as an ornamental. *P. aculeata* and *C. praecox* occur in sympatry through much of South America. *C. praecox* is distributed from central and northern Argentina throughout the arid regions of the west and north of South America (BURKHART & CARTER 1976); *P. aculeata* is arguably native and certainly cultivated and weedy in many of these

areas (MACBRIDE 1943, PEREZ-ARBELAEZ 1956, BURKART 1957). Botanical exploration of South American areas of sympatry could bring further instances of hybridization to light.

Whilst proliferation of names for very rare or ephemeral hybrids should be avoided, it is convenient to name well documented, common hybrids which are fertile, conspicuous or important (WAGNER 1969, 1983; STACE 1975). On this basis, the hybrid is formally described and named here.

There has been more than a century of controversy surrounding the delimitation of the genera *Parkinsonia* and *Cercidium* (e.g. WATSON 1876; SARGENT 1889; JOHNSTON 1924; BRENNAN 1963, 1980; CARTER 1974a; ISELY 1975; POLHILL & VIDAL 1981). WATSON (1876), BRENNAN (1963), ISELY (1975) and POLHILL & VIDAL (1981) chose to accept one genus. However, neither BRENNAN (1963) nor POLHILL & VIDAL (1981) made nomenclatural changes and WATSON (1876) and ISELY (1975) treated only the subset of species found in the USA. Recent flora treatments continue to recognise both genera (e.g. McVAUGH 1987, HICKMAN 1993). Morphological cladistic analysis shows that *Cercidium* sensu CARTER is a monophyletic group which is nested within the larger monophyletic group comprising *P. aculeata*, *P. africana* and *Cercidium* sensu CARTER (HAWKINS 1996). It is the intention of the first author to transfer *Cercidium* sensu CARTER to *Parkinsonia*. The new combination for *Cercidium praecox* is presented here and the hybrid is described as *Parkinsonia* × *carterae* in recognition of ANNETTA CARTER's many years of work on the group.

***Parkinsonia praecox* (RUIZ & PAVÓN) HAWKINS, comb. nova.**

Cercidium praecox RUIZ & PAVÓN, Fl. Peruv. 4: t. 376, (1830?); HOOKER & ARNOTT in Bot. Misc. 3: 208 (1833).

The basionym was validated by the illustration with analysis in volume 4 of RUIZ & PAVÓN'S Flora Peruviana, but the details of when this was published are still obscure. According to STAFLEU & COWAN (1983: 984) the first known reference to the volume being published is in 1830. In case this should later prove incorrect, the next available publication of the name is also given above.

***Parkinsonia* × *carterae* HAWKINS [*P. aculeata* L. × *Parkinsonia praecox* (RUIZ & PAVÓN) HAWKINS], hybrida nova.**

Type: Mexico. Santa Domingo, Guerrero; in the village of Santa Domingo 18.24N 100.44W. HAWKINS 43 (holotype MEXU!, isotypes CAS, FHO!, GH, K, TEX, UC).

Diagnosis: Arbor inter *P. aculeata* L. et *Parkinsonia praecox* (RUIZ & PAVÓN) HAWKINS foliis, folioliis, fructibus, intermedia et verisimiliter ex hybridatione harum specierum orta.

Description. Small to medium-sized shrub or low-branching, spreading tree (1.5–) 4–12 (–20) m tall, sometimes almost as broad. Bark of trunk grey-brown fissured, small branches green, shoots green-grey-brown and sub-glabrous to pubescent. Armature usually lacking, determinant spinescent axillary shoots lacking, stipules minute, indurate to 4 mm, very weakly spinescent, mucro of leaf rachis sometimes very weakly spinescent. Leaves bipinnate, pinnae paired-opposed on the rachis; rachis (4–20) –35 mm long; petiole 1–8 (–10) mm long, sometimes broad and flattened; mucro 0.7–5 (–8) mm long; pinnae (1–) 2–4 pairs, pinnular rachis slightly flattened, (2.4–) 6–12 (–25) cm long, 0.3–0.8 mm wide.

Leaflets (8-) 16-45 pairs spaced 2-4 leaflets/cm; 2.5-6 (-8.5) mm long, 1.2-3 mm wide, obovate-elliptic, weakly mucronate, only midvein visible, sometimes deciduous. Racemes (3-) 5-10 (-14) cm long, borne on short shoots; 6-12 (-25) flowers per raceme, pedicels 7-12 mm, jointed in the distal portion, 0.8-4 mm from the calyx. Flowers yellow, banner flecked orange, clawed; banner fully 12-16 mm long, 8-13 mm wide, claw 4-6 mm long; other petals ovate, 10-14 mm long, 6.5-11 mm wide, claw 1-2 mm long; sepals (5-) 6 (-8) mm long, narrowly ovate, reflexed in flower, sub-glabrous in bud becoming glabrous, (narrowly) imbricate; stamen filaments 7-9 mm long, densely hairy below; anther 10-12 mm long; ovary sometimes tinged deep red at anthesis, few scattered hairs to villous. Fruits brown-grey, linear 2.2-7.8 cm long 3.5-5 mm wide 2-3 mm thick.

Additional specimens examined (HAWKINS and HUGHES duplicates distributed as indicated).

Mexico. Baja California del Sur: La Paz, 24° 08'N 110° 18'W, 15 May 1986, R DOMINGUEZ C 234 (MEXU); 8 Mar 1988, R DOMINGUEZ C 677 (MEXU); Todos Santos, 23° 27'N 110° 13'W, 13 Aug 1989, R DOMINGUEZ C 901A (MEXU); La Paz, 24° 15'N 110° 30'W, 2 May 1993, HAWKINS JA 82 (FHO, K, MEXU, TEX, UC); HAWKINS JA 83 (FHO, K, MEXU, TEX, UC); HAWKINS JA 84 (CAS, FHO, K, MEXU, TEX, UC); HAWKINS JA 85 (EAP, FHO, K, MEXU, TEX, UC); Rancho El Imposible, km 185 on Hwy1 between La Paz and Villa Constitution, 15 km before Villa Morelos, 24° 60'N 111° 55'W, 4 May 1993, HAWKINS JA 91 (FHO, K, MEXU, TEX, UC); Guerrero: Río Florido, 5 km N Coyuca, W bank of the Rio Balsas, 18° 23'N 100° 43'W, 22 Feb. 1993, HAWKINS JA 25 (EAP, FHO, GH, K, MEXU, NY, TEX, UC); 6 Mar. 1993, HAWKINS JA 39 (CAS, EAP, FHO, GH, K, MEXU, NY, TEX, UC); Santo Domingo, 7 km N Coyuca, W bank of the Rio Balsas, 18° 24'N 100° 44'W, 6 March 1993, HAWKINS JA 42 (FHO, K, MEXU, TEX, UC); HAWKINS JA 43 (CAS, FHO, GH, K, MEXU, TEX, UC); HAWKINS JA 44 (CAS, FHO, K, MEXU, NY, TEX, UC); HAWKINS JA 45 (CAS, EAP, FHO, K, MEXU, TEX, UC); HAWKINS JA 46 (FHO, MEXU, TEX, UC); HAWKINS JA 49 (FHO, K, MEXU, TEX, UC); HAWKINS JA 50 (FHO, K, MEXU, TEX, UC); HAWKINS JA 51 (FHO, K, MEXU, TEX, UC); 28 April 1993, HAWKINS JA 73 (FHO, K, MEXU); HAWKINS JA 74 (FHO, K, MEXU); HAWKINS JA 75 (FHO, K, MEXU); HAWKINS JA 76 (FHO, K, MEXU); HAWKINS JA 78 (FHO, K, MEXU); Coyuca, 18° 22'N 100° 43'W, 11 May 1934, HINTON GB 6040 (BM); 25 March 1937, HINTON GB 9968 (BM, K, MEXU). Michoacan: Tacupa, 5 km N of Ciudad Altamirano on the road to Huetamo de Nunez close to the Rio Balsas, 18° 24'N 100° 41'W, 3 March 1993, HAWKINS JA 26 (CAS, FHO, K, MEXU, TEX, UC); HAWKINS JA 27 (FHO, MEXU, TEX); HAWKINS JA 28 (FHO, K, MEXU, TEX, UC); HAWKINS JA 29 (FHO, K, MEXU, TEX, UC); HAWKINS JA 30 (FHO, K, MEXU, TEX, UC); HAWKINS JA 35 (CAS, EAP, FHO, K, MEXU, NY, TEX, UC); 5 March 1993, HAWKINS JA 37 (CAS, EAP, FHO, GH, K, MEXU, NY, TEX, UC); 16 April 1988, HUGHES CE 1161 (FHO, K, MEXU, TEX, UC); HUGHES CE 1164 (FHO, K, MEXU); 14 Aug. 1991, HUGHES CE 1514 (FHO, K, MEXU, MO, NY); El Infiernillo, below the dam on waste ground next to the electric substation near the CFE headquarters, 18° 18'N 101° 55'W, 25 Nov. 1993, HUGHES CE 1846 (FHO, K, MEXU, NY, TEX); Oaxaca: 12 km S Tehuantepec, on the road to Salina Cruz, 16° 15'N 95° 13'W, 30 April 1981, R CEDILLO T 755 (MEXU); 5 km from Tehuantepec, on the Juchitan road, 16° 19'N 95° 09'W, 17 Feb. 1993, HAWKINS JA 18 (CAS, FHO, K, MEXU, NY, TEX, UC); HAWKINS JA 21 (CAS, EAP, FHO, K, MEXU, NY, TEX, UC); 10 March 1993, HAWKINS JA 53 (FHO, K, MEXU, TEX, UC); HAWKINS JA 54 (FHO, K, MEXU, TEX, UC). Puebla: 10 km S of Mitepec, close to the road running S from Huachinantla towards Atenango del Rio, in hills on the N side of the Balsas depression, 18° 12'N 98° 56'W, 19 Nov. 1993,

HUGHES CE 1820 (FHO, K, MEXU, NY, TEX). Sonora: 3.2 km (by road) N of Los Hoyos, 30° 10'N 109° 80'W, 23 April 1971, CARTER AM 5575 (K, MEXU, UC); Guaymas, 3 km from the centre of Guaymas, towards ferry terminal and near PEMEX terminal, 27° 56'N 110° 50'W, 26 Jan. 1992, HUGHES CE 1560 (FCME, FHO, K, MEXU, NY); Opposite a disused ironworks, between 1 and 2 km from Guaymas ferry terminal, approaching the junction of the Hermisillo – Obregon highway, 27° 56'N 110° 50'W, 17 May 1993, HAWKINS JA 130 (FHO, K, MEXU, UC); along the unpaved road to La India from the main Guaymas – Empalme highway, 27° 98'N 110° 98'W, 17 May 1993, HAWKINS JA 132 (CAS, FHO, K, MEXU, TEX, UC); HAWKINS JA 133 (FHO, K, MEXU, TEX, UC). **Honduras.** Comayagua: Los Mangos field evaluation trial site, near the village of El Taladro about 10 km WSW of the departmental town of Comayagua, 14° 27'N 87° 41'W, 8 Aug. 1990, all cultivated, HUGHES CE 1364 (FHO, TEX, UC); HUGHES CE 1365 (FHO, TEX, UC); HUGHES CE 1366 (FHO, TEX, UC); HUGHES CE 1367 (FHO, TEX, UC); HUGHES CE 1415 (EAP, FHO, MEXU). **Ecuador.** Loja: 5 km N of Catemayo, 3° 58'S 79° 23'W, 14 Jan 1998, LEWIS GP 3761 (LOJA, QCME, K, AAU).

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