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# Meiotic analyses of *Cucumis* hybrids and an evolutionary evaluation of the genus *Cucumis* (*Cucurbitaceae*)

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**Key words:** Angiosperms, *Cucurbitaceae, Cucumis, C. sativus, C. melo, C. metuliferus, C. anguria, C. zeyheri*; *C. myriocarpus* subsp. *leptodermis*, comb. nov. – Crossing experiments, meiosis of hybrids, polyploidy, isozymes, DNA analysis, evolution.

**Abstract:** Meiosis in seven interspecific *Cucumis* hybrids has been analysed i.a. in *C. metuliferus* × *C. zeyheri*, where the parents belong to different sections. In the triploid hybrids a remarkably high number of trivalents has been found. Additional data from literature on geographical distribution, cucurbitacins, flavonoid patterns, isozymes, C-banding, genome size, DNA amount and chloroplast DNA are used to discuss species relationships and evolution. The African cross-compatible group is divided into the *Myriocarpus* subgroup with the diploid species *C. africanus, C. myriocarpus* subsp. *leptodermis* and subsp. *myriocarpus*, and the *Anguria* subgroup with *C. anguria, C. dipsaceus, C. ficifolius, C. prophetarum, C. zeyheri* and all polyploids (except *C. heptadactylus*). It is argued that the Asian subg. *Melo* with x = 7 is derived from the African subg. *Cucumis* with x = 12; the latter contains all the polyploid species and has the most common basic chromosome number of the *Cucurbitaceae*. This phylogenetic advance is interpreted with concepts of the quantum model of evolution.

The genus *Cucumis* was recently subdivided into two subgenera (JEFFREY 1980).The Asian part of the genus, the subg. *Cucumis*, has the basic chromosome number x = 7 and includes as most important species *C. sativus* L. The majority of *Cucumis* spp. belong to subg. *Melo* with x = 12 as basic number and are distributed mainly in Africa. Polyploid species and cytotypes occur only in the African subgenus. A number of crosses between species of the two subgenera has been carried out in order to create new cucumber cultivars containing traits from African species, especially resistance. However, all these attempts have failed, and only fruit production was induced (BATRA 1953, KISHI & FUJISHITA 1969, 1970, DEAKIN & al. 1971, KHO & al. 1980, DEN NIJS & VISSER 1985). In vitro culture of embryos also was unsuccessful until now.

Chromosome pairing in meiosis and pollen fertility were studied in interspecific hybrids within either of the two subgenera (DANE & al. 1980, SINGH & YADAVA 1984) and in polyploids (DANE & TSUCHIYA 1979). The relationship of the species based on the meiotic results fits well with the classification by JEFFREY (1980), based on morphology, geography and crossability. The African subg. *Melo* was

Table 1. Origin of the *Cucumis* hybrids analysed, indicated by the IVT collection number, source (if known)

| Hybrid | Female parent | (Gbn), provider, source |
|---|---|---|
| C 77098 | *C. zeyheri* 4x | (1053), USDA (PI 299572), Cape province |
| C 77099 | *C. zeyheri* 4x | (1053), USDA (PI 299572), Cape province |
| C 78390 | *C. anguria* subsp. *anguria* | (0310), USDA (PI 233646), India |
| C 79352 | *C. ficifolius* 4x | (1729), USDA (PI 193967), Ethiopia |
| C 78441 | *C. prophetarum* | (1752), U. Sarup (India) |
| C 81515 | *C. anguria* subsp. *longipes* | (1736), Leningrad, Africa |
| C 81240 | *C. metuliferus* | (1734), Leningrad, Africa |

subdivided into four groups, of which two contain only one species, *C. metuliferus* NAUD. (group 1) and *C. hirsutus* SOND.(group 4). Most of the African species, i.e., *C. anguria* L., *C. dipsaceus* SPACH, *C. myriocarpus* NAUD., *C. prophetarum* L. and *C. zeyheri* SOND., including all the polyploids, together form group 2. Group 3 consists of *C. melo* L., *C. humifructus* STENT. and some relatives (JEFFREY 1980).

Supplementary biosystematic information is now available on morphology and geography (MEEUSE 1965, JEFFREY 1967), distribution of cucurbitacins (ENSLIN & REHM 1958) and of flavonoids (BROWN & al. 1969), isozymes (DANE 1976, 1983; ESQUINAS-ALCAZAR 1977, PERL-TREVES & al. 1985, STAUB & al. 1987), chromosome banding patterns (RAMACHANDRAN & al. 1985), chromosome lengths (SINGH & ROY 1974, RAMACHANDRAN & al. 1985), DNA amounts (RAMACHANDRAN & NARAYAN 1985) and chloroplast DNA's (PERL-TREVES & GALUN 1985). The available data allow the construction of a tentative model of relationships and evolution within the genus *Cucumis*.

Chromosome behaviour in meiosis of seven interspecific hybrids, including triploids, is analysed in the framework of the IVT *Cucumis* crossing program (DEN NIJS & VISSER 1985). All information available is summarized in an evolution model and in a note on classification.

### Material and methods

The plant material used is listed in Table 1. These hybrids were described by DEN NIJS & VISSER (1985).

Stamens of staminate flower buds were collected from plants grown in a glasshouse during the summer, they were stained in 0.5% acetocarmine for one hour at room temperature and squashed in 45% acetic acid. Meiotic configurations were examined at metaphase I.

## Results

The mean numbers (and ranges) of univalents, bivalents and trivalents for all hybrids studied by us and other authors were calculated and are listed in Table 2. The number of pollen mother cells analysed range from two to ten (only a small part

the parents are indicated by the IVT gene bank number (Gbn), the provider and the original

| Male parent | (Gbn), provider, source |
|---|---|
| *C. dipsaceus* | (0163), the Netherlands |
| *C. myriocarpus* | (0165), the Netherlands |
| *C. myriocarpus* | (0182), Copenhagen |
| *C. anguria* subsp. *anguria* | (0307), USDA (PI 196477), Brazil |
| *C. anguria* subsp. *longipes* | (1736), Leningrad, Africa |
| *C. zeyheri* | (0181), Copenhagen |
| *C. zeyheri* | (0181), Copenhagen |

of the flower buds are right for meiotic analysis). Pollen fertilities obtained from DEN NIJS & VISSER (1985) were added.

Moderately large numbers of bivalents were produced in the diploid hybrids. An exception was the hybrid between *C. metuliferus* and *C. zeyheri* (2 x), with up to 24 univalents (Fig. 1 a). This is the first report of a meiotic analysis of a hybrid between species, which belong to different groups (JEFFREY 1980).

The production of bivalents in the hybrid between *C. ficifolius* (4 x) and *C. anguria* (2 x) may indicate that one of the two genomes of the tetraploid parent is at least partly similar to the diploid genome of the other parent. Moreover, from the occurrence of 4 – 6 trivalents (and 5 – 8 bivalents) in this hybrid it may be concluded that both the genomes of *C. ficifolius* (4 x) are compatible in part with the genome of *C. anguria* (Fig. 1 b) and similar to each other. The situation in the hybrids with *C. zeyheri* (4 x) as one of the parents is somewhat different, since more univalents are found, especially in the hybrid obtained from the cross *C. zeyheri* (4 x) × *C. myriocarpus*. However, *C. zeyheri* (4 x) seems to be more closely related to *C. dipsaceus* than to *C. myriocarpus* or *C. zeyheri* (2 x), because of the formation of more trivalents (see Table 2).

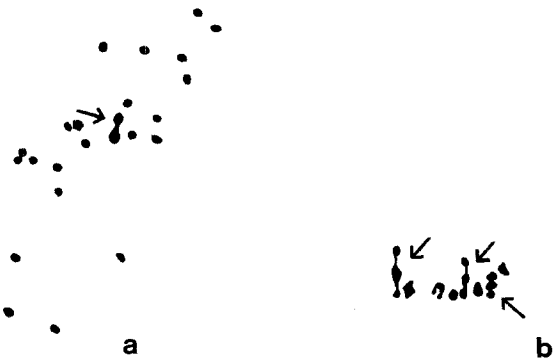


Fig. 1. *a* Meiosis of *Cucumis metuliferus* × *C. zeyheri*: 22 I + 1 II (arrow). – *b* Meiosis of *C. ficifolius* (4 x) × *C. anguria* showing a part of the chromosome set with three trivalents (arrows). × 1000

Table 2. Review of meiotic analyses and pollen stainability obtained in this study of *Cucumis* belong to group 2 except for *C. metuliferus*. Only polyploid levels are indicated; otherwise

| Hybrid combinations: female × male parent | | Source | Number of quadrivalents |
|---|---|---|---|
| *aculeatus* (4 x) | × *anguria-ang.* | D | 0 |
| | × *ficifolius* | D | 0 |
| | × *zeyheri* | D | 0 |
| *anguria-ang.* | × *africanus* | D | 0 |
| | × *anguria-long.* | S | 0.04 (0 – 1) |
| | × *dipsaceus* | D | 0 |
| | × *myriocarpus* | IVT | 0 |
| *anguria-long.* | × *anguria-ang.* | S | 0.12 (0 – 2) |
| | × *myriocarpus* | D | 0 |
| | × *prophetarum* | S | 0.12 (0 – 2) |
| | × *zeyheri* | IVT | 0 |
| *dipsaceus* | × *anguria-ang.* | S | 0.80 (0 – 2) |
| | × *anguria-long.* | S | 0 |
| | × *myriocarpus* | S | 0.12 (0 – 1) |
| | × *zeyheri* | D | 0.07 (0 – 1) |
| | | S | 0.18 (0 – 2) |
| *ficifolius* | × *zeyheri* | D | 0 |
| *ficifolius* (4 x) | × *anguria-ang.* | IVT | 0 |
| *figarei* (6 x) | × *aculeatus* (4 x) | D | 0 |
| *metuliferus* | × *zeyheri* | IVT | 0 |
| *myriocarpus* | × *africanus* | D | 0 |
| | × *leptodermis* | D | 0 |
| | × *prophetarum* | S | 0.20 (0 – 2) |
| *prophetarum* | × *anguria-ang.* | S | 0.12 (0 – 1) |
| | × *anguria-long.* | S | 0.06 (0 – 1) |
| | | IVT | 0 |
| | × *dipsaceus* | S | 0.14 (0 – 2) |
| | × *zeyheri* | S | 0.20 (0 – 2) |
| *zeyheri* | × *anguria-long.* | S | 0 |
| | × *myriocarpus* | S | 0.10 (0 – 1) |
| *zeyheri* (4 x) | × *dipsaceus* | IVT | 0 |
| | × *myriocarpus* | IVT | 0 |
| | × *zeyheri* | D | 0 |

## Discussion

**Crossability analyses.** DANE & al. (1980) and SINGH & YADAVA (1984) have already published meiotic analyses of hybrids. Their data are also listed in Table 2 for comparison with our results. The present knowledge of meiotic behaviour of *Cucumis* hybrids is summarized in Fig. 2: A few combinations were never carried out, and unsuccessful crosses are deleted.

Crosses between diploids. Several hybrids obtained on the diploid level show very high numbers of bivalents. This is especially true for the infraspecific crosses between the two subspecies of *C. anguria*. The hybrid between *C. myriocarpus* and *C. leptodermis* regularly forms 12 bivalents in meiosis (DANE & al. 1980). These

hybrids (IVT), by DANE & al. (1980: D), and by SINGH & YADAVA (1984: S). All species taxa are diploid

| Number of trivalents | Number of bivalents | Number of univalents | Pollen stainability % |
|---|---|---|---|
| 0.33 (0–2) | 9.61 (6–12) | 15.78 (22–11) | ? |
| 0.10 (0–1) | 11.80 (11–12) | 12.10 (14–1) | 75 |
| 0.28 (0–1) | 9.58 (6–12) | 16.0 (22–12) | 89 |
| – | 11.25 (8–12) | 1.50 (8–0) | 46 |
| – | 11.84 (10–12) | 0 | 80 |
| – | 10.26 (8–12) | 3.50 (8–0) | 16 |
| – | 11.50 (11–12) | 1.0 (2–0) | 42 |
| – | 11.68 (10–12) | 0.24 (4–0) | 80 |
| – | 7.08 (3–11) | 9.80 (18–2) | 85 |
| – | 11.72 (8–12) | 0 | 82 |
| – | 10.0 (9–11) | 4.0 (6–2) | 25 |
| – | 8.86 (0–12) | 3.06 (24–0) | 20 |
| – | 10.06 (8–12) | 3.88 (9–0) | 17 |
| – | 9.40 (6–12) | 4.86 (12–0) | 13 |
| – | 11.16 (8–12) | 1.40 (8–0) | 23 |
| – | 10.12 (0–12) | 3.04 (24–0) | 54 |
| – | 8.33 (8–9) | 7.33 (8–6) | ? |
| 5.40 (4–6) | 7.60 (5–8) | 4.60 (14–2) | 12 |
| 0.40 (0–1) | 12.20 (9–18) | 34.40 (42–21) | 49 |
| – | 3.90 (0–10) | 16.20 (24–4) | 0 |
| – | ? | ? | 97 |
| – | 12.0(12) | 0 | 97 |
| – | 11.0 (8–12) | 1.32 (8–0) | 22 |
| – | 10.84 (10–12) | 1.84 (5–0) | 17 |
| | 10.88 (9–12) | 2.0 (6–0) | 20 |
| – | 11.25 (11–12) | 1.50 (2–0) | 40 |
| – | 10.56 (7–12) | 2.20 (10–0) | 26 |
| – | 11.20 (10–12) | 1.0 (4–0) | 23 |
| – | 10.50 (8–12) | 2.96 (8–0) | 16 |
| – | 11.60 (11–12) | 0.28 (2–0) | 22 |
| 3.60 (2–4) | 8.60 (8–10) | 8.0 (14–4) | 5 |
| 1.80 (1–3) | 8.80 (8–10) | 13.0 (17–7) | 18 |
| 0.57 (0–3) | 10.80 (8–12) | 12.60 (16–9) | 41 |

results support the conclusion that these two taxa belong to the same species (MEEUSE 1965, DEAKIN & al. 1971, DANE 1983). A high number of bivalents is also found in *C. anguria* × *C. prophetarum* (SINGH & YADAVA 1984; present results). In these diploid $F_1$ hybrids pollen fertility is higher than 80%. This relation between high number of bivalents and excellent pollen stainability is not found in some other hybrids.

An average number of only 7 bivalents together with a pollen stainability of 85% is found in *C. anguria* subsp. *longipes* × *C. myriocarpus* (DANE & al. 1980). On the other hand, several diploid hybrids show more than 11 bivalents together with a pollen stainability of less than 46%. At least one of the species *C. anguria,*

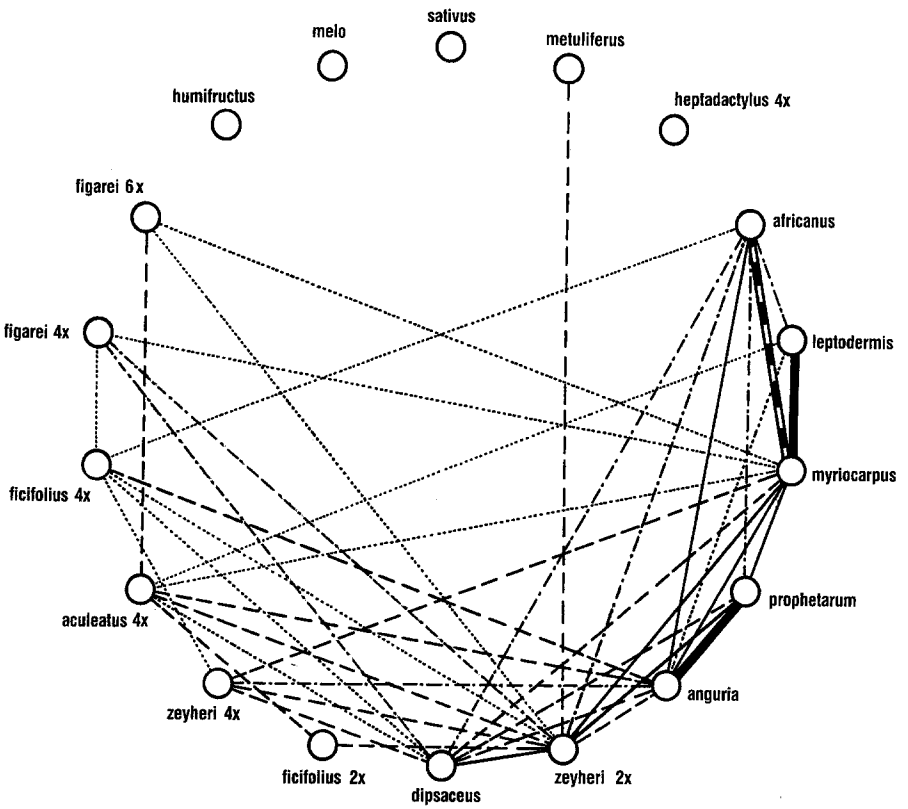


Fig. 2. Crossing polygon showing the results of meiotic analyses and fertility: ▬▬ >11 bivalents and pollen fertility >80%. ▬▬ number of bivalents unknown and pollen fertility 97%. ——— >11 bivalents and pollen fertility <46% (only *C. anguria* × *C. myriocarpus* with 7 bivalents and pollen fertility 85%). – – – <11 bivalents and pollen fertility <54%. – · – · – F 1 seed fertility reduced. ..... F 1 seed sterile. Lack of connecting line indicates cross not possible or not attempted

*C. myriocarpus, C. prophetarum* and *C. zeyheri* is involved as a parent of these hybrids (DANE & al. 1980, SINGH & YADAVA 1984; present results).

Crosses between diploids and polyploids. The production of trivalents in triploids indicates segmental autotetraploidy in one of the parents (STEBBINS 1950) or more probably the occurrence of reciprocal translocations. Chromosome alterations also can explain low amounts of trivalents in some interspecific crosses (DANE & al. 1980), e.g. in *C. ficifolius* (4x) × *C. anguria* (2x) with 4–6 trivalents. No strong conclusions can be drawn about the autoploid nature of the tetraploid parent, because only one successful cross has been reported so far (Table 2) and the segregation ratio of the genes for andromonoecy indicates amphidiploidy (VISSER & DEN NIJS 1984). The triploid hybrids obtained from crosses between *C. aculeatus* (4x) and some diploid species have very low amounts of trivalents, but show a remarkably high pollen stainability. The occurrence of univalents does not seem to affect a regular production of pollen. Fertile triploids were also found in other genera. The triploid cytotype of *Ornithogalum angustifolium* BOR. showed an average number of stainable pollen of 73% (VAN RAAMSDONK 1985a) and it pro-

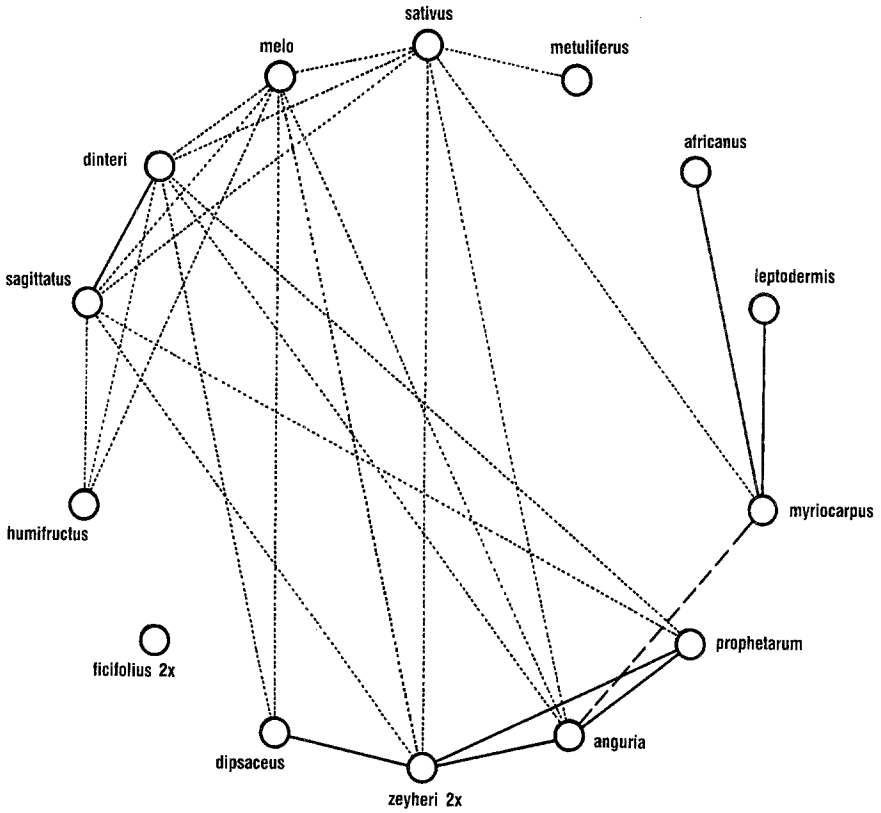


Fig. 3. Crossing polygon of diploid species showing the combinations in which only fruit induction was obtained, together with the fully successful crosses in which a good production of a F 2 or B 1 generation, or a high number of bivalents together with a high pollen fertility was obtained: ——— > 11 bivalents and pollen fertility > 80% and/or notable production of F 2 and B 1. – – – parents aberrant from the species (STAUB & al. 1987). ..... fruit induction only (no viable seeds)

duced hybrids after crossing with the diploid and tetraploid cytotypes of the same species (VAN RAAMSDONK 1985 b). The number of trivalents differs remarkably in crosses of *C. zeyheri* (4 x) with several diploid species (Table 2). The cross between the tetraploid and the diploid cytotype of *C. zeyheri* can not be regarded as infraspecific: The former apparently is an allopolyploid, since no quadrivalents are found (VAN RAAMSDONK & VISSER 1989).

A maximum of 18 bivalents was found in the pentaploid hybrid between *C. figarei* and *C. aculeatus*. Therefore, the parents must have at least one genome in common (DANE & al. 1980). In all successful crosses between species with different ploidy levels the female parent had the highest chromosome number (Table 2).

Crosses between different groups. Many crosses have been carried out between species of the African cross-compatible group and the other species; nearly all were unsuccessful (DEAKIN & al. 1971, KHO & al. 1980, DEN NIJS & VISSER 1985). Only fruits without fully developed seeds could be induced after cross pollination. The recently obtained hybrid between *C. metuliferus* and *C. zeyheri* (2 x) (DEN NIJS & VISSER 1985) is the only exception, and may act as a bridge between *C. sativus* and the African species. These results for diploids only are shown in

Fig. 3, together with the fully successful crosses in which a good production of a F 2 or B 1 generation, or at least a high number of bivalents together with a high pollen stainability could be obtained. The species of the *Melo* group and *C. sativus* appear to be able to produce fruits after crossing with a group including *C. prophetarum, C. anguria, C. zeyheri* and *C. dipsaceus*, but usually not with *C. africanus, C. leptodermis* and *C. myriocarpus*.

**Validity of results.** The conclusions based on the results of a research program are strictly valid only for the specimens involved in that study. It is therefore important to know whether the plants used are good representatives of a group (i.e. taxon, cytotype, species). STAUB & al. (1987), in an isozyme analysis of eight gene loci, found a main group of typical accessions in every species and a few aberrant accessions (with a deviating isozyme pattern) in *C. africanus, C. anguria* subsp. *longipes* and *C. myriocarpus*. However, plants they considered to be *C. africanus* have to be regarded as *C. zeyheri* (both 2 x and 4 x) (DEN NIJS & VISSER 1985). Some of the plants involved in the STAUB & al. (1987) study were used already earlier by DANE & al. (1980), e.g., those for *C. anguria* subsp. *longipes* × *C. myriocarpus*, had an aberrant isozyme pattern. In contrast, the *C. myriocarpus* specimen used in *C. myriocarpus* × *C. leptodermis* (DANE & al. 1980) was a typical one according to STAUB & al. (1987). The other parent, an accession of *C. leptodermis*, was so identified by PERL-TREVES & GALUN (1985) but regarded as *C. myriocarpus* by STAUB & al. (1987). Thus, we have based our conclusions on relationships as summarized in Fig. 2, only on plants representing the typical main type of each species according to STAUB & al. (1987).

**Delimitation of groups.** The taxonomy of two groups of *Cucumis* will be discussed, since one of these groups contains a number of species (African cross-compatible group; JEFFREY 1980) and the other could be of polyphyletic origin (*Melo* group; PERL-TREVES & GALUN 1985).

African cross-compatible group. Most African species belong to group 2 according to JEFFREY (1980) (Fig. 4). We propose to divide this group into two subgroups with the following species:

*Myriocarpus* subgroup: *C. africanus, C. heptadactylus* (4 x), *C. myriocarpus* subsp. *leptodermis* and subsp. *myriocarpus*;

*Anguria* subgroup: *C. aculeatus* (4 x), *C. anguria* subsp. *anguria, C. anguria* subsp. *longipes, C. dipsaceus, C. ficifolius* (2 x and 4 x), *C. figarei* (4 x and 6 x), *C. prophetarum* and *C. zeyheri* (2 x and 4 x).

Eight lines of evidence support this proposal:

– The crossability between the species parallels the two subgroups (Fig. 3). *C. myriocarpus* × *C. anguria* is not indicative of their relationship, since aberrant members of the species were used (STAUB & al. 1987). A high interfertility is found only within the two subgroups (Fig. 3).

– Fruit induction in the *Melo* group occurs only in combination with species of the *Anguria* subgroup and not with the members of the *Myriocarpus* subgroup (Fig. 3).

– The diploid species belonging to the *Myriocarpus* subgroup contain Cucurbitacin A in contrast to members of the *Anguria* subgroup (ENSLIN & REHM 1958) (Fig. 4).

– All the species of the *Anguria* subgroup exclusively exhibit allele 5 of a

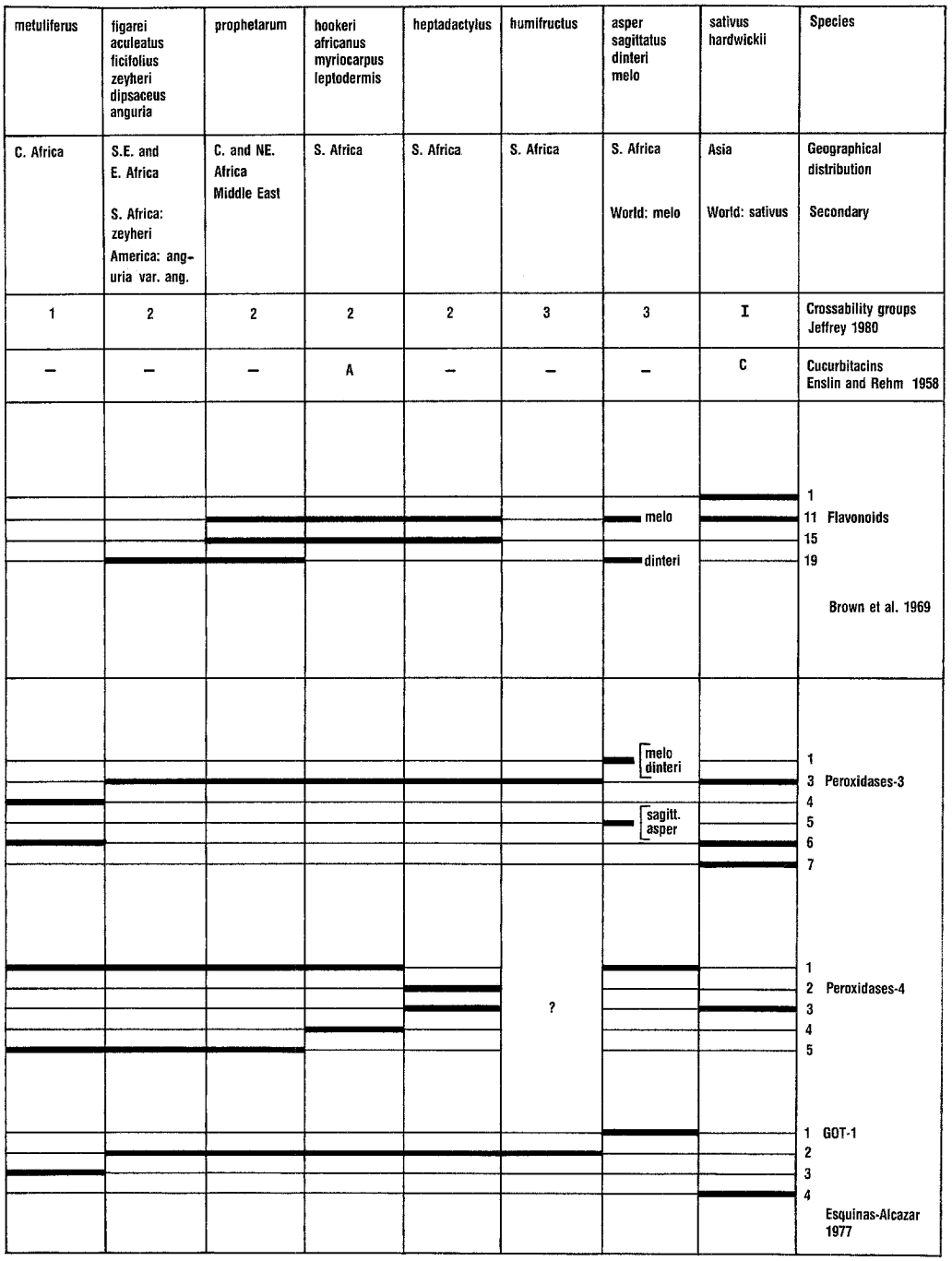


Fig. 4. Groups and species of *Cucumis*: distribution, crossability, cucurbitacins, flavonoid patterns, and isozymes (excl. *C. hirsutus*, group 4, because of paucity of relevant data)

particular peroxidase locus. This is replaced by allele 4 in the diploid members of the *Myriocarpus* subgroup, *C. heptadactylus* being the only exception (Esquinas-Alcazar 1977) (Fig. 4).

– The diploid species of the two subgroups differ basically in the presence or absence of one addition in the nucleotide sequence of the chloroplast DNA (Perl-Treves & Galun 1985).

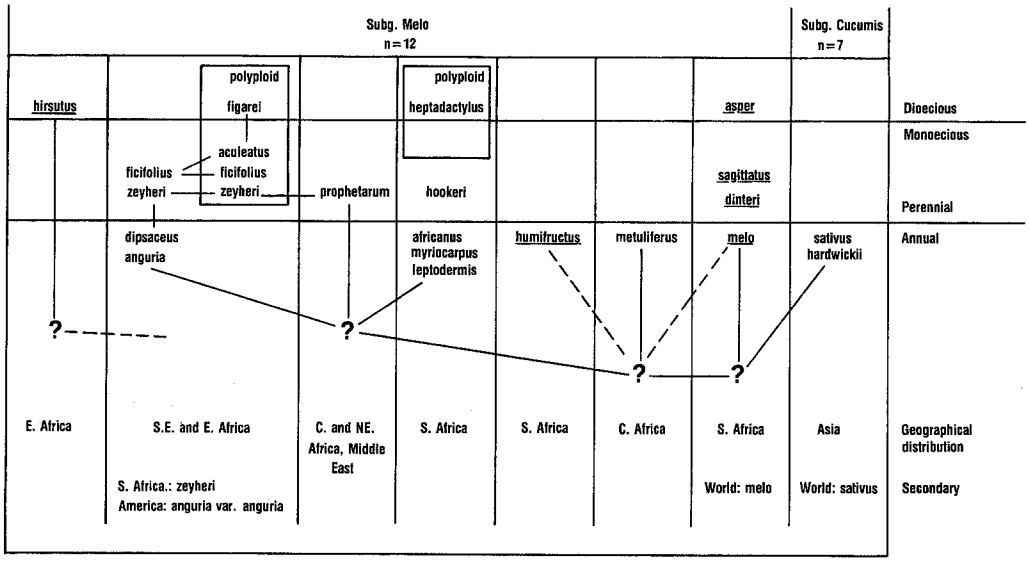


Fig. 5. Groups and species of *Cucumis* indications of polyploidy, sex expression, growth form, geographical distribution and assumed phylogenetic relationships (the latter according to PERL-TREVES & GALUN 1985)

– The species of the *Anguria* subgroup, including most polyploids, are found in SE. and E. Africa. The distribution of *C. prophetarum* extends to C. Africa and the Middle East and *C. zeyheri* is the only species of this subgroup which occurs in southern Africa. All the species of the *Myriocarpus* subgroup are located in southern Africa.

– The species of the two subgroups show different flavonoid patterns with *C. prophetarum* taking an intermediate position (BROWN & al. 1969) (Fig. 4).

– All polyploids except *C. heptadactylus* are crossable with at least one of the species of the *Anguria* subgroup. The interfertility of one diploid and one polyploid is uncertain because of scanty data: *C. prophetarum* was not included in the study of DANE & al. (1980) and only rarely used by KHO & al. (1980) due to misidentification (DEN NIJS & VISSER 1985); *C. figarei* (6x) was only used by DANE & al. (1980). It may be concluded that all polyploid species but *C. heptadactylus* have originated from species of the *Anguria* subgroup (Fig. 3).

*Melo* group. The species of this group differ in peroxidase-4 alleles and show deviating flavonoid patterns (BROWN & al. 1969, ESQUINAS-ALCAZAR 1977) (Fig. 4). The polyphyletic origin of the *Melo* group as indicated by PERL-TREVES & GALUN (1985) based on differences in the chloroplast DNA sequence is supported by our data.

*C. dinteri* and *C. sagittatus* are interfertile and were sometimes considered conspecific (DEAKIN & al. 1971, DANE 1980). The chloroplast DNA is identical (PERL-TREVES & GALUN 1985), but they differ in their isozyme pattern (ESQUINAS-ALCAZAR 1977) (Fig. 4).

JEFFREY (1980) included *C. humifructus* in the *Melo* group because of its hairy fruits. However, this species shows deviating flavonoid and isozyme patterns BROWN & al. 1969, ESQUINAS-ALCAZAR 1977) (Fig. 4) and it appears to be incapable of inducing fruit set after crossing with members of the *Anguria* subgroup (Fig. 3).

**Phylogeny.** African subgenus. Data on chromosome arm lengths and centromere position of *Cucumis* spp. were used by SINGH & ROY (1974) to discuss the general assumption of STEBBINS (1950) that in wild species the number of asymmetric chromosomes is less than in cultivated species. *C. anguria* and *C. dipsaceus* appeared to have less asymmetric chromosomes than *C. melo*. Differences are also found between several cultivars of *C. melo* (SINGH & ROY 1974).

It is difficult to decide whether a character state is primitive (plesiomorph) or derived (apomorph). However, polyploidy gives an almost certain indication of the direction of evolution. The distribution of annual and perennial growth, and of monoecy and dioecy is indicated in Fig. 5. Annuality is considered to be plesiomorphic together with other characters in *C. anguria* and *C. dipsaceus* (SINGH & ROY 1974) and because polyploidy, being apomorphic on principle, is exclusively found in perennials. The perennial species are located predominantly at the end of the branches of the evolutionary tree proposed by PERL-TREVES & GALUN (1985), comparable to the tree shown in Fig. 5. But there are differences in the arrangement of the species belonging to the African cross-compatible group and to the polyphyletic *Melo* group. Several possibilities exist for rooting the tree. The common ancestor of the genus could have been close to *C. metuliferus* and the *Melo* group. The same conclusion was reached by PERL-TREVES & GALUN (1985) based upon the "molecular clock" hypothesis.

Subgeneric relationships. In the literature two directions of evolution have been considered: the derivation of the basic number $x = 12$ from $x = 7$ by fragmentation (WHITAKER 1933, BHADURI & BOSE 1948, AYYANGER 1967), or $x = 7$ derived from $x = 12$ by fusion (TRIVEDI & ROY 1970). RAMACHANDRAN & SESHADRI (1986) refuse both interpretations; in their opinion the two subgenera are not closely related phylogenetically because of differences in number, size, organization and behaviour of chromosomes, and geographical distribution (RAMACHANDRAN & SESHADRI 1986). However, we support the taxonomic rank of subgenera as proposed by JEFFREY (1980) partly because of nomenclatural reasons. The large genetic differences can be explained by long geographic isolation. The following considerations bear on the relative age and relationship of the subgenera.

The basic number $x = 12$ is most common in the *Cucurbitaceae* (TRIVEDI & ROY 1970). The group with the longest polyploid series can be considered to be the oldest one (STEBBINS 1971), assuming the existence of a polyploid series clock. The subg. *Melo*, therefore, is most probably the older in the genus.

The derivation of the subg. *Cucumis* can be supported by the following observations:

An increased amount of heterochromatin (RAMACHANDRAN & al. 1985) as found in the *Scilla bifolia* L. group by GREILHUBER & al. (1981),where some derived species have more heterochromatin. The same trend was found in *Allium* L. (LOIDL 1983) and *Anacyclus* L. (EHRENDORFER & al. 1977).

Fixation of some gene-loci (DANE 1976, ESQUINAS-ALCAZAR 1977) was found exclusively in the Asian subgenus, and may be caused by genetic drift and/or migration. In some crops the number of polymorphic loci or the number of different alleles per locus appears to be lower in cultivated plants than in wild relatives (alfalfa: QUIROS 1983, tomato: RICK 1983, and maize: SMITH & al. 1985).

Inbreeding, drastic genetic changes and the migration of small populations as

aspects of the quantum model of speciation (GRANT 1980) seem to be important processes in the evolution of *Cucumis*. The founder effect resulting from small population sizes was discussed recently by LADIZINSKI (1985) as important for plant domestication.

The occurrence of strong isolation barriers between both subgenera is indicative for a fairly long evolution. MALLICK & MASUI (1986) suggest that the divergence between the subgenera could have started when the separation of Africa and India was taking place some hundred million years ago. However, the absence of *Cucumis* on the island of Madagascar militates against such a view. A more likely possibility is migration from Africa to Asia through the Middle East in a later period, together with the other processes which are part of the quantum model.

Comparable situations are found in *Begonia* L. and *Dorstenia* L., both genera occurring in Africa, Asia and S. America, but with their geographical centre of distribution in Africa. The most primitive pollen types in *Begonia* occur in Africa (VAN DER BERG 1985). Polyploidy in *Dorstenia* is only found in Africa, and the African sections exhibit the most primitive embryo sac types (HOEN 1985; pers. comm.).

## Taxonomic note

A subspecific status is proposed for the species *C. leptodermis*:

***Cucumis myriocarpus* NAUD. subsp. *leptodermis* (SCHWEICK.) VAN RAAMSDONK, comb. nov.**

Basionym: *C. leptodermis* SCHWEICKERDT in S. Afr. J. Sci. **30**: 359 (1933).

The name *C. myriocarpus* has priority over *C. leptodermis* because it was validly published by NAUDIN in 1859. No crossing barriers have been found between the two subspecies. They are almost allopatric. The geographical distribution of the subsp. *myriocarpus* ranges from Rhodesia through Transvaal and southern Bechuanaland to the eastern Cape Province and Natal. It is introduced elsewhere. The subsp. *leptodermis* is endemic to the Cape Province and the Orange Free State. The subspecies can best be distinguished by their different fruits (MEEUSE 1965). The subspecific level is chosen because of geographical and morphological distinctness.

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