

# Mixoploidy and cytotypes: a study of possible vegetative species differentiation in stapeliads (Asclepiadaceae)

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**Keywords:** adventitious roots, Asclepiadaceae, cytotypes, euploidy, growth forms, mixoploidy, Stapeliaceae

## ABSTRACT

Mixoploidy is common in proembryos and embryos as well as in meristems of radicles, primary, secondary and adventitious roots and in innovation shoots of stapeliad species (Asclepiadaceae). The proportion of polyploid cells in the meristem of single adventitious roots is significantly higher than in meristems of primary and secondary roots. This may lead to a complete polyploidisation of adventitious roots. Innovation shoots display a low percentage of polyploid cells, comparable to the condition found in primary and secondary roots. Nevertheless cells of different euploid levels are frequently found. During field studies, however, individuals of a given population were always found to have the same chromosome number; infraspecific polyploidy was found in only three out of 305 investigated stapeliad species. Genera with an orthotropic growth form were found to be diploid throughout, whereas the genera of which the members spread vegetatively by means of innovation shoots, comprise di-, tetra- and polyploid species. This phenomenon can be ascribed to ecological rather than morphological factors. The often proposed hypothesis that new cytotypes can have a vegetative origin is not found to be acceptable.

## UITTREKSEL

Miksoploïdie kom algemeen voor by proëmbrio's en embrio's asook by meristeme van kiemworteltjies, primêre, sekondêre en bywortels en by verjongingslote van aasblomspecies (Asclepiadaceae). Daar is in verhouding meer poliploïede selle in die meristeme van enkelvoudige bywortels as in meristeme van primêre en sekondêre wortels. Dit mag tot die algehele poliploïdisering van bywortels lei. Die persentasie poliploïede selle by verjongingslote is laag en kan vergelyk word met die toestand wat by primêre en sekondêre wortels aangetref word. Selle van verskillende euploïede vlakke word niemin dikwels aangetref. Tydens ondersoek in die veld is bevind dat individue in 'n bepaalde bevolking altyd dieselfde chromosoomgetal het; infraspesifieke poliploïdie is by slegs drie uit 305 aasblomspecies wat ondersoek is, aangetref. Genusse met 'n ortotropiese groeivorm was deurgaans diploïed, terwyl genusse waarvan die plante spreidende verjongingslote het, di-, tetra- en poliploïede spesies bevat. Hierdie verskynsel kan aan ekologiese eerder as morfologiese faktore toegeskryf word. Die hipotese wat dikwels voorgestel word dat nuwe sitotipes 'n vegetatiewe oorsprong kan hê, is nie aanvaarbaar bevind nie.

## CONTENTS

Introduction .....	67
Material and methods .....	67
Results .....	68
1. Mixoploidy in embryos and meristematic tissue of adult individuals .....	68
a. Proembryos and embryos .....	68
b. Radicles and secondary roots .....	68
c. Adventitious roots .....	69
d. Primordia of innovation shoots .....	69
2. Mixoploidy in plagiotropic and orthotropic genera .....	70
3. Chromosome number and ecology of populations .....	70
Discussion .....	71
Acknowledgements .....	72
References .....	72

The mixoploid character of many root tips, present as early as in the meristematic stage, has often hampered the determination of the chromosome number of single taxa. Due to this peculiarity the vegetative origin of new cytotypes has been suggested (Reese 1973). Even though only root tips had been studied at the time, Reese (1973) proposed a similar cytological concept for shoot tips, which was originally introduced by Sharma (1956), who suggested a vegetative species differentiation, but failed to submit convincing experimental proof. To test the hypothesis of vegetative cytotype differentiation, wide-ranging karyological studies were carried out on individuals, populations and genera. Data and material were collected during several periods of field work in southern Africa.

## MATERIAL AND METHODS

Field work was carried out during periods of several months' duration in southern Africa in 1983, 1986 and 1988. The material collected is cultivated in the Botanical Garden of the University of Münster. The present study is based mainly on the following taxa from the Cape Province, South Africa, and Namibia:

*Duvalia caespitosa* (Mass.) Haw.:  $2n = 44$ .

## INTRODUCTION

Previous casual collections and the karyological study of stapeliad species have elucidated the spectrum of chromosome numbers of this stem-succulent group of the Asclepiadaceae (preliminary summary by Albers 1983).

CAPE.—3118 (Vanrhynsdorp): 15 km S. *Meve* 147. 3119 (Calvinia): 40 km N of Niewoudtville. *Meve* 245. 13 km N of Niewoudtville. *Meve* 252.

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MS. received: 1990-04-17.

*Duvalia pubescens* N.E. Br.:  $2n = 44$ .

CAPE.—2816 (Oranjemund): Richtersveld, Hellskloof, *Albers & Meve* 33, 3017 (Hondeklipbaai): 3 km E of Kamieskroon, *Meve* 154, 2917 (Springbok): 8 km N of Concordia, *Meve* 222.

*Hoodia gordonii* (Mass.) Sweet:  $2n = 22$ .

CAPE.—3219 (Wuppertal): Biedouw Valley, *Albers et al.* K1301.

NAMIBIA.—2816 (Oranjemund): Lorelei, *Albers et al.* K1364.

*Orbea namaquensis* (N.E. Br.) Leach:  $2n = 22$ .

CAPE.—2817 (Vioolsdrif): 50 km N of Lekkersing, *Albers & Meve* 15, 2917 (Springbok): 4 km N of Steinkopf, *Albers & Meve* 112; 5 km N of Concordia, *Meve* 163.

*Pectinaria articulata* (Ait.) Haw. subsp. *borealis* Bruyns:  $2n = 22$ .

CAPE.—2816 (Oranjemund): Richtersveld, Hellskloof, *Albers & Meve* 32.

*Stapelia asterias* Mass.:  $2n = 22$ .

CAPE.—3321 (Ladismith): N of Calitzdorp, *Albers et al.* K1124.

*Stapelia garipeensis* Pillans:  $2n = 44$ .

CAPE.—2816 (Oranjemund): Richtersveld, Hellskloof, *Albers & Meve* 23, 24; Grootderm, *Jürgens s.n.*

*Stapelia hirsuta* L.:  $2n = 22$ .

CAPE.—3318 (Cape Town): Malmesbury, *Albers et al.* K1513, K1514, K1515.

*Trichocaulon dinteri* Berger:  $2n = 22$ .

CAPE.—(Oranjemund): Richtersveld, Beauvallon, *Albers et al.* K1346.

NAMIBIA.—2716 (Witputz): 8 km S of Rosh Pinah, *Albers & Meve* 45.

*Tridentea longipes* (Lückhoff) Leach:  $2n = 22$ .

CAPE.—2816 (Oranjemund): Richtersveld, Numees, *Albers & Meve* 38, 39.

NAMIBIA.—2716 (Witputz): 38 km N Rosh Pinah, *Albers & Meve* 76.

Earlier chromosome counts (Reese & Kressel 1967; Reese 1971; Albers 1974, 1975, 1976, 1981; Albers & Delfs 1983; Albers & Austmann 1987; Albers, Austmann & Meve 1988, 1990) have also been used in the present study.

Population studies were carried out in grid squares. Individual plants, stem parts and fruits were collected within each plot. Seeds of fruits which had already set in habitat could be harvested from a number of plants in the Botanical Garden of the University of Münster. Root tips were collected from individual plants transplanted to the greenhouse, from rooting stems (adventitious roots) and from germinated seeds. Furthermore, the meristems of the stem tip, the proembryo and the embryo were studied. Apart from the latter, mitotic equatorial plates

were generally used to count chromosome numbers. Sections and squash preparations were produced and stained according to standard techniques (Snow 1963). For the embryo sections, the nuclei were measured and the ploidy level estimated according to the different diameters of these nuclei.

## RESULTS

Within the Stapelieae, two different growth forms are known. In southern Africa the genera *Hoodia*, *Quaqua* and *Trichocaulon* are characterized by an orthotropic growth form, while other genera, such as *Duvalia*, *Huernia*, *Orbea*, *Pectinaria*, *Piarranthus*, *Stapelia* and *Tridentea* display plagiotropic growth forms. In the latter taxa the axis ceases to grow at an early stage. Basally, numerous innovation shoots are formed, which are often lying on the ground, lending a mat-like appearance to the plant (Albers *et al.* 1989). These lateral shoots form adventitious roots. In order to clarify the extent and qualitative significance of mixoploidy, embryos as well as root- and shoot-primordia of individuals of these two growth form types were studied.

### 1 *Mixoploidy in embryos and meristematic tissue of adult individuals*

#### a. Proembryos and embryos

In *Trichocaulon dinteri*, *Duvalia caespitosa* and *D. pubescens*, single polyploid cells can be found as early as the proembryo stage. Even though the ploidy level cannot always be established with certainty by means of counts in equatorial plates, the size of the nucleus and the number of chromocentres allow such a judgement. The chromocentres are extraordinarily prominent in meristematic cells of the Asclepiadaceae and, as Czeika (1956) has already pointed out, for *Echidnopsis cereiformis* Hook. f. (Stapelieae), it is easy to differentiate between diploid and polyploid cells. Polyploid cells are also found in the tissue of mature embryos (<5%). Whether chromosome numbers are exclusively doubled, or whether higher ploidy levels occur, cannot always be determined with certainty, judging from the number of chromocentres. The polyploid cells are single cells evenly dispersed throughout the whole tissue of the cotyledons, the hypocotyl and the radicle.

#### b. Radicles and secondary roots

Between 1.9% and 6.3% polyploid cells occur in the apical region of the radicle (Table 1). These figures represent the mean of different root tips of an individual plant; individual values, however, ranged from 0 to 8.3%.

Polyploid cells do not simply possess a double chromosome number. Cells with 33 chromosomes were observed in diploid species and cells with 55, 66 and, very rarely, 77 and 88 chromosomes were seen in tetraploid species. There are obviously no divergent aneuploid cells. Merely one individual with  $2n=22 + 1B$  was found in the East African *Echidnopsis scutellata* (Deflers) Berger. Irregularities during the anaphase were also never detected.

TABLE 1. — Percentage of aberrant polyploid cells in the meristematic area of the radicle

Species	2n	No. of cells examined	% aberrant polyploid cells
<i>Duvalia caespitosa</i>	44	1 074	6,3–
<i>Duvalia pubescens</i>	44	262	5,0
<i>Stapelia asterias</i>	22	538	2,4
<i>Stapelia garipeensis</i>	44	107	1,9
<i>Trichocaulon dinteri</i>	22	3 653	3,9

Cells with chromosome numbers above the diploid level of a species are scattered over the whole cross section of the apex with a slight increase in number in the protoderm.

Species with orthotropic growth possess an allorhizal root system. Even though examination of the secondary roots of *Trichocaulon dinteri* occasionally revealed small sectors of triploid cells in the periblem and the plerome, the percentage of polyploid cells in the apical regions corresponds with the lower value already found in the radicles. The primary roots studied support this observation.

#### c. Adventitious roots

In species with mat-like growth forms, the number of shoots can increase considerably during a single growth period. Their adventitious roots have previously been studied by Reese (1973). In tips of adventitious roots, he demonstrated the entire spectrum of different ploidy levels; however, he did not compare adventitious roots with radicles, primary and secondary roots.

Apart from single euploid nuclei, polyploid layers and sectors can be found more frequently in adventitious roots

(Figure 1). This root type therefore displays more cytochimaera features than the ones previously mentioned (Reese 1973: fig. 1). Although the adventitious roots normally contain the expected chromosome number, the share of (aberrant) polyploid cells, which did not reach 10% in radicles and secondary roots, can rise to more than 50% in adventitious roots of *Duvalia* and *Huernia* species. In rare cases entire adventitious roots attain a higher ploidy level (see also Reese 1973).

Reese (1973) mentions two chromosomally aberrant examples in which a tripling of the basic number could be observed, apart from normal diploid values. This euploidy has, however, been found in many species presently studied. Root tips of diploid species can contain cells with  $2n=22$ , 33, 44 and 66 chromosomes (Figure 1A). Penta- to octoploid cells (Figure 1B, C) can frequently be found in tetraploid species, and hepta- and octoploid cells in hexaploid species.

A haploid cell with 11 chromosomes was observed only twice: in the tetraploid *Duvalia vestita* Meve, and in the diploid *Pachycymbium carnosum* (Stent) Leach. No explanation for this unusual karyological condition can be offered.

The number of triploid and pentaploid cells is occasionally very high; these cells may even make up the entire root. Adventitious roots of innovation shoots, sequentially branching off the same plant, do not change in their karyological composition. Thus the proportion of polyploid cells to diploid cells does not increase with time.

#### d. Primordia of innovation shoots

In apical meristems of innovation shoots, relatively few polyploid cells are found. Of the twelve examined individuals belonging to the genera *Duvalia*, *Orbea*, *Pectinaria* and *Piaranthus*, only three plants showed

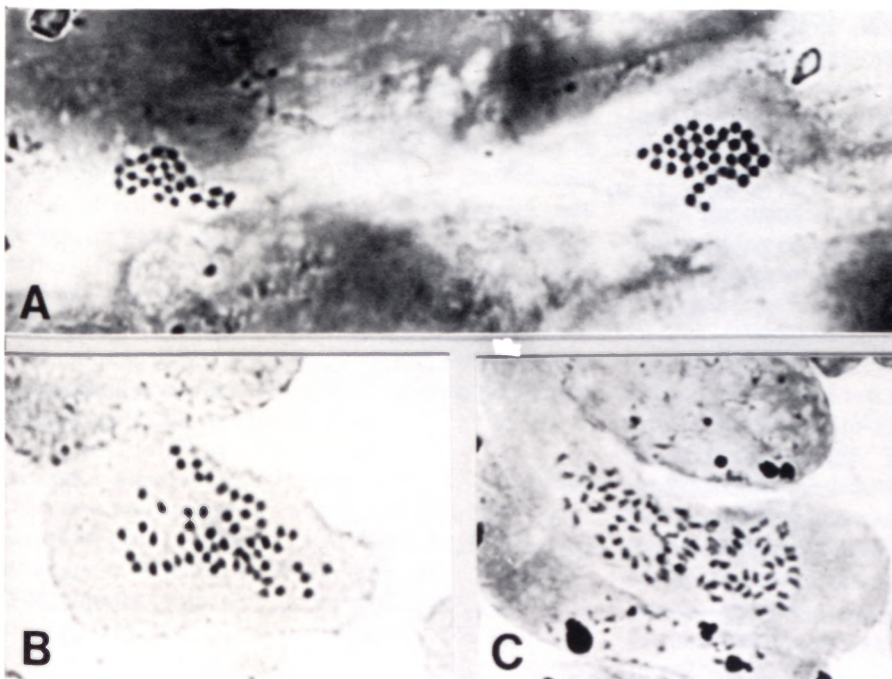


FIGURE 1. — Metaphase plates in root tip meristems. A, *Duvalia elegans* ( $2n=22$ ) with a normal and an aberrant equatorial plate ( $22 < - > 33$  chromosomes); B, *D. vestita* ( $2n=44$ ) with 55 chromosomes; C, *D. caespitosa* ( $2n=44$ ) with 77 chromosomes. All  $\times 1600$ .

TABLE 2.—Mixoploidy in the apical area of innovation shoots

Species	2n	Ploidy levels found	% equatorial plates counted
<i>Duvalia caespitosa</i> (147)	44	4×	91
		5×	7
		7×	2
<i>Duvalia caespitosa</i> (245)	44	4×	98
		7×	2
<i>Pectinaria articulata</i> subsp. <i>borealis</i>	22	2×	97
		3×	3

mixoploidy in the apical area. In these plants the percentage of polyploid cells of different ploidy levels was also small (Table 2). Exclusive occurrence of unequal multiples of haploid chromosome numbers, apart from the expected diploid numbers, is particularly conspicuous.

### 2 Mixoploidy in plagiotropic and orthotropic genera

The above-mentioned peculiarities have been found predominantly in adventitious roots. Nevertheless, differences between genera of different growth forms are smaller than expected. In orthotropic genera 7.7% of the individuals display mixoploidy, while this number is about 9.5% in plagiotropic genera (Table 3).

### 3 Chromosome numbers and ecology of populations

Growth forms in the Stapelieae have been discussed recently by Albers *et al.* (1989). Studies concerning ecology and population dynamics in the tribe are not

available. However, several months of field work allow us to recognize some clearcut tendencies. Plagiotropic species are regularly associated with xerophytic shrubs (about 0.5–1.0 m high), but rarely with succulent shrubs. They grow generally at the shaded bases of these shrubs. The fine-grained soil found in this habitat, due to reduced erosion and the accumulation of drifting sand, furnishes the ideal substrate for stapeliads. This preference for a certain habitat expresses itself in the ephemeral character of these species; and in highly variable population sizes and densities in space as well as in time. This behaviour, which characterises pioneer plants, is particularly conspicuous in disturbed areas.

One population of *Duvalia caespitosa* (Touwsrivier, Karoo), initially consisting of 33 individuals (and a total of 648 shoots) has been observed since 1983 and considered suitable for studies of population karyology as well as population dynamics. The high density of individuals, which causes meshing of individual plants in several places, is in part a consequence of vegetative reproduction by means of innovation shoots. As demonstrated by vegetative reproduction in cultivation, every shoot can be the starting point for a new plant. Even so, no individuals have been found for which chromosome numbers in adventitious roots or in apical meristems were higher than  $2n=44$  throughout, the normal chromosome number for the tetraploid *D. caespitosa*.

Observations on this stand, repeated in 1986 and 1988, demonstrate clearcut changes within the whole stapeliad population: only a few individuals of *D. caespitosa* were left in 1988, whereas another species, *Stapelia pillansii* N.E. Br., was becoming more frequent. Populations of *Tridentea longipes* (Grasvlakte, Richtersveld), *Stapelia hirsuta* (Malmesbury) and *Orbea namaquensis* (N of Lekkersing, Richtersveld) belonging to the same growth

TABLE 3.—Chromosome numbers and extent of mixoploidy in individuals and species of different growth forms

Growth form	Genus	Chromosome sets	Nos examined		Mixoploid individuals	% mixoploidy
			Species	Individuals		
Orthotropic	<i>Hoodia</i>	2n=22	6	9	—	—
	<i>Quaqua</i>	2n=22 (33, 44)	7	55	4	7.3
	<i>Trichocaulon</i>	2n=22 (33, 44)	7	14	2	14.3
Total			20	78	6	7.7
	<i>Duvalia</i>	2n=22 (33, 44) 44 (11, 55, 66, 77, 88) 66 (77, 88)	14	201	18	9.0
	<i>Huernia</i>	2n=22 (33, 44) 44 (66) 66	54	106	6	5.7
	Plagiotropic	<i>Orbea</i>	2n=22 (44) 44 (66)	18	45	5
	<i>Pectinaria</i>	2n=22 (33)	3	13	2	15.4
	<i>Piранthus</i>	2n=22 (33, 44)	6	104	6	5.8
	<i>Stapelia</i> (incl. <i>Tromotriche</i> )	2n=22 (33, 44, 66) 44 (55, 66, 88) 66 (88)	39	108	17	15.7
	<i>Tridentea</i>	2n=22 (44)	15	39	5	12.8
Total			149	616	59	9.6
Total orthotropic and plagiotropic spp.			169	694	65	9.4

form, also provided no evidence for the formation of new cytotypes.

Orthotropic species in general form stable, long-lived populations on fully sun-exposed stands. Habitat observations in populations of *Trichocaulon dinteri* in the Richtersveld (Beauvallon) illustrate in addition the strong influence of topographic and edaphic factors on orthotropically growing species. Seventeen out of 19 individuals of a small population, restricted to a small hill (6 m<sup>2</sup>) with very coarse and permeable substrate, grew on the microclimatically more moderate south-western slope. In contrast, no plant could be found on the sandy and level area around that hill. The clearcut boundary of the population, however, has to be attributed to the occurrence of rather unstable quartzite sands. They create a high-risk habitat for the slow-growing *Trichocaulon* plants, which are incapable of vegetative reproduction.

Investigations of root tips of primary and secondary roots and seedlings grown from seeds harvested from individuals of *T. dinteri* at this locality did not yield any new karyological information. Only a few single cells differed from the diploid chromosome number in the manner discussed earlier. Since no innovation shoots were formed and thus no vegetative reproduction occurred, formation of different cytotypes is considered to be impossible in this growth form.

#### DISCUSSION

Endopolyploidy has been found in a vast number of species throughout the vascular plants (John & Lewis 1968). On the other hand, a low level or absence of endopolyploidy seems to characterize a smaller number of species Tschermak-Woess (1956). Endomitotic polyploidisation commonly occurs in the zone adjacent to the apical meristem (Fenzl & Tschermak-Woess 1954). This fact has been confirmed by the present observations in radicles and both secondary and primary roots of the Stapelieae, in which a relatively low percentage of aberrant chromosome numbers has been found in the apical zone.

A different point of view, however, needs to be taken for the adventitious roots widespread in the Stapelieae. The conspicuous mixoploid character of some adventitious roots has been mentioned in earlier studies on chromosome numbers in the Stapelieae (Reese 1971; Reese & Kressel 1967). Reese (1973) comments on the different degrees of polysomaty in some stapeliad species, and develops his own ideas about their origin. His suggestion that the adventitious roots, and to a lesser degree the secondary roots, tend towards mixoploidy, was confirmed in the present study. The mixoploidy level rises in the meristems of adventitious roots. According to Reese, cells of different polyploid levels become involved as early as the formation stage of the primordia.

Endopolyploidisation commonly leads to a doubling of chromosome numbers (Tschermak-Woess 1971). Occasionally higher polyploid cells have been observed (summary in Tischler & Wulff 1953–1963: 321–336). Though they occur in the stapeliads in extraordinarily high numbers, they have not been mentioned at all by Czeika (1956) and only as an oddity by Reese (1973). They are

found in different root types as well as in shoot tips. While valencies of euploid cells commonly exceed the diploid value, an equatorial plate has been found in *Duvalia vestita* and *Pachycymbium carnosum* with 11 chromosomes.

Mitotic irregularities during the anaphase have never been noted here. It is questionable whether a nucleus fragmentation observed by Czeika (1956) in older tissue of *Echindopsis cereiformis* (Stapelieae) was responsible for the formation of aneuploid nuclei, since amitoses are more or less disorganized processes (Nagl 1976) and are never followed by cell divisions (Nagl 1978).

Since the number of cells with different polyploid levels, especially in adventitious roots of plagiotropically growing shoots, can be considerable and since these polyploid cells can in extreme cases constitute the whole root, this phenomenon can be identified as a source of obviously wrong chromosome numbers in the literature. Some stapeliad species have been thought of as triploid and therefore as potential hybrids (Reese & Kressel 1967). Control counts have, however, unambiguously established the diploid character of these species. In contrast, triploidy has been proven in a natural hybrid (*Duvalia caespitosa*  $2n=44 \times$  *Huernia pillansii*  $2n=22$ ; Albers & Meve unpubl.), which was collected by Bruyns (1981).

A small percentage of polyploid cells, comparable to those found in radicles and secondary roots, has been found in apical meristems of innovation shoots, which enlarge the body of individual plants of plagiotropic species. Since every shoot roots as it comes into contact with the soil, it forms a possible starting point for a new, genetically identical plant.

Speculative formation of new cytotypes by means of mixoploid meristems in this vegetative process, could not be proven in individuals of larger populations. The possibility of such a process is also contradicted by results of karyological studies in apical meristems of innovation shoots, which have never been found to be exclusively polyploid. The exclusive presence of polyploid cells in a small percentage of adventitious roots had previously led to such speculations (Reese 1973). The different mode of formation of adventitious roots (from parenchymatic tissue adjacent to the outer phloem) and of innovation shoots (exogeneously from axillary buds) must also be taken into account.

The fact that species of the genera *Hoodia*, *Quaqua* and *Trichocaulon* (a total of 19 species was investigated) with orthotropic growth forms, are exclusively diploid, seems to support the hypothesis of cytotype formation, since tetraploidy and hexaploidy are widespread in the genera with plagiotropic growth forms. However, this clearcut distinction between the two morphologically different groups must be attributed to habitat conditions rather than to growth form. *Hoodia*, *Trichocaulon* and *Quaqua* (p.p.) predominantly inhabit extremely dry and relatively stable biotopes in the winter rainfall area of southern Africa and their populations could be shown to be highly constant during the time of our studies over five years. Most other genera, in contrast, are confined to far more unstable karroid areas, in which they are apparently often relatively short-lived.

The formation of different ploidy levels in the plagiotropic growth form obviously is not caused by the branching off of cytologically different innovation shoots, but has been achieved generatively by promotion of polyploid races in the conquest of new habitats (e.g. Hanelt 1966). The possible vegetative formation of new cytotypes requires a high percentage of different infraspecific cytotypes. Extensive investigations of species and subspecies has so far only revealed two cytotypes each in *Orbea variegata* (L.) Leach, *Huernia hislopilii* Turill subsp. *hislopilii*, and *Duvalia polita* N.E. Br. In terms of stem and flower morphology, each pair member is indistinguishable from the other; the two cytotypes of the first species, however, inhabit ecologically clearly distinct habitats. In *D. polita* there are indications of mixed populations with diploid and tetraploid cytotypes. In summary, there are no clues for an enlarged number of cytotypes nor for a special mode of origin for the existing ones.

Angiosperms tend to form mosaic tissues; the degree to which mosaic tissues are produced is more or less species-specific. This condition, which can occur as early as in the apical meristems, however, obviously does not lead to the formation of new cytotypes under natural conditions, even though such a mechanism has been suggested several times (Sharma 1956; John & Lewis 1968; Reese 1973). This fact is surprising in the light of the successes of plant breeding research in the production of polyploid strains.

#### ACKNOWLEDGEMENTS

Our studies have been made possible by financial support of the Deutsche Forschungsgemeinschaft, the CSIR (RSA) and the University of Stellenbosch (RSA). For advice on many aspects we are grateful to Mr M.B. Bayer and Mr L. Leach, both formerly at the Karoo Botanical Garden, Worcester, RSA. Prof. J.J.A. van der Walt, Dept. of Botany, University of Stellenbosch, has supported our work in various ways. Finally we wish to thank Dr Sigrid Liede for translation of our manuscript, and numerous other colleagues in South Africa, Namibia, Lesotho and Zimbabwe.

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