

# Morphology of *Opuntia aurantiaca* (jointed cactus) biotypes and its close relatives, *O. discolor* and *O. salmiana* (Cactaceae)

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The hypothesis that *Opuntia aurantiaca* Lindley is a hybrid which originated in the dry northern region of Argentina was investigated using quantitative data. Sixty specimens were cultivated under uniform greenhouse conditions and 41 OTUs were selected for morphological study. Using 88 vegetative characters a correlation matrix was generated and subjected to principal component analysis. The resulting scatter diagrams showed the intermediate position of the four biotypes of *O. aurantiaca* between the putative parents, *O. discolor* Britton and Rose and *O. salmiana* Parm.

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Die hipotese dat *Opuntia aurantiaca* Lindley 'n hibried is wat in die droë, noordelike deel van Argentinië ontstaan het, is met behulp van kwantitatiewe data ondersoek. Sestig plante is onder eenvormige toestande in 'n glashuis gekweek en 41 operasionele taksonomiese eenhede is vir die morfologiese studie geselekteer. Ag-en-tagtig vegetatiewe kenmerke is gebruik om 'n korrelasiematriks, wat aan 'n hoofkomponente-analise onderwerp is, op te stel. Die verkreë verstrooiingsdiagramme het getoon dat die vier biotipes van *O. aurantiaca* 'n intermediêre posisie tussen die moontlike ouers, *O. discolor* Britton and Rose en *O. salmiana* Parm., inneem.

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## Introduction

*Opuntia aurantiaca* Lindley is a serious weed introduced to rangeland in South Africa. The original account of the cactus by Lindley (1833) and subsequent records by a number of authors (Arnold 1977; Moran & Annecke 1979) gave its distribution as South American. Moran *et al.* (1976) found that *O. aurantiaca* only occurred in disturbed areas in South America and was not recorded there before 1905. They concluded, on the basis of this and historical evidence, that the taxon was only recently introduced into South America from the West Indies. Arnold (1977) made a taxonomic study of *O. aurantiaca* and its relatives and using these data, additional historical evidence and distributional data, reported that the taxon was probably restricted in its natural distribution to the Entre Rios region of Argentina and the southern extremity of Uruguay. The species was not recorded in South America prior to 1905 and Arnold postulated that the reason for this was that it is a hybrid of relatively recent origin which is restricted to disturbed areas. In a more recent critical review of the biological control of the cactus, Moran & Annecke (1979) accept that the plant is of hybrid origin but point out that the actual origin of the type specimen is still unknown.

Morphologically *O. aurantiaca* is a highly variable taxon and Zimmerman (unpublished observations; Moran & Annecke 1979) distinguished three forms within the South American representatives of the species. In 1977 Arnold described four morphological forms, only one of which, the typical form, occurs in South Africa, having been introduced as an horticultural specimen and first recorded by McGibbon in 1858 (Moran *et al.* 1976).

Arnold's (1977) evidence for the hybrid origin of *O. aurantiaca* is based on seed sterility, pollen morphology, cytology, insect associations, distribution, ecology and morphology. The latter provides the strongest evidence, as the morphological range of variation of *O. aurantiaca* is intermediate between two possible parent species, *O. salmiana* Parm. and *O. discolor* Britton and Rose. Plants of *O. aurantiaca* at the two extremes of the range share many features in common with the other two morphologically distinct species. Information given by Arnold (1977) and characters measured and recorded in this study are presented in Table 1 which illustrates the affinity between the four biotypes of *O. aurantiaca* and the two related species. Arnold (1977) designated the A biotypes as being allied to

**Table 1** The morphological biotypes of *Opuntia aurantiaca* and their affinities with related species

Species and biotype	Habit	Basal cladodes	Aerial cladodes	Length of spines (mm)			Affinity
				Basal cladodes	Aerial cladodes	Flower colour	
<i>O. aurantiaca</i> Lindley A <sub>2</sub>	Semiprostrate to erect	Flattened, 60–230 mm long, 21–32 mm broad and 11–18 mm thick	Flattened, 40–147 mm long, 14–24 mm broad and 5–15 mm thick	11–31	11–29	Bright yellow	Typical form of <i>O. aurantiaca</i> —allied to <i>O. discolor</i>
A <sub>1</sub>	Semiprostrate ascending	Flattened, 65–125 mm long, 18–19 mm broad and 16–18 mm thick	Flattened, 50–90 mm long, 14–19 mm broad and 10–13 mm thick	11–39	11–38	uncertain	Closely resembles form A <sub>2</sub> —allied to <i>O. discolor</i>
B <sub>1</sub>	Ascending	Cylindrical-terete, 68–92 mm long, 11–13 mm broad and 11–13 mm thick	Cylindrical-terete 20–50 mm long, 7–11 mm broad, 7–11 mm thick	6–11	7–15	Creamy-white with pink	Most closely allied to <i>O. salmiana</i>
B <sub>2</sub>	Ascending	Cylindrical-terete, 34–85 mm long, 16–22 mm broad and 16–21 mm thick	Cylindrical-terete, 26–134 mm long, 11–19 mm broad, 11–18 mm thick	7–28	7–26	Pale yellow	Applied to <i>O. salmiana</i> —intermediate between forms A <sub>2</sub> and B <sub>1</sub>
<i>O. discolor</i> Britton and Rose	Semiprostrate	Flattened, 40–120 mm long, 18–23 mm broad and 16–19 mm thick	Flattened, 47–77 mm long, 16–23 mm broad and 11–17 mm thick	15–38	13–37		
<i>O. salmiana</i> Parm.	Erect	Cylindrical-terete, 35–230 mm long, 10–20 mm broad and 10–20 mm thick	Cylindrical-terete, 13–320 mm long, 8–11 mm broad and 8–11 mm thick	1,3–6,5	2–6,2		

*O. discolor*, with A<sub>2</sub>, which is found in South Africa and South America, being the typical form of the species and thus listed first in the table. The B biotypes are allied to *O. salmiana* and along with the A<sub>1</sub> biotype are only found in Argentina and/or Uruguay. A<sub>1</sub> and B<sub>1</sub> were so designated as they are the biotypes most closely related to *O. discolor* and *O. salmiana* respectively. The A<sub>2</sub> and B<sub>2</sub> biotypes have been described as separate species, *O. montevidensis* Speg. and *O. maldonadensis* Arech. respectively, but these species are no longer recognized as being different from *O. aurantiaca* (Arnold 1977). The affinities between the biotypes and their allied species are apparent in the photographs showing their general growth habit. (Figures 1 & 2).

The present investigation was initiated to establish relationships between the four biotypes of *O. aurantiaca* and its reputed parents on a quantitative basis. Hybridization has long been illustrated using quantitative data (Anderson 1949) and more recent studies have shown the advantages of ordination in this type of study (Schueler & Rising 1976; Schilling & Heiser 1976; Crowe & Parker 1981). If these biotypes of *O. aurantiaca* show the affinities with the putative parents that have been proposed, more detailed quantitative studies should illustrate this relationship more exactly.

### Materials and Methods

Plants were raised from cladodes obtained from South

America and South Africa and grown under uniform conditions in a quarantine greenhouse at the University of Port Elizabeth. In all, some 60 plants were produced but only 41 of these were selected for detailed study (Table 2). For the four *O. discolor* plants, three cladodes were obtained from Tucuman, Argentina and one from Bolivia. Four *O. salmiana* plants were raised from cladodes obtained from Tucuman. Three *O. aurantiaca* A<sub>1</sub> biotype plants were grown from cladodes collected in Santa Elena, Argentina. Altogether 21 A<sub>2</sub> biotype plants were used in the analyses. Cladodes originated from the eastern Cape, South Africa (3), Cerro Montevideo (3), Cerro Carmelo (3) and Colonia (3) in Uruguay, and Gualeguay (3), Colon (3) and Gualeguaychù (3) in Argentina. Three B<sub>1</sub> biotypes were raised from cladodes originating from Paraná, Argentina, while six B<sub>2</sub> biotypes were grown from cladodes obtained from Victoria (3) and Campana (3) in Argentina.

The cladodes were rooted in water before planting them in a sandy loam in plastic pots 200 mm deep and 180 mm in diameter. After approximately 1½ years the plants were reasonably well established and they were studied morphologically. Data were collected in the winter months (June, July and August) when virtually no growth was taking place and the plants were not flowering.

The characters chosen for the analyses (Table 3) were selected by observing the plants for morphological characters which seemed to differ between the biotypes and the

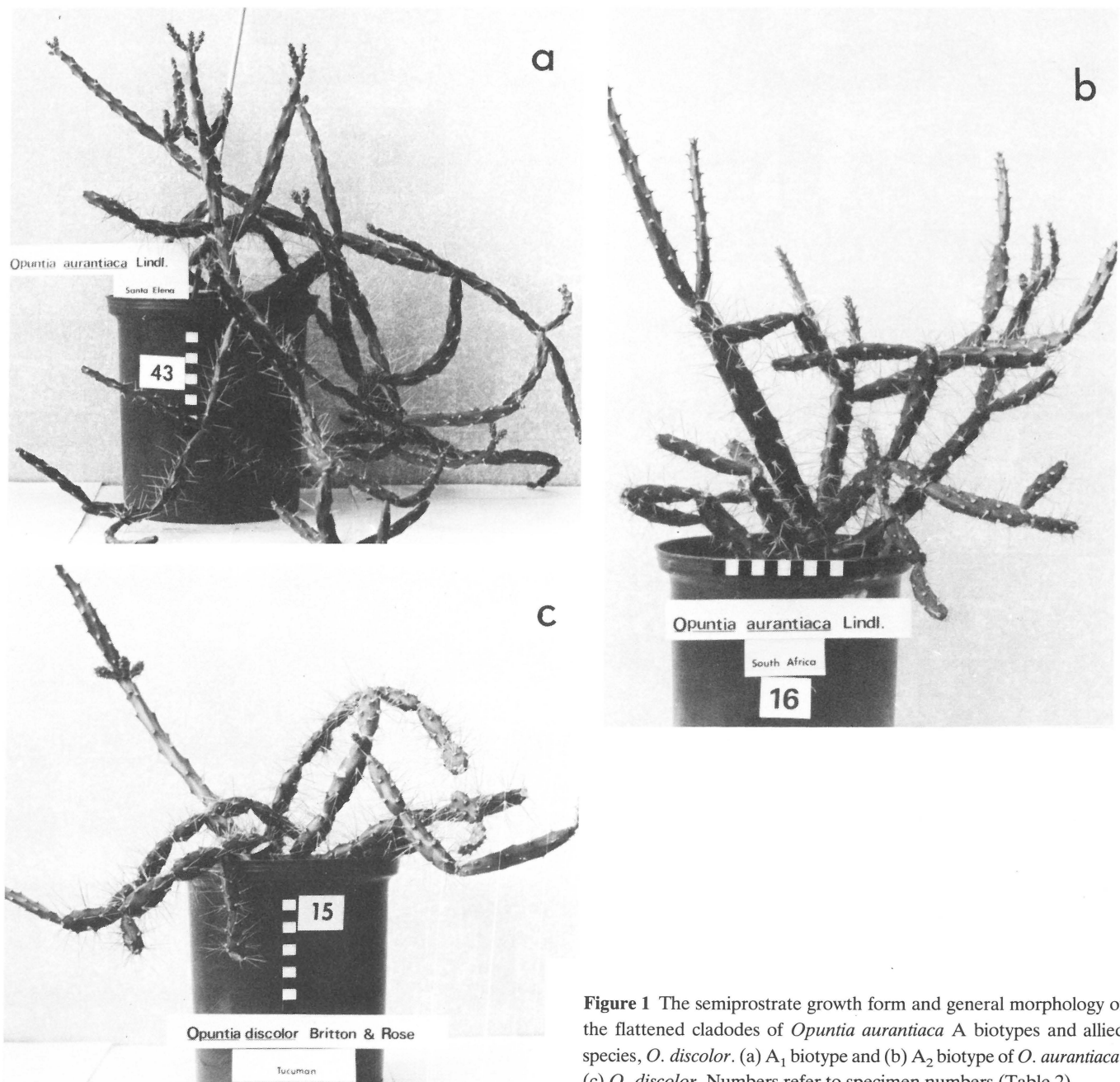
reputed parents. The characters can be divided into four major groups; those related to the whole plant (19), the basal, the median and the terminal cladodes (23 characters each). The 23 cladode characters were recorded for the cladodes in different positions on the plant because they differed quite markedly, especially in some specimens (Figures 1 & 2, Table 1). Of the 88 characters ( $n$ ) used in the study, 36 were quantitative characters obtained from measurements or counts and calculated mean values where possible, and 52 were qualitative characters (Table 3). Qualitative characters, such as growth habit (3–8) or branching pattern (14–18), were subdivided into two-state characters to facilitate coding.

The characters of the 41 operational taxonomic units — OTUs ( $t$ ) were measured and noted on coded data sheets. Missing data occurred in the case of one specimen (no. 53, OTU 38) as the terminal cladodes were of insufficient size to be measured. Consequently mean values obtained from related specimens (nos. 36 & 43, OTUs 36 & 37) were

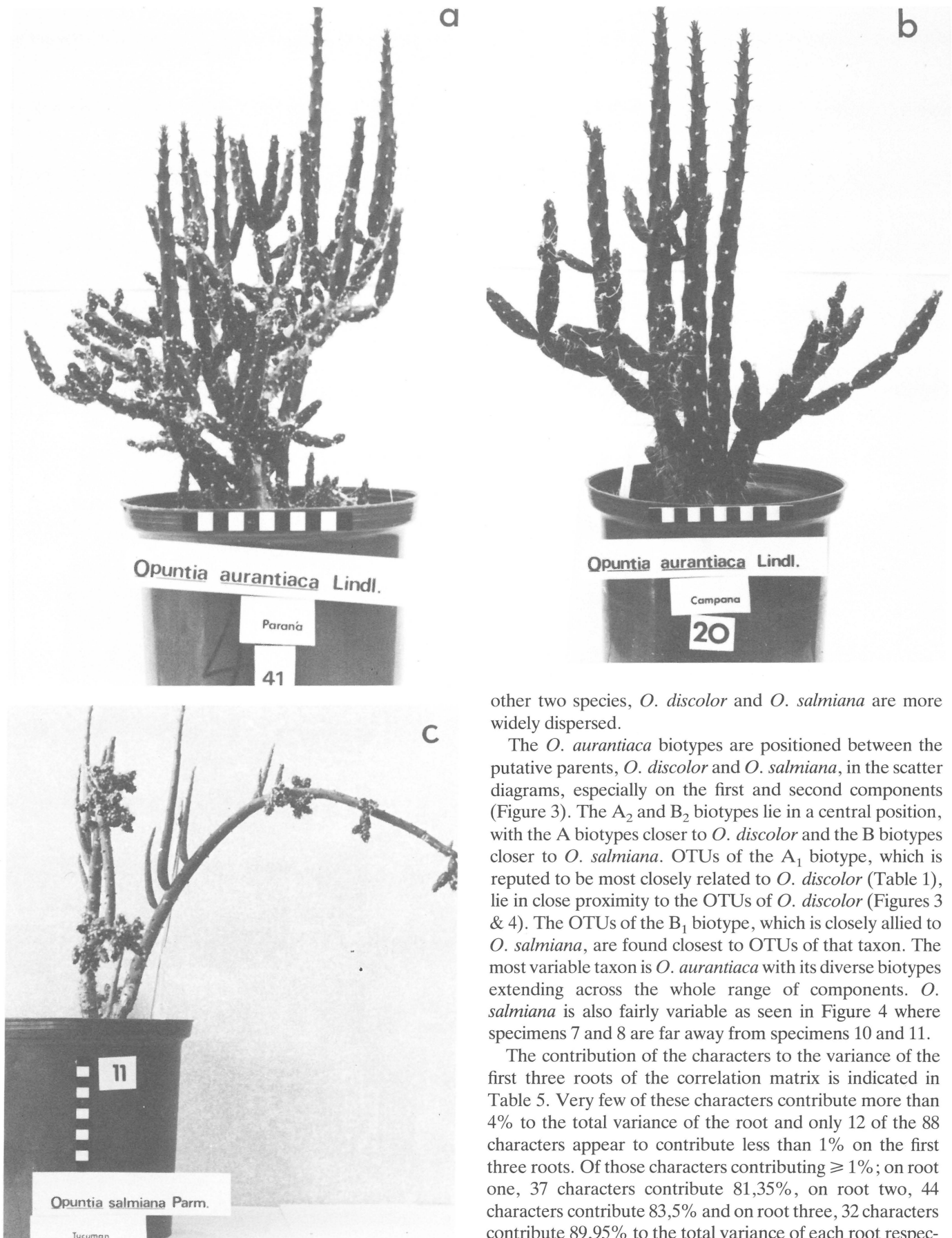
calculated for characters 66–88 for this OTU. The  $88 (n) \times 41 (t)$  data matrix was analysed by principal components analysis on the correlation matrix (Orloci 1967). Results of the ordination are expressed in two-dimensional scatter diagrams. The contribution of the individual characters to the variation in the direction of principal components was evaluated according to the method of Orloci (1968) as this technique illustrates the importance of the characters which separate the OTUs on the scatter diagrams (Lubke & Phipps 1973).

### Results

The ordination of the 41 OTUs on the two-dimensional scatter diagrams is shown in Figures 3 & 4. These first three components only account for 47% of the total variance (Table 4) of the original 88 characters, but do describe the relationship between the OTUs in a meaningful way. The  $A_2$ ,  $B_1$  and  $B_2$  biotypes of *O. aurantiaca* form fairly tight clusters on these axes. In contrast the  $A_1$  biotype and the



**Figure 1** The semiprostrate growth form and general morphology of the flattened cladodes of *Opuntia aurantiaca* A biotypes and allied species, *O. discolor*. (a)  $A_1$  biotype and (b)  $A_2$  biotype of *O. aurantiaca*; (c) *O. discolor*. Numbers refer to specimen numbers (Table 2).



**Figure 2** In contrast to Figure 1, the more erect growth form and cylindrical cladodes of *Opuntia aurantiaca* B biotypes and allied species, *O. salmiana*. Note also the shorter spines. (a) B<sub>1</sub> biotype and (b) B<sub>2</sub> biotype of *O. aurantiaca*; (c) *O. salmiana*. Numbers refer to specimen numbers (Table 2).

other two species, *O. discolor* and *O. salmiana* are more widely dispersed.

The *O. aurantiaca* biotypes are positioned between the putative parents, *O. discolor* and *O. salmiana*, in the scatter diagrams, especially on the first and second components (Figure 3). The A<sub>2</sub> and B<sub>2</sub> biotypes lie in a central position, with the A biotypes closer to *O. discolor* and the B biotypes closer to *O. salmiana*. OTUs of the A<sub>1</sub> biotype, which is reputed to be most closely related to *O. discolor* (Table 1), lie in close proximity to the OTUs of *O. discolor* (Figures 3 & 4). The OTUs of the B<sub>1</sub> biotype, which is closely allied to *O. salmiana*, are found closest to OTUs of that taxon. The most variable taxon is *O. aurantiaca* with its diverse biotypes extending across the whole range of components. *O. salmiana* is also fairly variable as seen in Figure 4 where specimens 7 and 8 are far away from specimens 10 and 11.

The contribution of the characters to the variance of the first three roots of the correlation matrix is indicated in Table 5. Very few of these characters contribute more than 4% to the total variance of the root and only 12 of the 88 characters appear to contribute less than 1% on the first three roots. Of those characters contributing  $\geq 1\%$ ; on root one, 37 characters contribute 81,35%, on root two, 44 characters contribute 83,5% and on root three, 32 characters contribute 89,95% to the total variance of each root respectively. Thus the characters contributing to the variance in this ordination are widely dispersed among most of the characters. The important characters are not confined to any particular sets or morphological region of the plants but are dispersed throughout the range of characters selected for the analysis (Table 5).

**Table 2** List of *Opuntia* specimens cultivated at the University of Port Elizabeth as of 22-7-1979

Specimen No.	OTU No.	Species or biotype	Place of origin
1, 2	—	<i>O. discolor</i>	—
3	1	<i>O. discolor</i>	Bolivia
4, 6, 15*	2, 3, 4	<i>O. discolor</i>	Tucuman, Argentina
5	—	<i>O. discolor</i>	Tucuman, Argentina
7, 8, 10, 11 <sup>+</sup>	5, 6, 7, 8	<i>O. salmiana</i>	Tucuman, Argentina
9	—	<i>O. salmiana</i>	Tucuman, Argentina
12, 13, 14	9, 10, 11	<i>O. aurantiaca</i> B <sub>2</sub>	Campana, Argentina
20 <sup>+</sup> , 58	—	<i>O. aurantiaca</i> B <sub>2</sub>	Campana, Argentina
25	—	<i>O. aurantiaca</i> B <sub>2</sub>	Victoria, Argentina
34, 42, 50	27, 28, 29	<i>O. aurantiaca</i> B <sub>2</sub>	Victoria, Argentina
16*, 17, 19	12, 13, 14	<i>O. aurantiaca</i> A <sub>2</sub>	Eastern Cape, South Africa
18, 56, 57	—	<i>O. aurantiaca</i> A <sub>2</sub>	Eastern Cape, South Africa
24, 46, 47	15, 16, 17	<i>O. aurantiaca</i> A <sub>2</sub>	Cerro Montevideo, Uruguay
27, 39, 40	18, 19, 20	<i>O. aurantiaca</i> A <sub>2</sub>	Gualeguaychu, Argentina
28	—	<i>O. aurantiaca</i> A <sub>2</sub>	Gualeguaychu, Argentina
21	—	<i>O. aurantiaca</i> A <sub>2</sub>	Colon, Argentina
23, 31, 32	21, 22, 23	<i>O. aurantiaca</i> A <sub>2</sub>	Colon, Argentina
22, 37, 51	24, 25, 26	<i>O. aurantiaca</i> A <sub>2</sub>	Cerro Carmelo, Uruguay
26	—	<i>O. aurantiaca</i> A <sub>2</sub>	Cerro Carmelo, Uruguay
29	—	<i>O. aurantiaca</i> A <sub>2</sub>	Colonia, Uruguay
33, 35, 44	30, 31, 32	<i>O. aurantiaca</i> A <sub>2</sub>	Colonia, Uruguay
30, 38, 48	33, 34, 35	<i>O. aurantiaca</i> A <sub>2</sub>	Gualeguaychu, Argentina
36, 43*, 53	36, 37, 38	<i>O. aurantiaca</i> A <sub>1</sub>	Santa Elena, Argentina
54	—	<i>O. aurantiaca</i> A <sub>1</sub>	Santa Elena, Argentina
41 <sup>+</sup> , 45, 49	39, 40, 41	<i>O. aurantiaca</i> B <sub>1</sub>	Paraná, Argentina

\* Illustrated in Figure 1

<sup>+</sup> Illustrated in Figure 2

**Table 3** List of morphological characters and character-states used in the numerical analysis

Whole plant		
1.	Plant height (mm)	_____
2.	Plant width (mm)	_____
3.	Growth habit — erect	Yes/No
4.	— ascending	Yes/No
5.	— scrambling	Yes/No
6.	— intricately branched	Yes/No
7.	— ascending to declinate	Yes/No
8.	— declinate	Yes/No
9.	Abscission of cladodes on touch	Easy/Not easy
10.	Number of cladodes arising from tuber (mean)	_____
11.	Number of cladodes arising from basal cladodes (mean)	_____
12.	Number of cladodes arising from second cladode above tuber	_____
13.	Total number of cladodes per plant	_____
14.	Branching pattern — apical	Yes/No
15.	— subapical-single	Yes/No
16.	— subapical-whorled	Yes/No

**Table 3** cont.

17.	— lateral-opposite	Yes/No
18.	— lateral-whorled	Yes/No
19.	Stem type — short cladodes with limited terminal growth only/not only short cladodes/only short cladodes	
<b>Basal cladode(s)</b>		
20.	Mean length (mm)	_____
21.	Mean width (mm) (across flattened face)	_____
22.	Mean thickness (mm)	_____
23.	Width/thickness (mean)	_____
24.	Length/width (mean)	_____
25.	Mean no. of areoles/cladode	_____
26.	Cladode shape — spherical	Yes/No
27.	— cylindrical-terete	Yes/No
28.	— cylindrical-compressed	Yes/No
29.	— clavate-compressed	Yes/No
30.	— clavate-gibbous and compressed	Yes/No
31.	— fusiform	Yes/No
32.	Areole shape	Circular/Not circular
33.	Mean no. of spines per areole	_____
34.	Mean length of longest spine (mm)	_____
35.	Mean length of all spines (mm)	_____
36.	Angle between cladode surface and longest spine	_____
37.	Spine colour — white	Yes/No
38.	— banded	Yes/No
39.	— blotched	Yes/No
40.	— brown-tipped	Yes/No
41.	— brown	Yes/No
42.	Glochids visible as distinct area (not necessarily brown)	Yes/No

**Median cladodes**

Character nos. 43–65 the same as character nos. 20–42 but for the median cladodes.

**Terminal cladodes**

Character nos. 66–88 the same as character nos. 20–42 but for the terminal cladodes.

**Table 4** Roots of the correlation matrix

Root number	Value of root	Percentage of total variance accounted for	Accumulated percentage
1	22,08	25,1	25,1
2	11,01	12,5	37,6
3	8,27	9,4	47,0
4	5,55	6,3	53,3
5	4,00	4,5	57,8
6	3,72	4,2	62,0
7	2,75	3,1	65,1
8	2,55	2,9	68,0
9	2,36	2,7	70,7
10–42	25,71	29,3	100,0
Total variance	88,00	100,0	

**Table 5** Contribution of the characters to the variance of the first three roots of the correlation matrix

Character No.	Character	Percentage of		
		Root 1	Root 2	Root 3
<b>Whole plant</b>				
1	Plant height (mm)	0,14	1,62	4,68

Table 5 cont.

Character No.	Character	Percentage of		
		Root 1	Root 2	Root 3
2	Plant width (mm)	2,28	0,11	0,45
3	Growth habit — erect	2,27	1,22	1,85
4	— ascending	0,71	0,26	1,73
5	— scrambling	0,38	0,04	0,05
6	— intricately branched	0,46	1,08	0,25
7	— ascending to declinate	0,76	0,23	0,34
8	— declinate	0,08	1,70	0,11
9	Abscission of cladodes on touch	2,42	0,70	1,06
10	Number of cladodes arising from tuber cladode (mean)	0,05	1,07	3,31
11	Number of cladodes arising from basal (mean)	0,00	1,81	0,09
12	Number of cladodes arising from second cladode above tuber	0,86	0,07	6,12
13	Total number of cladodes per plant	0,93	1,20	0,12
14	Branching pattern — apical	0,13	0,88	1,00
15	— subapical-single	0,14	0,03	1,24
16	— subapical-whorled	0,84	0,21	0,29
17	— lateral-opposite	0,85	1,24	0,10
18	— lateral-whorled	2,74	1,23	0,02
19	Stem type short cladodes with limited terminal growth only	2,27	1,22	1,85
	<b>Basal cladodes</b>			
20	Mean length (mm)	0,34	3,51	0,13
21	Mean width (mm) (across flattened face)	3,12	0,27	1,24
22	Mean thickness (mm)	0,00	4,50	1,77
23	Width/thickness (mean)	2,51	2,22	0,19
24	Length/width (mean)	0,57	2,80	1,41
25	Mean no. of areoles/cladode	0,03	3,64	0,43
26	Cladode shape — spherical	0,09	0,49	0,00
27	— cylindrical-terete	1,95	1,57	0,00
28	— cylindrical-compressed	2,04	0,07	0,01
29	— clavate-compressed	2,34	2,44	0,23
30	— clavate-gibbous and compressed	0,50	0,45	0,14
31	— fusiform	0,39	0,20	3,20
32	Areole shape	0,06	1,17	2,15
33	Mean no. of spines per areole	0,07	1,05	1,54
34	Mean length of longest spine (mm)	2,93	1,04	0,04
35	Mean length of all spines (mm)	2,92	0,81	0,12
36	Angle between cladode surface and longest spine	0,12	1,09	0,00
37	Spine colour — white	1,31	1,32	1,12
38	— banded	0,68	0,03	0,00
39	— blotched	0,66	1,33	0,06
40	— brown-tipped	1,53	0,17	0,45
41	— brown	0,01	0,66	0,11

Table 5 cont.

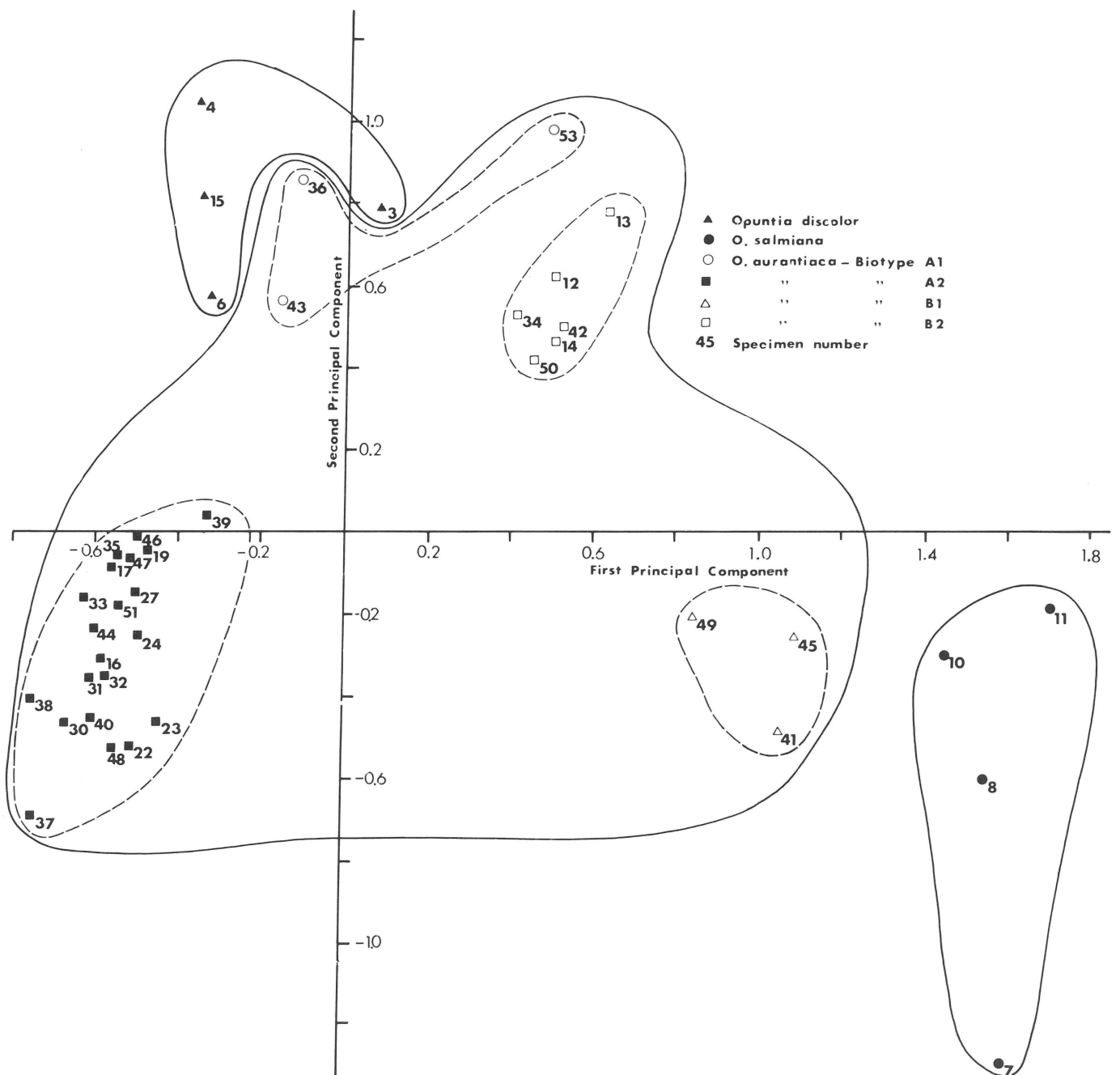
Character No.	Character	Percentage of		
		Root 1	Root 2	Root 3
42	Glochids visible as distinct area (not necessarily brown)	1,77	1,44	4,56
	<b>Median cladodes</b>			
43	Mean length (mm)	0,03	0,08	7,10
44	Mean width (mm) (across flattened face)	2,60	0,86	0,60
45	Mean thickness (mm)	0,02	4,63	0,55
46	Width/thickness (mean)	2,79	0,60	0,06
47	Length/width (mean)	0,75	0,32	5,47
48	Mean no. of areoles/cladode	0,80	0,01	5,66
49	Cladode shape — spherical	0,54	1,33	0,32
50	— cylindrical-terete	2,75	0,92	0,13
51	— cylindrical-compressed	0,64	1,28	0,10
52	— clavate-compressed	1,21	1,05	0,00
53	— clavate-gibbous and compressed	2,27	2,13	0,25
54	— fusiform	1,04	1,16	3,41
55	Areole shape	0,02	0,89	2,31
56	Mean no. of spines per areole	1,06	0,05	6,35
57	Mean length of longest spine (mm)	2,75	2,07	0,16
58	Mean length of all spines (mm)	0,55	0,08	0,01
59	Angle between cladode surface and longest spine	0,53	1,91	0,01
60	Spine colour — white	1,75	2,20	0,00
61	— banded	0,43	0,46	0,00
62	— blotched	2,32	0,03	0,22
63	— brown-tipped	0,14	0,03	0,02
64	— brown	0,86	1,62	0,04
65	Glochids visible as distinct area (not necessarily brown)	2,48	1,41	1,37
	<b>Terminal cladodes</b>			
66	Mean length (mm)	3,13	0,41	0,07
67	Mean width (mm) (across flattened face)	3,34	0,68	0,18
68	Mean thickness (mm)	0,01	4,71	0,07
69	Width/thickness (mean)	2,11	0,71	0,01
70	Length/width (mean)	1,99	0,09	1,03
71	Mean no. of areoles/cladode	0,33	0,76	0,30
72	Cladode shape — spherical	2,26	0,03	1,63
73	— cylindrical-terete	0,33	1,77	0,23
74	— cylindrical-compressed	0,61	1,51	0,11
75	— clavate-compressed	2,69	1,13	0,25
76	— clavate-gibbous and compressed	1,95	1,81	0,23
77	— fusiform	0,62	1,35	2,96
78	Areole shape	0,34	0,81	4,21
79	Mean no. of spines per areole	1,46	0,02	2,45
80	Mean length of longest spine (mm)	1,65	3,26	0,62
81	Mean length of all spines (mm)	1,71	2,60	0,65
82	Angle between cladode surface and longest spine	0,43	0,27	1,04

**Table 5** cont.

Character No.	Character	Percentage of		
		Root 1	Root 2	Root 3
83	Spine colour — white	0,21	2,06	0,44
84	— banded	0,20	0,96	0,07
85	— blotched	0,06	0,00	0,34
86	— brown-tipped	0,11	0,19	0,27
87	— brown	0,01	0,86	1,30
88	Glochids visible as distinct area (not necessarily brown)	1,85	0,65	3,83
Total percentage		99,98	99,95	99,99

**Discussion**

The hypothesis that *Opuntia aurantiaca* is of hybrid origin (Arnold 1977) is supported in this quantitative analysis of the morphological variation of the biotypes of the species and its putative parents. In a simple ordination of specimens of *Iris* on two-character scatter diagrams, Anderson (1949) illustrated introgressive hybridization and the relationship between the hybrids and the parents. Using a large number of characters in a principal component analysis of the correlation matrix a more effective ordination can be achieved. One would expect that the hybrids would show the highest affinity and thus the highest correlation coefficients with their parents, as was observed by Heiser *et al.*



**Figure 3** Ordination of the 41 specimens of *Opuntia aurantiaca* and its close relatives on the first and second principal components. The lines grouping the species and biotypes were subjectively drawn. Numbers refer to specimen numbers (see Table 2).

(1965) and Schilling & Heiser (1976). Analysis of the correlation matrix by principal component analysis thus places the OTUs of the hybrids closest to the reputed parents.

In this study the affinity between the A biotypes and *O. discolor*, and the B biotypes and *O. salmiana* is illustrated in Figure 3. The A<sub>1</sub> and B<sub>1</sub> biotypes, reputed to be most closely allied to *O. discolor* and *O. salmiana*, respectively, (Arnold 1977) are closest to those species on the scatter diagrams (Figures 3 & 4). In particular the OTUs of the A<sub>1</sub> biotype are in close proximity to the dispersed cluster of *O. discolor*. If more than 3 OTUs in each case had been available for study

a more complete picture of this relationship may have been apparent. From these scatter diagrams, *O. aurantiaca* appears to be the most variable taxon with *O. discolor* the least variable and most closely allied to *O. aurantiaca*. The difficulty in obtaining living material made it impossible to include more OTUs of the 'parent' species in the analysis.

Other studies have been made using principal component analysis to show hybrid/parent relationships. Rising (1968) inferred the presence of hybrid chickadees (*Parus*) where the ranges of two species overlapped, and Heiser *et al.* (1965) and Schilling & Heiser (1976) found that the hybrids of *Solanum* species, in all but one case, were positioned

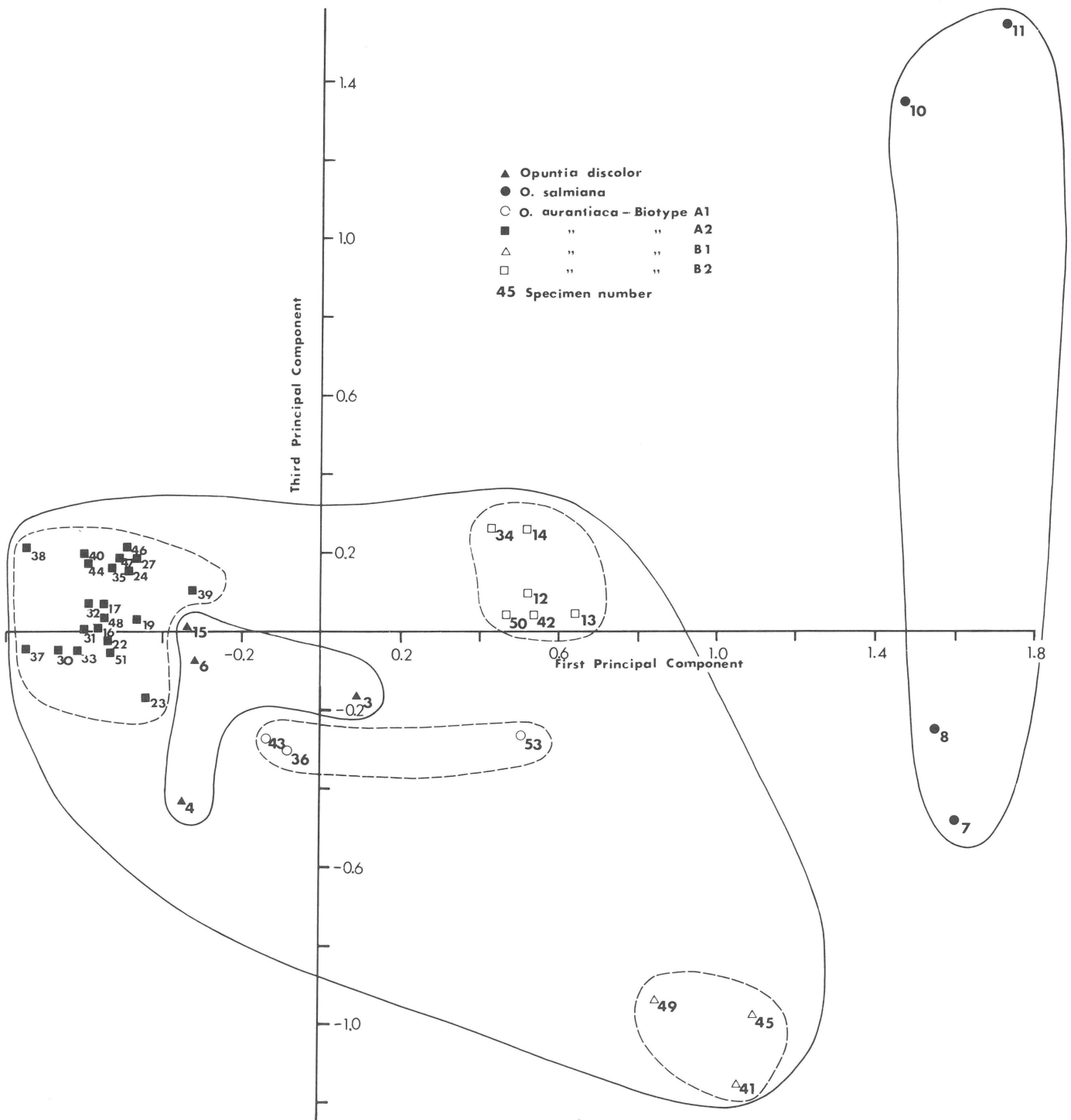


Figure 4 Ordination of the 41 specimens of *Opuntia aurantiaca* and its close relatives on the first and third principal components (see Figure 3 for details).



between their parents on the scatter diagrams produced by principal component analysis. Crowe & Parker (1981) found that *Bidens connata*, supposedly of hybrid origin and derived from *B. frondosa* and *B. cerna*, was intermediate between the supposed parents on the first two components of a principal component analysis. Their study was substantiated by cytological data.

The quantitative analysis of morphological data using this technique is thus a useful method of showing hybrid origins. This type of analysis is particularly useful when a number of hybrid species and their parents are under investigation, as for example in the study of Schilling & Heiser (1976) on *Solanum* species and hybrids. These authors point out that some degree of caution is necessary in the interpretation of the results. Morphologically a species may appear to be intermediate between two others through divergent evolution from one of those species, not necessarily from hybridization. Likewise a hybrid may in some cases be morphologically different from the parent species or not be positioned intermediately in one dimension on principal components, as observed by Whitehouse (1970) and Crowe & Parker (1981).

In the final analysis, the genetic relationship between the OTUs under study is important. The morphological characters selected may be controlled by a few genes and intermediate character states may thus not be reflected in the hybrid species. In this study the characters chosen all seemed to contribute more or less equally to the roots of the first three components (Table 5). This was partly due to the similarity of characters selected from the cladodes of the different regions of the plant. In some cases there was a significantly large contribution to the variance of a root by a character from the three regions (for example, no 23, 46 and 69—width/thickness ratio), but this was an exception rather than the rule. Quantitative analysis of the morphological form of the OTUs of the three species and the biotypes of *O. aurantiaca* served to substantiate the evidence of a few characters presented in Table 1. Thus, the semiprostrate, long-spined, flattened cladodes of *O. discolor* are also characteristic of the A biotypes of *O. aurantiaca* (Figure 1), whereas the *O. salmiana* form, of which the B biotypes of *O. aurantiaca* are part, has cylindrical or terete ascending cladodes with short spines.

The ecological importance of the growth form and morphological features of the four biotypes is not known. The only biotype which has been studied in detail with respect to its control in South Africa is the typical A<sub>2</sub> biotype (Zimmerman 1977, 1979). Taxonomic studies on weedy species of hybrid origin are important in that the agents of biological control, such as insect species or fungal pathogens, may be related to the parents as well as the hybrids. In an

effort to control spreading of the jointed cactus in South Africa the search for biological control agents continues (Moran & Annecke 1979). These authors accept the theory of hybrid origin of *O. aurantiaca*, but report that Zimmerman observed that *O. discolor* is sterile and possibly a hybrid. If this is the case, and it still has to be substantiated, further studies of other *Opuntia* species will be necessary to determine the true parents of *O. aurantiaca*.

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