PHYTON
ANNALES REI BOTANICAE

VOL. 40, FASC. 1 PAG. 1–208 30. 6. 2000

Phyton (Horn, Austria)	**Vol. 40**	Fasc. 1	1–42	30. 6. 2000

Cucurbita pepo (Cucurbitaceae) – History, Seed Coat Types, Thin Coated Seeds and their Genetics

By

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With 46 Figures

This paper is the modified and enlarged version of a talk given at the First International Oil Pumpkin Conference in Wies (Steiermark, Austria) on August 10, 1999

Key words: *Cucurbita pepo* L., *C. pepo* subsp. *gumala* TEPPNER subsp. nova, *C. pepo* var. *flogra* TEPPNER var. nova, *C. pepo* var. *georgica* TEPPNER var. nova, *Cucurbitaceae*. – Anatomy, seed coat types. – Genetics, history of cultivars, morphology, taxonomy.

Summary

TEPPNER H. 2000. *Cucurbita pepo (Cucurbitaceae)* – History, seed coat types, thin coated seeds and their genetics. – Phyton (Horn, Austria) 40 (1): 1–42, 46 figures. – English with German summary.

The pecularity of flowering shoots of *Cucurbitoideae* with male inflorescence, female flower, next order shoot and tendril in and beside the leaf axil are interpreted as primary axillary shoot with two basal lateral shoots, whose lowermost internodes are reduced.

Cucurbita pepo L. subsp. *gumala* TEPPNER subsp. nova, *C. pepo* subsp. *pepo* var. *georgica* TEPPNER var. nova and *C. pepo* subsp. *pepo* var. *flogra* TEPPNER var. nova are

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described as new taxa. *C. pepo* subsp. *gumala* is regarded as one of the possible progenitors of *C. pepo* subsp. *pepo*.

With the help of the herbals from the 16th century it is shown, that the horticultural groups pumpkin, vegetable marrow, scallop, acorn and ornamental gourds were already present during this time in Europe.

The testa consists of the five layers epidermis (1), hypodermis (2), sclerenchyma (3), aerenchyma (4) and chlorenchyma (5). 0 is the sign for the outer walls of placenta epidermis, ( ) around the number mean that this layer need not be obligatorily present in the ripe dry seed; bold numbers indicate lignification. According to these symbols the four main testa types in the r i p e seeds may be characterised as follows:
thick coated (most *C. pepo* types) **1.2.3.4.**5.
semi-thick coated (in the F_2 from a thin × semi-thin cross) (0).**2.4.**5.
semi-thin coated (*C. pepo* var. *georgica*) (0).**4.**5.
thin coated (*C. pepo* var. *styriaca*, var. *oleifera* and var. *flogra*) 1.4.5.

From the testa structure of the phenotypes in the F_2 from the cross thin × semi-thin it is estimated, that 6–12(–15) genes should be responsible for the studied characters and, consequently, an allele constellation as in var. *styriaca* must be very rare, which is the reason for the uniqueness of this variety.

The first evidence of oil production from thick coated seeds in Styria dates back to 1735. The thin coated mutant must have segregated from the normal *C. pepo* around 1870–1880 in Styria.

Zusammenfassung

TEPPNER H. 2000. *Cucurbita pepo* (*Cucurbitaceae*) – Geschichte, Samenschalen-Typen, dünnschalige Samen und deren Genetik. – Phyton (Horn, Austria) 40 (1): 1–42, 46 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die auffallende Eigenheit der Sprosse blühender *Cucurbitoideae* mit männlichem Blütenstand, weiblicher Blüte, Fortsetzungssproß und Ranke in bzw. neben der Blattachsel wird als primärer Achselsproß mit zwei basalen Seitensprossen nächster Ordnung gedeutet, deren unterste Internodien reduziert sind.

Cucurbita pepo L. subsp. *gumala* TEPPNER subsp. nova, *C. pepo* L. subsp. *pepo* var. *georgica* TEPPNER var. nova und *C. pepo* subsp. *pepo* L. var. *flogra* TEPPNER var. nova werden als neue Taxa beschrieben. *C. pepo* subsp. *gumala* wird als einer der Ausgangspunkte für die Evolution von *C. pepo* subsp. *pepo* angesehen.

An Hand von Kräuterbüchern aus dem 16. Jahrhundert wird gezeigt, daß die gartenbauchlichen Gruppen pumpkin, vegetable marrow, scallop, acorn und Zierkürbisse bereits damals in Europa vorhanden waren.

Die Testa besteht aus den fünf Schichten Epidermis (1), Hypodermis (2), Sklerenchym (3), Aerenchym (4) und Chlorenchym (5). 0 steht im folgenden für die Außenwände der Plazenta-Epidermis und ( ) um eine Zahl für eine im reifen, trockenen Samen nicht absolut obligatorisch vorhandene Schichte; fette Zahlen deuten Verholzung an. Danach sind die vier unterschiedenen Testa-Typen in r e i f e n Samen folgendermaßen verschieden:
dickschalig (Hauptmasse von *C. pepo*) **1.2.3.4.**5.
halb-dickschalig (in der F_2 aus der Kreuzung dünn × halb-dünn) (0).**2.4.**5.
halb-dünnschalig (*C. pepo* var. *georgica*) (0).**4.**5.
dünnschalig (*C. pepo* var. *styriaca*, var. *oleifera* und var. *flogra*) 1.4.5.

Aus dem Testa-Bau der Phänotypen in der F_2 der Kreuzung dünn × halb-dünn wird abgeschätzt, daß ca. 6–12(–15) Gene für die studierten Merkmale verantwortlich sein dürften und daher eine Allel-Konstellation wie in var. *styriaca* überaus selten sein muß, was die Einzigartigkeit dieser Varietät erklärt.

Der erste Nachweis für das Ölpressen aus dickschaligen Samen in der Steiermark datiert aus dem Jahre 1735. Die dünnschalige Mutante dürfte um 1870–1880 in der Steiermark aus dem normalen *C. pepo* herausgespalten haben.

1. Introduction

Cucurbits have always fascinated us. Although they came to us in Europe after the discovery of the Americas, they took up a very important place in our life and also entered our fairy tales in the form of Cinderella's pumpkin coach. The Halloween tradition of the New World is also catching up in European countries. And of course, every Styrian is proud of his/her Styrian 'Kern-Öl'. And other way round Styrian 'Kern-Öl' and Styrian pumpkin seeds are winning increasing international popularity (O'NEILL 1998, BROADBENT & MACLEAN 1998). I use here the term 'thin coated' (correctly proposed by SCHÖNINGER 1950: 322: 'dünnschalig') instead of the incorrect 'nackt', 'unbeschalt', 'naked', or 'hull- less'.

2. Morphology

Probably the most outstanding morphological feature of *Cucurbitoideae* is the fact, that on flowering shoots four axillary products seem to arise side by side from one leaf axil, and from them, the next order lateral shoot is situated more or less and the tendril completely outside and beside the leaf axil. This basic arrangement of male inflorescence, female flower, vegetative shoot and tendril is easily and clearly seen e.g. in *Luffa* (Fig. 1). This unique structure has engaged morphologists for more than hundred years and completely different hypotheses have been proposed. From all these, only the last thesis about this subject, the minutious and excellently illustrated work of LASSNIG 1997 is discussed here. According to him the next order lateral shoot as the primary axillary product is confirmed. The inflorescence and the tendril are the two first axillary products of this shoot. The diagrammatical interpretation is shown in Fig. 2. Due to the reduction of internodes the first two nodes of the axillary shoot and the lowermost node of the inflorescence are incorporated in the axil of the subtending leaf. In *Cucurbita* the inflorescence is reduced usually to one male or one female flower per leaf axil.

The tendril in *Cucurbita* is a very complex structure. On the basis of LASSNIG 1997: 111–115, 126–130, and my own observations I conclude, that the common stalk of the single tendrils is an offshoot of the primary axillary shoot; the longest and lowermost single tendril is a metamorphous leaf – the only leaf – of this shoot; the further single tendrils are a leaf rosette of a shoot in the axil of the first single tendril (Fig. 2).

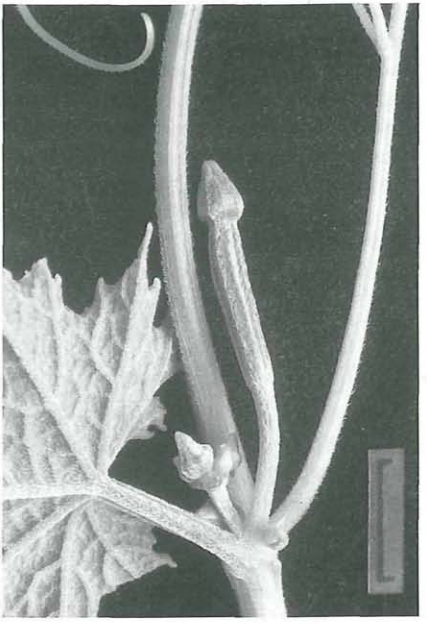


Fig. 1

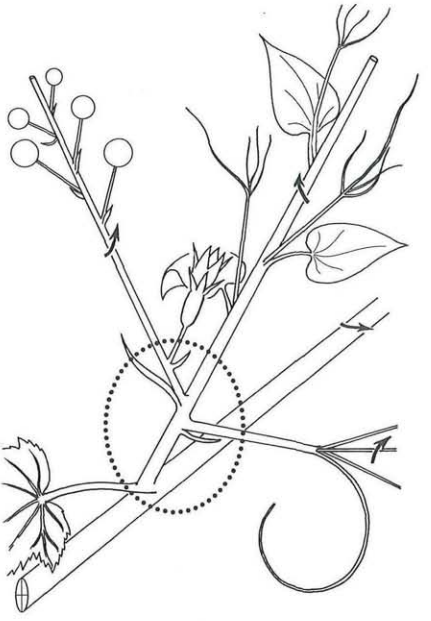


Fig. 2

Fig. 1. *Luffa acutangula*, leaf axil of an adult, blooming plant. From left to right: scale, male inflorescence, female flower, next order shoot (the bud at the base of the female flower) and tendril. – Scale bar = 1 cm.

Fig. 2. Diagrammatic interpretation of the bauplan of the axillary structures in Fig. 1. – The parts within the dotted circle are reduced and incorporated in the leaf axil. The arrows indicate the direction of the ontogenetic leaf spiral on the respective shoots. – Based on LASSNIG 1997 and own observations and interpretations.

The orientation of the tendril depends on the twining direction of the ontogenetic leaf spiral; if the spiral ascends to the right, the tendril stands on the right side of the leaf. On the next order lateral shoot the position changes to the left side, on the next to the right and so on. On the primary axis (seedling axis) in c. 50% of the plants the tendril is on the right side of the leaf, in the other c. 50% on the left side (checked in *Cucurbita pepo* and *Luffa acutangula*).

Another curiosity, the androecium structure, has been investigated and explained by CHAKRAVARTY 1958; see also SINGH & DATHAN 1998: 69–70.

3. Diversity

Let us start with the Vinous (it means long-shooted, i.e., having elongated internodes) Styrian Oil Pumpkin, *C.pepo* L. subsp. *pepo* (in the sense of DECKER 1988) var. *styriaca* GREBENŠČIKOV 1950: 199, 201 (Fig. 26, 27, 39). *C. pepo* is a very variable species with innumerable cultivars. To the same

subspecies belong e.g., zucchini and vegetable spaghetti (so called due to its ability to turn into sphagetti-like threads during cooking). The horticultural groups pumpkin, vegetable marrow, cocozelle and zucchini are all together members of *C.p.* subsp. *pepo* (PARIS 1998: 51) [ribs of the fruit continuing the ribs of the peduncle (Fig. 36, 40)].

To the second subspecies, *C. pepo* subsp. *ovifera* (L.) DECKER 1988: 11(other treatments, e.g. GREBENŠČIKOV in SCHULTZE-MOTEL & al. 1986: 941–944 are not considered by DECKER) belong e.g., scallops or patissons in bush and vine forms, with white or orange rind, most of the ornamental gourds, the crown-gourd and 'Jack be little' (with furrows continuing the ribs of the peduncle as in acorn, scallop etc.), the latter is to be found quite regularly in the seed trade today. The edible horticultural groups of this subsp. are scallop, acorn, crookneck, and straightneck (PARIS 1998: 51). – Compare also NAUDIN 1856, ALEFELD 1866: 217–225, HARZ 1885: 814–819, BAILEY 1937, CASTETTER 1925, DECKER-WALTERS 1990, PARIS 1986, 1989, 1996, 1998. The subspecific treatment by DECKER in combination with the horticultural groups of PARIS seems to be a very practical way to have an oversight over the immense diversity in *C. pepo*.

One should keep in mind, that all these forms of the botanical species *C. pepo* freely interbreed among each other.

The unnumbered infraspecific names in *C. pepo* are listed by ANDRES 1995.

4. Pollination

In the native distribution area of the genus *Cucurbita*, in the Americas, the squash or gourd bees of the genera Xenoglossa and Peponapis (Anthophoridae-Eucerini) are its legitime pollinators. They collect pollen from *Cucurbita* only and are not only adapted to collect the very large pollen grains of *Cucurbita* (*C. pepo* up to 100–200 µm) but also to visit the flowers early in the morning, when other bees are hardly awake (HURD & LINSLEY 1967, HURD & al. 1971, FREE 1970: 297–301).

Since *Cucurbita* flowers have abundant nectar (*C. pepo* c. 100 µl, c. 36–45 % sugar, NEPI & al. 1996) and the flowers remain open till late in the morning (PORSCH 1910: 156–160, 173–177, GRIDIN 1939, FREE 1970: 298, NEPI & PACINI 1993, SHARMA & LAL 1998: 162), they always find facultative pollinators like honey bees, wild bees, some wasps etc., so that pollination in cultivated *Cucurbita* is usually no problem (bad weather conditions excepted). Consequently, the best time for hand pollinations is in the early morning up to c. 8.00–9.00 MEZ. Female buds can be successfully pollinated at the day before opening (NEUMANN 1952: 540, NEPI & PACINI 1993: 532 and own observations). SHARMA & LAL 1998: 162 report the interesting observation that the anthers open on the evening before the flowers open. Mr. G. DEUTSCH's observation on the F_2 of a *C. pepo* cross and mine on *C. pepo* var. *flogra* in Graz showed that the slits of the thecae were open along the whole length but not widened at c. 21.00 MEZ !

5. Phylogeny

Ancestors of the cultivated cucurbits are surely wild types of *C. pepo* subsp. *ovifera* (L.) DECKER from the U.S.A. and probably also the wild *C. pepo* subsp. *fraterna* (BAILEY) ANDRES 1987: 71 from Mexico. With their ovoid fruits with whitish stripes, they look quite similiar to some ornamental gourds. But it is hardly understandable why these gourds should give rise to the high variability, that is seen in *C. pepo*. And surely enough, in the last few years, many hypotheses have arosen, which support a multiple origin of *C. pepo* and postulate a lineage of Mexican elements as an other source (BAILEY 1943, ANDRES 1987, ANDRES & al. 1986, DECKER & WILSON 1986, DECKER 1988, DECKER & NEWSOM 1988, DECKER-WALTERS 1990, DECKER-WALTERS & al. 1993, ROBINSON & DECKER-WALTERS 1997: 73).

My restricted knowledge of Central American Cucurbits allows me only the speculation, that a form such as *C. pepo* subsp. *gumala* TEPPNER (publ. h.l., chap. 14; Fig. 3, 24, 25) from Guatemala (received 1988 by courtesy of Mrs. SCHEIDT, Gießen, Germany), with its strongly ribbed fruits, the 5 main- and 5 second-order-ribs of the peduncle continuing as the 10 main ribs of the fruits and the very thick and hard rind, has enough qualities to be one of the progenitors of *C. pepo* subsp. *pepo* and for an understandig of all the variability in cultivated *C. pepo* as a whole.

6. History

The history of *C. pepo* is only fragementarily known. The main sources are the archaeological records (oldest seeds: from nearly 9 000 B.C., Oaxaca Valley in Mexico, WHITAKER & CUTLER 1971, WHITAKER 1981: 461, SMITH 1997; up to 30 000 B.C. in Florida according ROBINSON & DECKER-WALTERS 1997: 24), old paintings (examples from *C. pepo* in ZEVEN & BRANDENBURG 1986 and REITERER & REITERER 1996: 26–27, 45), old tapestries (KOSTUCH & ZEMANEK 1998), archaeology in Europe (scanty results: MOFFETT 1995) and the descriptions and figures in the herbals. COLUMBUS had seen squashes on his first voyage but there is only one entry in the log book, on December 3, 1492, which is referable to squashes (KINGSBURY 1991: 26). The following text is arranged according horticultural groups, the figures from the herbals are presented in chronological order.

The first clear descriptions and figures of *Cucurbita* in a printed herbal were produced by FUCHS 1542 and 1543. Cucurbita/Kürbis of FUCHS is – correctly – our *Lagenaria*. The present day *Cucurbita* is united (1543) in Cap. 257 'Von Cucumern' together with *Cucumis sativus* ('gemeyn Cucumern, Gurchen'), water melons and melons. Two cultivars of *Cucurbita pepo* are described: 'Türckischer Cucumer or Cucumer/ Cucumis turcicus' (Fig. 4) and 'Meer Cucumer, Cucumer marinus or Zucco marin' (Fig. 5). Meer Cucumer is doubtless a pumpkin; PARIS 1989: 426 compares it with cv. Small Sugar (figured in ROBINSON & DECKER-WALTERS 1997: 76). According

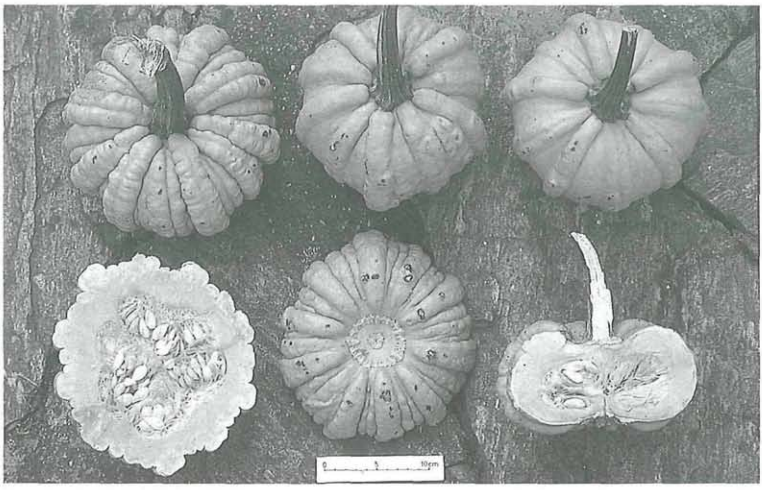


Fig. 3. *Cucurbita pepo* L. subsp. *gumala*. Fruits from different plants showing variability in the development of the ribs. Ten ribs are at least always present. – Scale bar = 10 cm.

to BAILEY, who used the reverse redrawing in GERARD's Herball (1636, reproduced in BAILEY 1929: 85) the Türckisch Cucumer should be '... undoubtedly a *C. Pepo* of the vegetable marrow kind ...'. But PARIS 1989: 426, 429 interpretes it also as pumpkin. Because FUCHS describes the fruits as 'seer groß' (= very large; Fig. 6) and since I have seen a pumpkin cv. with nearly cylindrical fruits of c. 40–50 × 26–30 cm in Wies (Fig. 7) which fits well with the Türckisch Cucumer (only the ribs are much shorter), I am sure that PARIS' interpretation is correct. Both cvs. seem to have similarities with the progenitor of the Styrian Oil pumpkin.

The woodcuts of FUCHS or redrawings of them were used by many later authors. The Meer Cucumer, figures in BOCK 1546, which he named 'Indianisch öpffel, Summer öpffel or Zucco marina' because he is against the merging with Cucumers (cucumbers and melons). 'Etlich wöllen obgerürte öpffel und die Cucumeres mengen / und sprechen es seien Türckische Cucumeren / das gefelt mir gar nit / ursach alle Cucumeres seind feüchter Art und gar nit werhafftig / darumb so nenne ich diese frucht Summer öpffel / Indianisch öpffel / Mala Indiana / Crocea / Lutea / Citrina / Nigra u. eins andern namen Zucco marina' (fol. 316/verso). [Some want to merge the above mentioned apples and the cucumers and say that they are Turkish Cucumers / I disagree totally / because all Cucumers are of wet character and not at all armed. Therefore I call this fruit Summer apples / Indian apples / Mala Indiana / Crocea / Lutea / Citrina / Nigra and with an other name Zucco marina.] According to the description (cap. 100, fol. 315/verso)

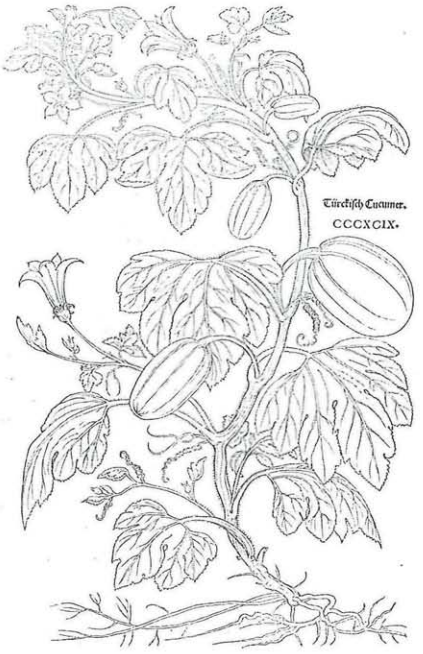


Fig. 4

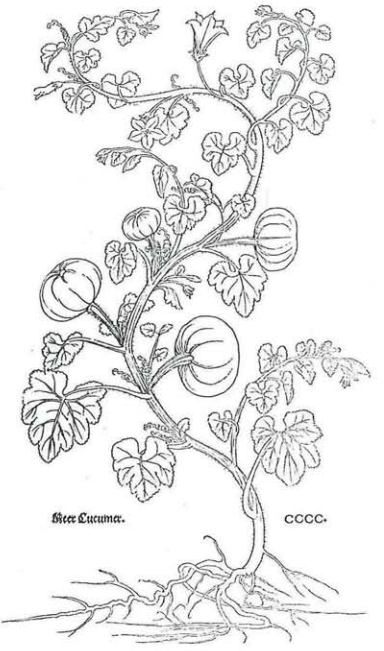


Fig. 5

Fig. 4. Türckisch Cucumer or Cucumer/Cucumis turcicus from FUCHS 1543 plate CCCXCIX. – *Cucurbita pepo* subsp. *pepo* / pumpkin. (Universitätsbibliothek Graz).
Fig. 5. Meer Cucumer, Cucumer marinus or Zucco marin from FUCHS 1543 plate CCCC. – *Cucurbita pepo* subsp. *pepo* / pumpkin.

a lot of cultivars must have been known to him: 'Under andern seind auch die schöne Summer öpffel so auff der erden ligen / und in einem Summer mit der gantzen substantz wachsen blüen und zeittig werden zu uns kommen / etlich seer groß / etlich klein / etlich ganz rund / etlich lang / zum theil süsse / zum theil bitter / Von farben etliche gold oder wachsgele / die andern bleich gele und etlich weiß'. And on fol. 316/recto '... / etlich glatt, etlich mit vielen groben rippen / ...' [The beautiful summer apples that lie on the earth / and grow, bloom and become ripe with total vigour in one summer is one among the others that have come to us / some are very big / some small / some completely round / some long / partly sweet / partly bitter / The colour sometimes golden yellow or yellow / the others pale yellow and some white. ... / some smooth, some strongly ribbed/ ...]

Furthermore BOCK 1546 reports, that the fruit flesh can be cooked like apples or turnips, that the peeled seeds can be used like almonds and even the healing efficacy concerning the blodder is mentioned already (original paragraph reproduced in TEPPNER 1999: Fig. 1).

ten waſſen ſaftig beſetzt. Der Türckiſch Cucumer iſt dem gemeinen mit ſtengel/kraut/heſſtlin/blettern/blůmen vñ öpffel etwas gleich/aber aller ding gröſſer. Die bletter ſeind vil tieffer zerſchnitten/grüner/vnd gegem dem ſtyl nit wie die Ephew bletter auſgeſchnitten. Die blůmen ſeind vil gröſſer/geſtalt wie die glocken/doch vornen in fünff oder ſechs teyl zerſpallten/gantz ſaffranfarb. Die öpffel werden ſeer groß/vnd gantz vñ gar geel. Die wurtzel iſt holtzecht. Der Zucco marin oder Meer Cucumer iſt mit ſtengel/heſſtlin/blettern/blůmen vnd wurtzel dem Türckiſchen gar änlich/aber aller ding kleiner. Die bletter ſeind auch mehr den Ephew blettern gleich/dann des Türckiſchen. Die öpffel ſeind gantz rund/geſtrömt/vñ an der farb erſtlich grün/darnach geel. Die Curul-

Fig. 6. FUCHS 1543, Cap. CCLXVII, part of the text with the descriptions of the two *C. pepo* subsp. *pepo* cultivars Türckisch Cucumer and Meer Cucumer. – A translation of the paragraph: The Turkish Cucumer is to some extent similar in stem, herbage, tendril, leaves, flowers and fruits to the common [cucumber] / but in all respects bigger. The leaves are deeper dissected / greener / and near the petiole not so cut out as in ivy. The flowers are much more bigger / bell formed / but in the front divided in five or six parts / totally saffron coloured. The fruits turn very big and completely yellow. The root is woody. The Zucco marin or Meer Cucumer is in respect to it's stem, tendril, leaves, flowers and root very similar to the Turkish one / but smaller in all parts. The leaves are also more similar to ivy / than to the Turkish one. The fruits are completely round / stripped / and the colour is at first green and then yellow.

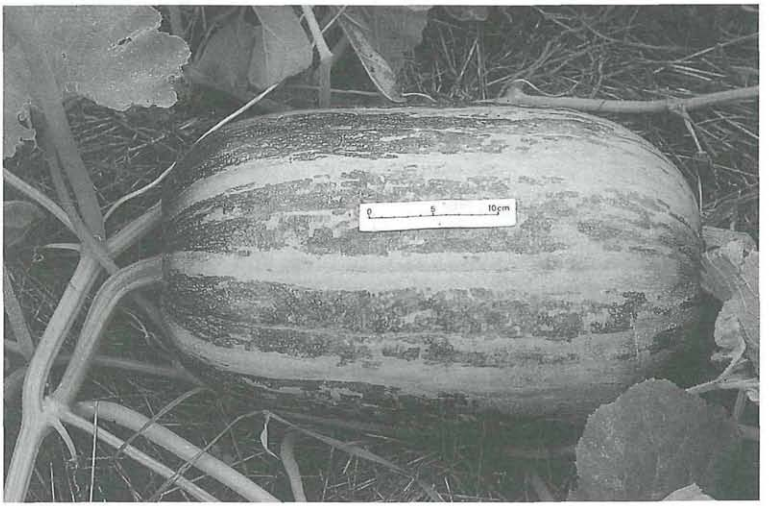


Fig. 7. *C. pepo* subsp. *pepo*, horticultural group pumpkin, with cylindrical fruits (and thick coated seeds). – Landwirtschaftliches Versuchszentrum Wies, Steiermark, Austria; August 18, 1999. – Scale bar = 10 cm.

The next work of great interest is the manuscript herbal of Georg Öllinger in Nürnberg, finished in 1553; therefore many images of this voluminous work must be much older. Only 50 selected images edited by Lutze & Retzlaff 1949 are published in print; but now the whole herbal is accessible in a very nice colour microfiche edition. One of the cucurbit pictures represents a plant (Fig. 8), which is similar to the Türckisch Cucumer of Fuchs. In Lonicerus 1557: 286/verso a round (Cucumis marinus, Indianisch öpffel) and an elongate fruited pumpkin (Melopepo) are also illustrated. As to pumpkin in Dodonaeus 1583: 657 the two of Fuchs can be found on p. 654 (Pepo maior oblongus = Türckisch Cucumer) and 655 (Pepo rotundus minor = Meer Cucumer). Matthiolus 1586: 293 shows another figure (Fig. 14) with ten stronger ribs from the one end of the fruit to the other. In Tabernaemontanus 1591 not all figures are interpretable for me with certainty. *Cucurbita* species are assigned to Melopepo, Pepo, Cucurbita and Cucumis. Pumpkins of the species *C. pepo* may be Pepo maximus oblongus (p. 178; Fig. 15), Cucurbita indica (p. 182, similar to the Meer Cucumer) and Cucumis turcicus II (p. 184, on which in the meantime sharp ribs have 'grown').

Soon after the first pumpkin drawings, the scallops appeared in different herbals and therefore must have been of some abundance; a remarkable fact because the scallops were nearly forgotten in Central Europe and the actual abundant use as a vegetable is a new development of the last decennia. The first picture seems to be the beautiful image in Öllinger 1553 (Fig. 9) which shows a strong bush with disk like fruits. The next magnificent manuscript herbal worth mentioning is that from Conrad Gessner which had its origin around ca. 1560 and which is much better known by its facsimile editions than the little earlier work of Öllinger. Gessner (a) furnishes excellent drawings of a scallop bush (fol. 344a/verso, not dated) and of the fruit (fol. 301/recto, dated 1561). Dodonaeus 1583: 655 adds a semibush or vine scallop (only one tendril in the figure) with discoid fruits (Fig. 12). According to Paris 1996: 10, a scallop figures already in Dodonaeus 1554. The variability of the scallops is well documented in Tabernaemontanus 1591 with bush and vine types and different fruit forms (Fig. 16–18).

The first figure of a fruit with the typical shape of a vegetable marrow (tapering to the peduncle) seems to be one of the four fruits on fol. 357/verso of Gessner (Fig. 11; dated 1561). Although this fruit, with its ten ribs along the whole length of the fruit, and weighing c. 8 kg, looks quite similar to the Giraumon de Patagonie de Naudin 1856: 37 = *C. pepo* var. *patagonica* Naud. ex Harz 1885: 815, it has a distinctly smaller length : width ratio. A vegetable marrow with a similar ratio but unribbed and most probably much smaller fruits should be the Cucurbita indica minor of Tabernaemontanus 1591: 182 (Fig. 19) in which the bush type is very re-

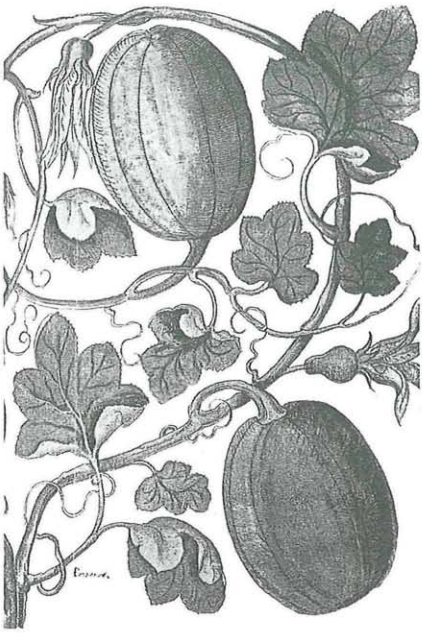


Fig. 8

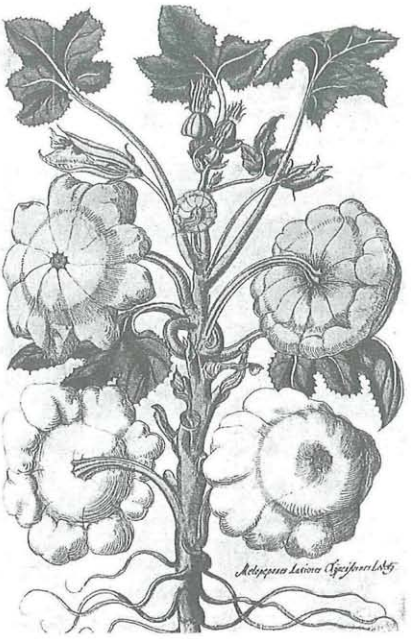


Fig. 9

Fig. 8. A pumpkin (*C. pepo* subsp. *pepo*) from the manuscript herbal of G. ÖLLINGER 1553; the right half of a two pages illustration on p. 90–91 of the original (LUTZE & RETZLAFF 1949: Bild 49).

Fig. 9. A scallop (*C. pepo* subsp. *ovifera*) with strong bushy growth habit from the manuscript herbal of G. ÖLLINGER 1553 (LUTZE & RETZLAFF 1949: Bild 47, p. 419 of the original).

markable in respect of the evolution of Zucchini; the name Cucurbita longa in the respective figure legend of the original is a mistake, which can be easily seen from the text. PARIS 1996: 10 cites a painting of J. BEUCKELAER from 1566 with vegetable marrow fruits.

The only figures which I had in my hands that probably can be brought in connection with acorn are TABERNAEMONTANUS 1591: 179 Pepo Indicus minor angulosus (Fig. 20) and probably also the Pepo minor Indicus IV (Fig. 21, from p. 180).

The early presence of ornamental gourds can be traced back as far as to BOCK 1546 (where mention of bitter fruits is to be found). The first figure of a pyriform type seems to be a painting in the herbal of ÖLLINGER (Fig. 10). The first figure in a printed book is most probably in DODONAEUS 1583:660: from the leaves and flowers his Cucurbita sylvestris (Fig. 13) must be a pyriform ornamental gourd (instead of the name and the bifid tendrils); curiously this woodcut illustration was classified by TABERNAEMONTANUS 1591: 183 as Coloquint das Weiblein or Colocynthis foemina.

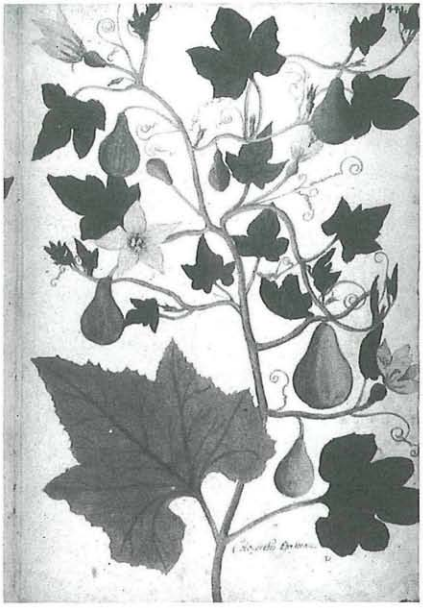


Fig. 10. An ornamental gourd (*C. pepo* subsp. *ovifera*) from the manuscript herbal of G. ÖLLINGER 1553: 441 (ÖLLINGER 1553b, colour microfiche edition, Edition Helga Lengenfelder, München, with permission).

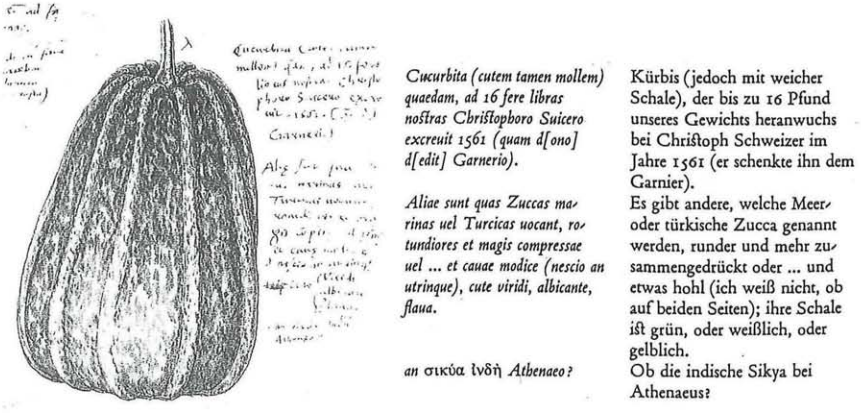


Fig. 11. *Cucurbita pepo* subsp. *pepo*. Painting of a vegetable marrow type from the manuscript herbal of C. GESSNER, fol. 357/verso (Faksimileausgabe, Urs Graf Verlag, Dietikon-Zürich, with permission).

Fig. 12

Fig. 13

Fig. 12. Pepo latus, a semibush or vinous scallop (*C. pepo* subsp. *ovifera*) from the herbal of DODONAEUS 1583: 655. (Universitätsbibliothek Graz).

Fig. 13. Cucurbita sylvestris from the herbal of DODONAEUS 1583: 659, apparently a pyriform ornamental gourd (*C. pepo* subsp. *ovifera*).

Warted gourds seem to have appeared late: One with oblong fruits could be Pepo indicus minor oblongus (TABERNAEMONTANUS 1591: 179), if not a *Cucumis*. A good picture of a warty and ribbed flat round type is Cucurbita verrucosa of BAUHIN & CHERLER 1651: 222 (Fig. 22). A painting of J. A. VAN DER BAREN 1657 shows warted cultivars, two round and an obovoid one (REITERER & REITERER 1996: 27–28).

Further figures out of herbals are reproduced in BAILEY 1929. STURTEVANT 1919: 212–219, gives an analysis of the *C. pepo* cultivars treated in the herbals (merged with some types of *C. maxima* and *C. moschata*). PARIS 1989, 1996, 1998 discusses his eight horticultural groups in relation to history.

Thus, we see that enough types of both cultivated subspecies of *C. pepo* were present in Europe in the 16th century to allow a rapid evolution of

Fig. 14

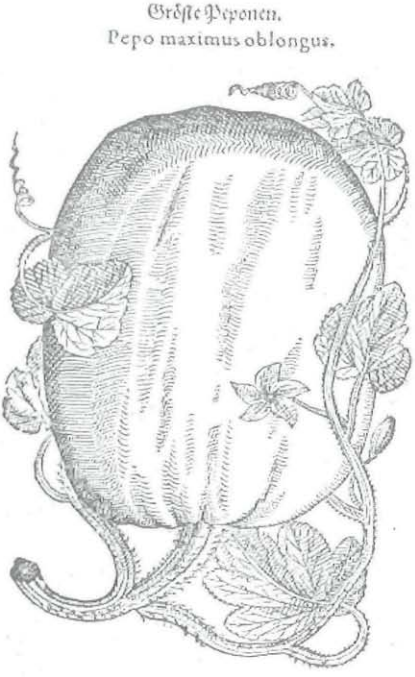


Fig. 15

Fig. 14. Cucurbita indica, a pumpkin (*C. pepo* subsp. *pepo*) from the herbal of MATTHIOLUS 1586: 293. (Universitätsbibliothek Graz).

Fig. 15. Gröste Peponen, a pumpkin (*C. pepo* subsp. *pepo*) from the herbal of TABERNAEMONTANUS 1592: 178. (Universitätsbibliothek Graz).

new cultivars. A sign of its popularity can be seen in the fact that a cucurbit is used as a symbol for plumpness in a poem from 1626 (printed anonymous 1646: 134) from a member (G.T.) of the 'Fruchtbringende Gesellschaft' (Fig. 23), a literaric association in Weimar, Germany (1617–1680).

An other point of historical interest is a *Cucurbita pepo* cross undertaken in 1763 by KÖLREUTER, who mainly worked with *Nicotiana, Verbascum* and *Dianthus*. It is one of the first scientific crosses in plants. KÖLREUTER 1766: §63 gives a short account of his cross of a Cucurb. indica × Cucurb. Pepo maxima with a full fertile intermediate progeny. He therefore concluded, that these two and other varieties belong to the same species. ("Man sieht also wohl, dass diese hier angegebene Varietäten dem Wesentlichen nach eben so wenig von einander unterschieden sind, als ein Schoosshündchen von einer englischen Dogge, und folgliche beyde, nebst

Fig. 16

Fig. 17

Fig. 16 and 17. Schildt Peponen and Köpffelkürbs, two bushy scallops (*C. pepo* subsp. *ovifera*) from the herbal of TABERNAEMONTANUS 1591: 178 and 181 respectively.

einer Menge [not all !] anderer Sorten, unter eine Gattung [means species in the work of KÖLREUTER] gehören." [Thus one sees, that the here mentioned varieties differentiate essentially from one another as less as a lapdoggy from a Great Dane and therefore both belong, along with many other sorts [not all !], to the same genus [means species in KÖLREUTER's work]]. – KÖLREUTER used crossability, e.g. also in §62 concerning *Sida*, as a character for delimitation of species!). But he did not state, that all Cucurbits belong to only one species as erroneousely supposed by NAUDIN 1856: 7–8. Admirable is also the comprehensive work on *Cucurbita* crosses (*C. maxima, C. moschata, C. pepo*) and its documentation by DUCHESNE. This lead to the first satisfying delimitation of *Cucurbita* taxa based on genetic (crossing) barriers which is principally accepted till today (DUCHESNE in LAMARCK 1786: 148–159!! See NAUDIN 1856: 8–9 and PARIS 2000).

The first mention of a cucurbit in Styria (as vegetable) is supposed to be a handwritten menues dated January 16, 1596 (REITERER & REITERER

Fig. 18

Fig. 19

Fig. 18. Klein Indianisch Schildtpeponen, a vinous scallop (*C. pepo* subsp. *ovifera*) from the herbal of TABERNAEMONTANUS 1591: 179.

Fig. 19. Klein Indianischer Kürbs, a bushy vegetable marrow (*C. pepo* subsp. *pepo*) from the herbal of TABERNAEMONTANUS 1591: 179.

1996: 64, 65; if the interpretation of the word 'Kabaß' as cucurbit by these authors should be correct; *Lagenaria* must also be taken into consideration). The oldest known reference of peeled seeds (for oil production) dates back to February 26, 1735 (KUNDEGRABER 1988: 193). The oldest printed informations concerning Styria are probably MAYER 1772 (p. 27: cucurbits need a lot of water to grow) and anonymous 1773 (see TEPPNER 1982).

Let us come back to the point where we started and that is the *C. pepo* var. *styriaca*. The use of fruit flesh (and much more rarely of the flowers) as food (WREDOW 1819: 99–100, KULMER & WEBER 1990, WAGNER & LAMMERHUBER 1997, REITERER & REITERER 1996: 96–106, especially rich in ideas and excellent photos: SEIDL 1998) and of the fruits as fodder is generally known but is restricted and economically not important. Mostly only the seeds are harvested and the opened fruits remain on the field. In times bygone, the harvesting took place only manually (Fig. 27) but in recent times different types of motorised harvesters have been invented (Fig. 26).

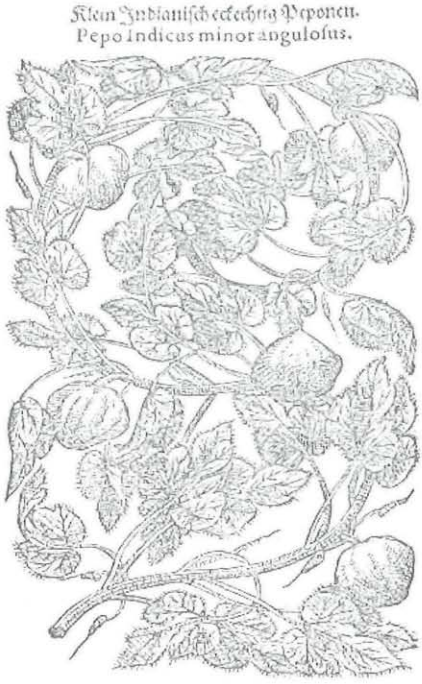


Fig. 20

Fig. 21

Fig. 20 and 21. Klein Indianisch eckechtig Peponen and Klein Indianisch Peponen, two acorns (*C. pepo* subsp. *ovifera*) from the herbal of TABERNAEMONTANUS 1591: 179 and 180 respectively.

7. Seed Coat Types

The seed testa in *Cucurbita* is a five-layered structure originating from the outer integument. The wild trait (thick coated, Fig. 31, 45) is represented by a strong lignification of the four outer layers and therefore such seeds have a thick and hard, more or less whitish to ochre seed coat (FICKEL 1876, HÖHNEL 1876, HARZ 1885: 811–814, ROSEN 1920, PRYM – VON BECHERER 1955, SINGH & DATHAN 1972, 1998). According to the numbering of the layers in Fig. 31 ripe seeds of this type have the seed coat structure **1.2.3.4**.5. (bold numbers indicate lignification).

The main characteristic of the Styrian Oil Pumpkin is the dark green colour of the thin coated seeds, which makes it so very much special. This arises due to the fact that the four outer layers of the seed coat lack the usual lignification of the cell walls completely (Fig. 32, 39) (HEINISCH & RUTHENBERG 1950, STUART & LOY 1983), moreover the fifth layer, the chlor-

Fig. 22. The warty ornamental gourd Cucurbita verrucosa BAUHIN & CHERLER 1651: 222. (Courtesy of F. SPETA, Linz).

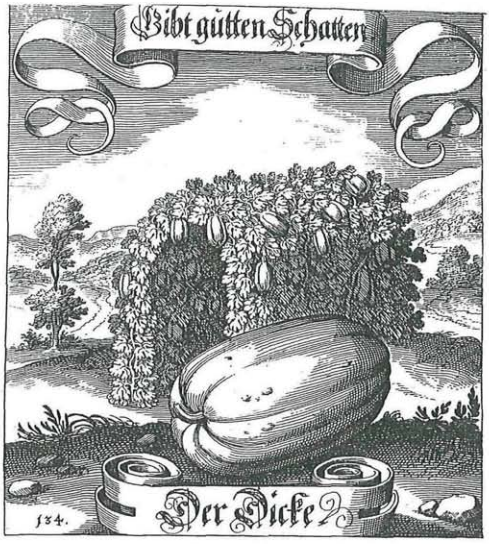
enchyma, has more cell layers than in some thick coated types (according to STUART & LOY 1983: 492).

In the full grown but unripe seed all five layers are developed (Fig. 32, upper row) (here and in the following all records concern the face of the seed – if not otherwise indicated):

1. Epidermis
2. Hypodermis: (0–) 3–5 (–6) layers of cells
3. Sclerenchyma: 1–2 cell layers
4. Aerenchyma: 1–3 cell layers
5. Chlorenchyma: 8–10 (–12) cell layers

During the late phases of seed development, when – the epidermis excepted – testa cells collapse, the layers 2 and 3 are largely or totally resorbed (Fig. 32, lower row); at best only a thin, compact, hyaline layer usually remains. Thus, outside chlorenchyma, only the thin aerenchyma, no or hyaline remains of 2 and 3 and the hyaline epidermis exist. In respect to the basically 5-layered structure ripe thin coated seeds possess essentially a 1.4.5.-testa! This is, in addition to the protochlorophyll content (for protochlorophyll chemistry see ELLSWORTH & NOWAK 1974), the main reason for the dark green colour of the thin coated seeds. Because of the destruction of 2–3 and the collapse of 4–5 during the ripening process already, no remarkable differences can be seen in the seed coat structure between fresh ripe seeds immediately taken from the fruit and dried seeds afterwards soaked.

In the developing thin coated seeds a deficiency in lignin (mainly in 2–4) and of cellulose (mainly in 1) was detectable at 20 days post anthesis (STUART & LOY 1983: 498–499, 1988: 192–194). The more or less total



Es dicket Kürbis kraut sehr guten schatten gibt/
Man pflegt mit seinem saft den Pferden auch zu raten/
Das sie von Fliegen nicht und Mücken seind betrübt:
Der Dicke Nahme mir auch kommet recht zu staten:
Ist einer dicke schon/so wird er doch geliebt/
Wan er sich völlig übt in Tugendhaften thaten/
Dahin wil zielen ich zu nacht und auch zu tag'/
Und iedem recht zuthun ein gros verlangen trag'
G. T. 1626.

Fig. 23. A cucurbit as a symbol of plumpness in 'der Fruchtbringenden Geselschaft Nahmen/Vorhaben/Gemählde und Wörter...' (Anonymous 1646: 134; Vincentz Verlag Hannover; with permission). A translation of the poem:
A very good shade gives the plump pumpkins herbage /
with it's sap you can the horses rub /
which them relief brings from flies and gnats:
The plump one is a name for me suitable:
Even when plump / is one loved all the same /
If he in his life virtuous deeds commits /
Thus in night and at day do I aspire /
To do everybody right is my only desire.

degradation of 2–3 and of the cell content of 1 seems to coincide with the decline of testa weight from day 20 post anthesis to the ripe seeds 55 days post anthesis found by STUART & LOY 1988: 192–194. During this period a rapid growth of the embryo takes place, using the materials stored in the testa (STUART & LOY 1988: 194, VINING & LOY 1998: 67).

The profuse chlorenchyma leads to the fact that more protochlorophyll is dissolved during roasting and pressing, giving the Styrian 'Kürbiskern-

öl' or Styrian 'Kernöl' ('Schwarzes Gold' = black gold, sometimes also called 'Grünes Gold' = green gold) its deep luxuriant colour. The deep colour is an important quality criterium in Styria.

It is very important to remember that true (typical, high quality) var. *styriaca* seeds have no lignified margin (Fig. 39)! This character was sometimes neglected purposely by cucurbitologists or breeders who regarded the seeds only in context of industrial oil production (GREBENŠČIKOV 1954a: 164, 166). For the use of the seeds as 'Knabberkerne' (snack seeds) as a delicacy or for medicinal purposes this is also a very important character. In var. *styriaca* only a thin 'pseudomargin' occurs: this type of margin is the vascular bundle along with collapsed and longitudinally folded testa parenchyma and the other layers and has nothing to do with any lignification of the coat. Furthermore the seeds are of the large and broad category (c. 2 × 1 cm when dry).

8. Thin Coated Seeds and Genetics

The thin coated seed character is genetically recessive in relation to thick coated. Originally, it was presumed to be caused by two major genes (H/h and N/n) and some modifier genes (GREBENŠČIKOV 1950: 203 and especially SCHÖNINGER 1950, 1952, 1955). This opinion, with some reservations or doubts, was more or less accepted by later authors (WEILING & PRYM – VON BECHERER 1951: 148, MUDRA & NEUMANN 1952: 102, PRYM – VON BECHERER 1955) except for GREBENŠČIKOV 1954a, who opposed it vehemently: He was of the opinion that only one strongly dominant major gene H/h exists along with some modifier genes, which are effective in the condition hh. WHITAKER 1974: 141 in his gene list followed GREBENŠČIKOV but gives no gene symbol. ROBINSON & al. 1976: 563, 565 proposed the gene symbol n instead of the original h and the modifier genes were omitted (identical in HUTTON & ROBINSON 1992: 105). It is difficult to say whether these genes mutated in the new or the old world. But anyhow, they segre-

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Fig. 24–25. *Cucurbita pepo* subsp. *gumala*. – Fig. 24. Fruit from the top and transverse section. Scale bar = 1 cm. – Fig. 25. Leaves, female and male flower. Scale bar = 10 cm.

Fig. 26. A motorized harvester (firm Moty-Landmaschinen Mayer, A-8523 Frauental, Styria) at work, surroundings of Leibnitz (Styria), September 25, 1994.

Fig. 27. Traditional manual pumpkin seed harvest. In the foreground the Hackscheit or Hackbårten, the knife for halving the fruits. Between Schwanberg and Deutschlandsberg, Western Styria, September 29, 1982.

Fig. 28–30. *Cucurbita pepo* subsp. *pepo* var. *flogra*. – Fig. 28. An entire plant at harvest time. – Fig. 29. Fruits at different degrees of ripeness, one in longitudinal section. Scale bar = 10 cm. – Fig. 30. Dry seeds. Scale bar = 1 cm.


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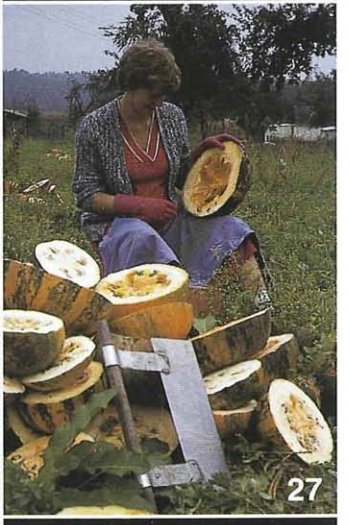
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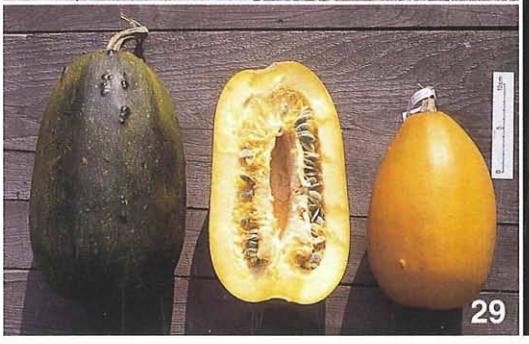
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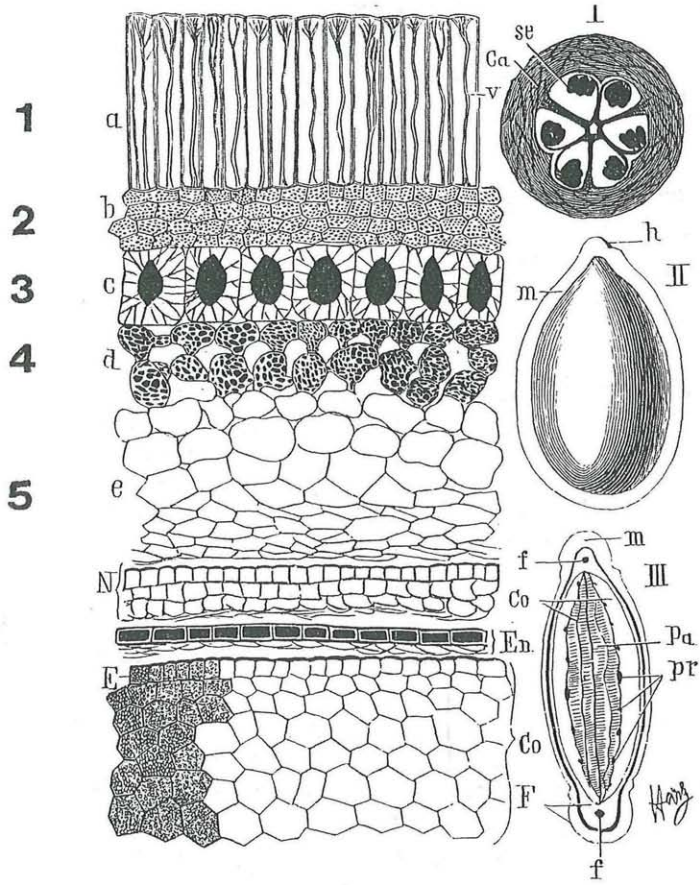

Fig. 45. Cucurbita Pepo. I Querſchnitt der Frucht. Ca Fruchtwand. se Samen. II Same. h Nabel. m Randſchwiele. III desgl. Querdurchſchnitt. T Samenſchale. f Gefäßbündel derſelben. Co Cotyledonen. Pa deren Palliſadenſchichte. pr deren Procambiumſtränge. IV Ein Theil des Samens quer durchſchnitten. a Oberhautzellen. v deren Verdickungsleiſten. b, c, d, e zweite, dritte, vierte und fünfte Teſtaſchichte. N Ueberreſte des Eikernes. En Ueberreſte des Endoſperms. Co Cotyledo. E deſſen Oberhaut.

Fig. 31. Figure of *Cucurbita pepo* seeds (thick coated), including a transverse section of the seed coat of a ripe seed, from HARZ 1885: 813. – Numbering of the testa layers in this paper: 1 = epidermis, 2 = hypodermis, 3 = sclerenchyma, 4 = aerenchyma, 5 = chlorenchyma. Additional 0 used for the placenta epidermis as in text, not shown in this figure.

gated from the normal field pumpkin in Styria (in the old sense, including Lower Styria, now in Slovenia) sometime in the 19th century.

9. Vinous Styrian Oil Pumpkin, Processing and History

The exact time and place of origin are still shrouded in mystery. The common mode of processing the thick coated seeds was to peel them (after soaking in hot water), the peeled seeds (embryos with the adherent chlorenchyma) (ROCHEL 1826: 99, FUCHS 1930: 34–36, KUNDEGRABER 1988: 193) were then milled in the so-called 'Schmiermühlen'. The resulting pap ('Öl-Sterz') was then roasted and 'ausgeschlagen' (it means hammered out) in an 'Ölkuh' (= oil-cow; FUCHS 1930: 30, Fig. 1) or pressed for oil. LILIEN 1824: 146 found the peeling method of the Styrians too cumbersome, which lead to his refusal to cultivate pumpkins as an oil crop in his domain SSW. of Budapest in Hungary. ULBRICHT 1886: 239 in West Hungary on the other hand accepted the method, even though he wished for a peeling machine. In other parts of Austria (rarely in Styria) thick-coated seeds were crushed in 'Stampfen' as whole, without peeling (BORCSÁNYI 1804: 23, ROCHEL 1826: 99, GAMERITH 1979: 41). That peeled seeds give a higher yield of oil is known since a long time (BORCSÁNYI 1804: 33–34). Old processing techniques are also described in BELANI 1940. The appearance of the thin coated mutant naturally simplified this tedious process. Surprisingly, no written information could be found about the origin of this new cultivar. All the efforts of Mr. O. GROLLEGGER (Trahütten, Styria) and myself to find any information on this topic in the 'Landwirthschaftliche Mittheilungen für Steiermark. Organ für Landwirtschaft und Landeskultur', edited by the 'K.K. Landwirthschafts-Gesellschaft in Steiermark' (before July 1884: 'Der steirische Landbote.'), a very important monthly agricultural journal of Styria, has at least till now failed. However the few available evidence support the view that the true breeding thin coated type appeared approximately between 1870 and 1880 (PREGEL in TSCHERMAK-SEYSENEGG 1934: 41, BUCHINGER 1944: 77, 1948: 12, TEPPNER 1982: 60–62, 1999). From the text of ULBRICHT 1886: 239–240 it is apparent, that in Hungary thin coated seeds were not known at that time.

10. Breeding of Oil Pumpkins

The first scientific crossing experiments for breeding oil pumpkins were undertaken in Germany (anonymous 1925). BUCHINGER 1944, 1948 summarized the experiments in Europe up to the 40's.

Modern breeding programs are carried out with the aim to increase the number of placentas. The basic bauplan of the gynoecium in the *Cucurbitaceae* is of five carpels, but *Cucurbita* has usually only three. Modern cultivars produce a higher percentage of fruits with four or five placentas. It is said that one placenta more can give as much as 10% more seed yield (NEUMANN 1952: 536, c. 20%, MUDRA & NEUMANN 1952: 102). Even Styrian

farmers, who grow their own land races, often select in this direction. Further efforts concern e.g. content of oil and antioxidants (HILLEBRAND & al. 1996, MURKOVIC & al. 1997), virus resistance (LELLEY & HENGLMUELLER 1999), high fruit yield, seed size and colour etc.

In the Austrian 'Österreichische Sortenliste 2000' (= Austrian cultivar list 2000, http://www.bfl.at/institut/pflbau/sorten/oe) actually six cultivars of oil pumpkins are registered. 'Gleisdorfer Ölkürbis' (WINKLER 1999 a,b), and 'Wies 371' (PELZMANN 1999) are the best known of them. Breeding efforts are also being undertaken in the USA and Hungary and in other countries which may have their own cultivars.

Crossing with Styrian oil pumpkin is difficult, when lines with wild type seeds are involved. Altough the thin coat character segregates in the F_2 generation, a lignified margin remains on the seeds, which is not easy to eliminate. In the 30's TSCHERMAK-SEYSENEGG in Vienna, produced an oil pumpkin with bush habit, which was soon known as 'TSCHERMAK-Kürbis' (*C. pepo* var. *oleifera* PIETSCH 1942: 388–389). The material which I recieved in the past under this name (no original material) had such a margin; according to the literature also the original material had this margin at least partly: BUCHINGER 1944: 77, 1948: 13, HEINISCH & RUTHENBERG 1950: 168. SCHÖNINGER 1950: 324, Abb. 3 even figures the lignified sclerenchyma in the margin of var. *oleifera*. The specimen chosen as neotpe (chap. 14) also shows partial lignification. But in the sample No. PEP 411/1977, generously provided by the Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, only an exaggerated parenchyma without lignification forms a prominent rim, therefore a pseudomargin; probably continuated selection may have eliminated the lignification.

I, myself tried in 1974–1977 a triple cross of Styrian oil pumpkin with an ornamental gourd (chosen for resistance) and an unnamed local zucchini (for bush habit). It is interesting to note that the crop plant character 'bush' is dominant over the wild type character 'vine' (GREBENŠČIKOV 1954b, 1958, MUDRA & NEUMANN 1952: 102, DENNA & MUNGER 1963), because it is usually estimated that only 1% of the useful mutant characters are dominant (GOTTSCHALK & WOLFF 1983: 12). The desired and derived result: a multi purpose garden squash of the vegetable marrow type (Fig. 28–30). This variety also had this lignified margin. Growing c. ten plants a year I needed many years of selection, in the first generations after selfing, later (since 1991) after open pollination, to eliminate it. At that time I yet had faith in the one gene theory and therefore I neglected to try a classification of the margin types and to count them. But some doubts about the correctness of the one gene theory arised from the difficulties of elimination. I also trusted that all cucurbits should have a five layered ripe seed coat as reported in all the literature. Thus, I omitted to check the seed coat anatomy in the different generations. So I can only say that the resulted variety has the same

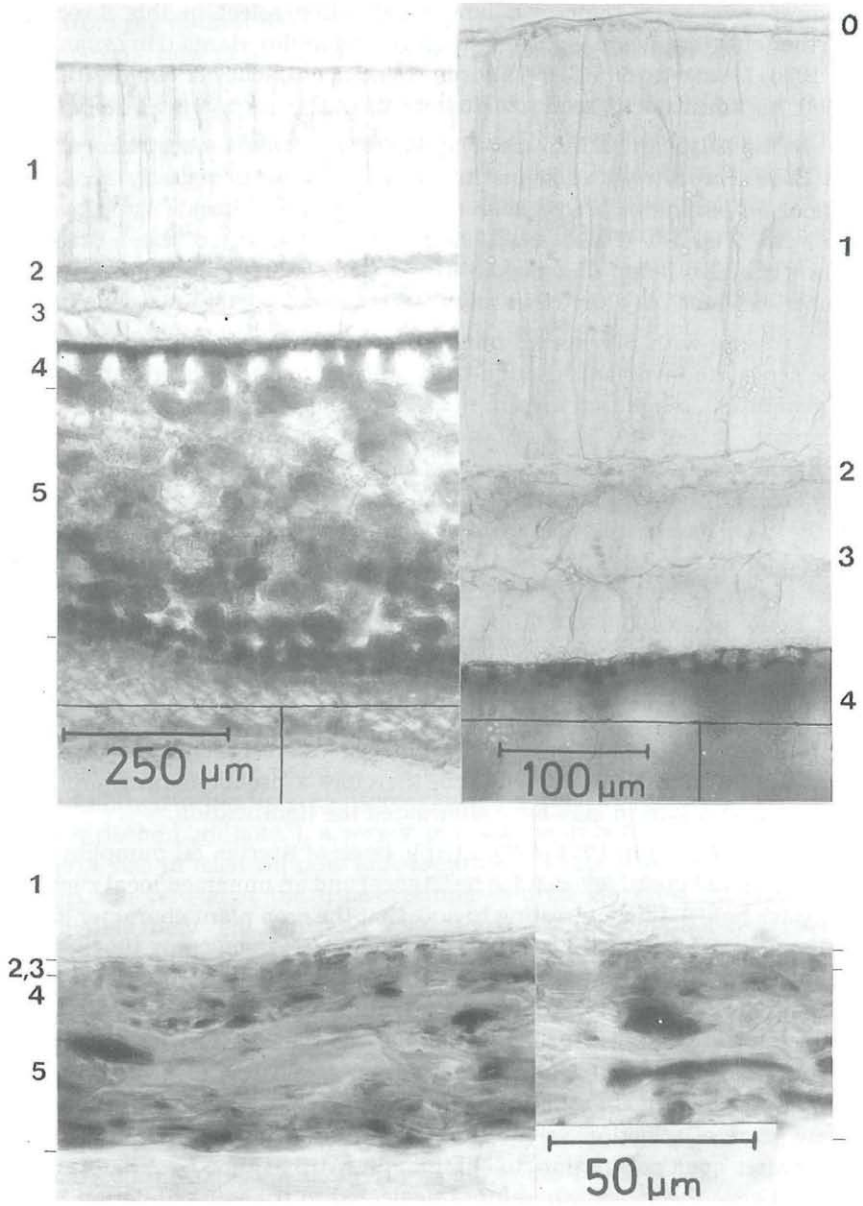

Fig. 32. Transverse sections of the testa of *Cucurbita pepo* subsp. *pepo* var. *styriaca*. Upper row: full sized but unripe, fresh seeds. – Below: ripe, dry seeds soaked for 24^h in water. From the epidermis only the basal part is shown. The scale bar is the same for both figures. – Hand sections in glycerine, not stained.

1.4.5.-testa (Fig. 33) without any lignification in the ripe seed as var. *styriaca*. A remarkable difference to actual cvs. occurs only in the margin, in which 1-3 was observed to be degenerated in my variety. Now I have given it the name *C. pepo* var. *flogra* TEPPNER (publ. h. l., chap. 14). It was tested by the Landwirtschaftliches Versuchszentrum Wies (1985) and by Saatzucht Gleisdorf (1990) but I couldn't find a single taker for my variety.

11. The Semi-thin Seed Envelope Type

It is sometimes said that seed coat mutations occurred elsewhere in *C. pepo* and other species as well (e.g. ROBINSON & al. 1976:565). Precaution is necessary in such cases, because often peeled seeds are offered for sale. Once I recieved alleged thin coated seeds from a market in Cancun, Yucatán, Mexico (Fig. 34; courtesy of Mrs. G. HÖDL-KUFFNER, Graz, 1997) which turned out to be a thick-coated *C. argyrosperma*.

Other mutants really exist, but I had the fortune to have one, from *C. pepo*, in my hands only once. It was a local field pumpkin cultivar from Georgia (former USSR), which was used there as a vegetable and for seeds (received 1993, courtesy of Dr. R. FRITSCH, Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany; gene bank collection number PEP 1540/1986). I classify it as *C. pepo* var. *georgica* TEPPNER (publ. h. l., chap. 14). The flat-round to somewhat elongated fruits were ribbed and had an orange coloured flesh (Fig. 36, 37). The seed coat of the narrower seeds is thinner than in the wild type, but is thick enough to hide the chlorenchyma, which is scarcely visible (Fig. 38). A lignified margin is also present. It seems it is best to name this type 'semi-thin'.

The result of the anatomical check was very surprising. In the ripe seed, epidermis, hypodermis and slerenchyma are usually completely lacking or are destructed to a thin, collapsed and largely resorbed hyaline layer (Fig. 35). The lignified aerenchyma is strongly developed, 2–4(–5) layered; the innermost cells are very large (Fig. 35). Due to the collapsing of the c. 8 layered parenchyma in the ripe seed the aerenchyma is much thicker than the parenchyma. Usually, the outer walls of the placenta epidermis are – even in the dry seed – appressed to the aerenchyma or to the remains of 1–3 (Fig. 35); sometimes it may be lacking because of the manipulations. Thus the ripe semi-thin seed envelope has the structure (0).4.5. (0 for the placenta epidermis and brackets for not absolutely obligatory in dry seeds outside the fruit).

12. A Thin Coated × Semi-thin Coated Cross (*C. pepo* var. *styriaca* × var. *georgica*)

12.1.

To cast some light on the genetics of the seed coat, I crossed var. *georgica* with the Styrian Oil Pumpkin (as mother) with the result that the

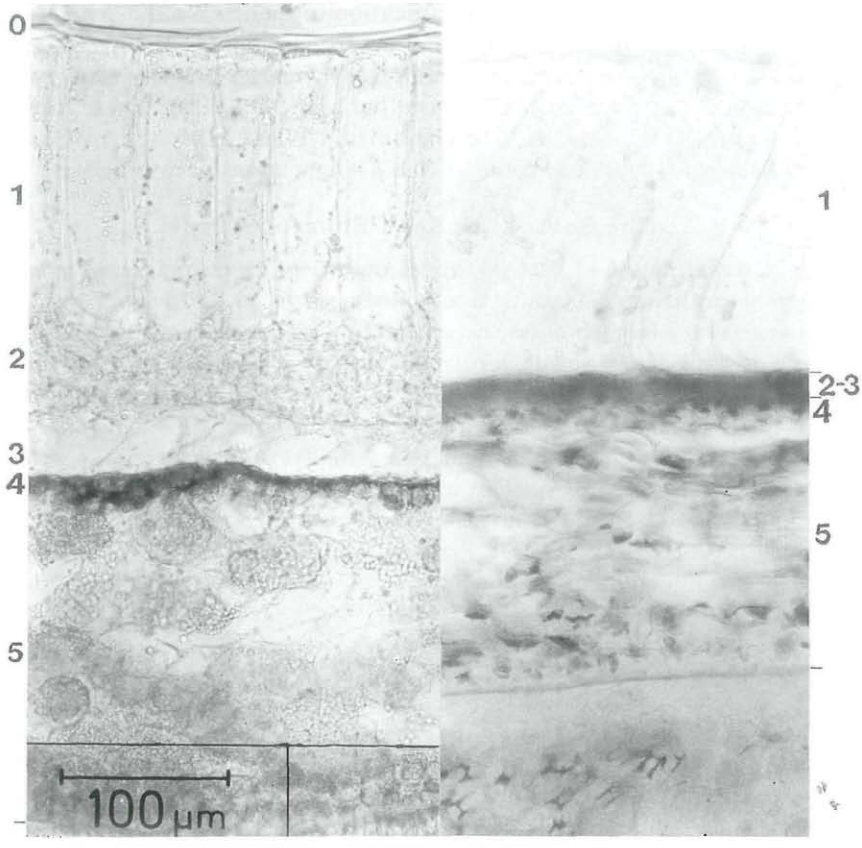

Fig. 33. Transverse sections of the testa of *Cucurbita pepo* subsp. *pepo* var. *flogra*. Left: full sized but unripe seed; right: a ripe, fresh seed. – Hand sections in glycerine, not stained. – The scale bar is the same for both figures.

seeds from the F_1 generation (Fig. 40, 41) were semi-thin ! S e m i - t h i n is also d o m i n a n t over thin coated !! Segregation in the F_2 produced plants with very different combinations of seed coat characteristics.

The limited resources of area and staff permitted no larger experiments. Unfortunately the plague of zucchini yellow mosaic virus in 1997 was the severest till now [e.g. SZITH 1999 and Kleine Zeitung (Graz), Aug. 12, 1997, p.8, Aug. 14, 1997, p.9] so that only one selfed gynoecium reached maturity and a number of plants didn't carry even a single fruit, thus hindering further observations. In 1999 the situation was little better. Therefore ripe fruits from only 12 F_2-plants are at our disposal.

In spite of great variability in the details, the 12 F_2 plants may be grouped for the seed coat characters in the ripe seeds as follows:

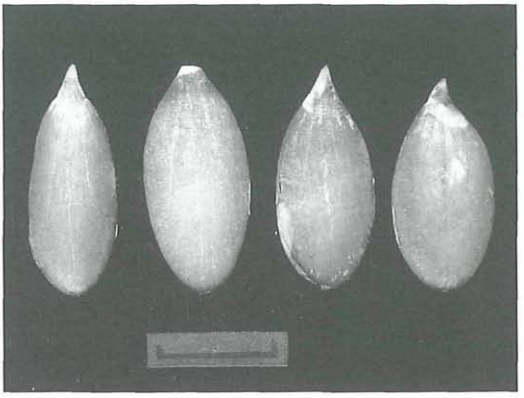

Fig. 34. *Cucurbita argyrosperma.* Peeled seeds (embryo and chlorenchyma) offered for sale on a market in Cancun, Yucatán, Mexico, 1996.

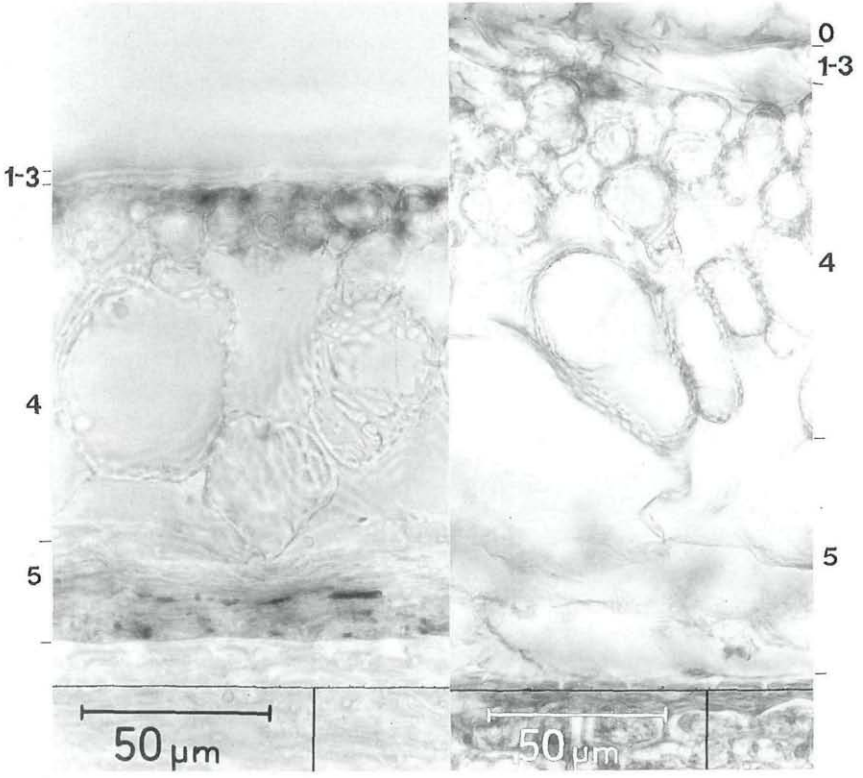

Fig. 35. *Cucurbita pepo* subsp. *pepo* var. *georgica.* Transverse sections of the testa of ripe seeds (PEP 1540/1986). At the left a hand section not stained, at the right a microtome section stained (safranine / fast green).

4 thick coated (including collapsed epidermis and different protochlorphyll content)
1 semi-thick coated: a new type, described later
4 semi-thin coated (including lignified sclerenchyma in the margin and individuals which also produce seeds with semi-thick seed coat in the same fruit)
3 thin coated (including collapsed epidermis or lignified sclerenchyma in the margin)

We hope for the possibility to treat the full F_2 variability of the testa structure in a subsequent paper. So I will characterize here only the new seed coat type and the two extremes of the other segregants.

12.2. Semi-thick Seed Coat

This type is found up till now only under the segregants of this thin × semi-thin cross. In only one individual all seeds had this character uniformly; but which was also accompanied by very uneven thickness of the coat and lignified sclerenchyma in the margin. Other three individuals, counted for the semi-thin group, had a mixture of seeds with semi-thin and semi-thick seed coats in one and the same fruit.

The presence of a well developed, lignified hypodermis (Fig. 44) of 4–5 cell layers in semi-thick is the main characteristic that distinguishes it from semi-thin. Layer 3 degenerates very early during the development or only scattered sclerenchyma cells remain and are lignified only at a small scale (in contrast the epidermis degenerates late). The size of the aerenchyma cells and the number of cell layers [2–4(–5)] is usually intermediate between semi-thin and thin. The chlorenchyma has ca. 8–10 cell layers. The epidermis is very rudimentary and represents a very thin hyaline hide. The outermost layer is the placenta epidermis once more. Thus the seed coat structure is essentially (0).**2.4**.5. Semi-thick and semi-thin seed coats cannot be distinguished by the naked eye only.

Fig. 36–38. *Cucurbita pepo* subsp. *pepo* var. *georgica*. – Fig. 36. Ripe fruits of two different individuals. Scale bar = 10 cm. – Fig. 37. Transverse section of a fruit . Scale bar = 1 cm. – Fig. 38. Ripe, dry seeds. Scale bar = 1 cm.

Fig. 39. *Cucurbita pepo* subsp. *pepo* var. *styriaca*. Ripe, dry seeds of a land race of Western Styria. – Scale bar = 1 cm.

Fig. 40–41. F_1 of the cross *Cucurbita pepo* subsp. *pepo* var. *styriaca* × var. *georgica*. – Fig. 40. Fruits of five different individuals. Scale bar = 10 cm. – Fig. 41. Ripe dry seeds. In the right seed the aerenchyma is partly removed. – Scale bar = 1 cm.

Fig. 42–43. Two segregants out of the F_2 of the same cross. – Fig. 42. Thick coated type with dark green chlorenchyma. – Fig. 43. A thin coated type with collapsed epidermis and lignified sclerenchyma in the margin. – Scale bar = 1 cm.


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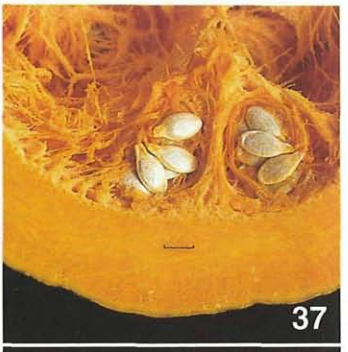
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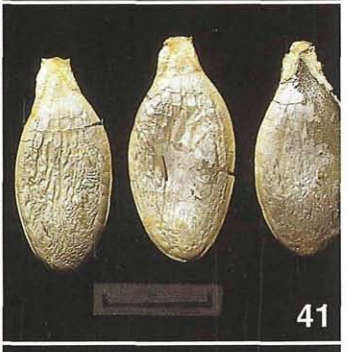
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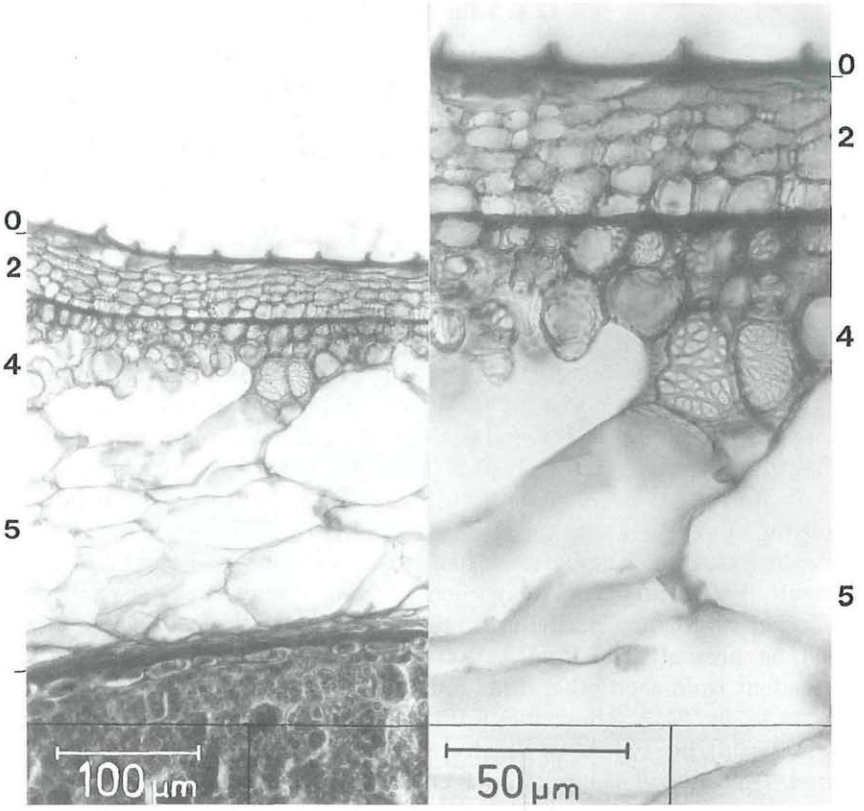

Fig. 44. Semi-thick testa type (transverse section) in a segregant of the F_2 from the cross thin × semi-thin (*C. pepo* var. *styriaca* × var. *georgica*). Dry seed, soaked, microtome section, stained (safranine / fast green).

The hypodermis is always present around the hilum in semi-thin coated seeds. In some individuals (in our sample three out of four), it can apparently extend in a part of the seeds over the whole surface of the seed.

12.3. Thick Coated Seed

In the progeny of the thin × semi-thin cross the character thick coated segregates! One of these is represented in Fig. 42 and 45. This one is especially remarkable due to its very dark green chlorenchyma (high protochlorophyll content) which seems to be a new combination. At least till now I have never seen a thick coated seed with such a dark green chlorenchyma.

12.4. Thin Coated Seed

Not even one of the three plants was identical with the thin coated parent. From the thin coated group, one with lignification of sclerenchyma in the margin is chosen here. In this individual the epidermis is also collapsed (Fig. 43 and 46) and the chlorenchyma is especially thick. The seed shape is much narrower than in the thin coated parent, which also seems to be a new combination.

12.5. Evaluation of the Number of Genes Involved in the Seed Coat Characteristics

It is clear that a lignification gene does not intervene in the biosynthesis of any cell wall materials (polysacharides, lignine) but decides only about the deposition of the material for the cell wall thickenings. Sometimes in the semi-thin coated seeds layers 2–3 remain in the margin, even with cell content; in this case both layers show no trace of lignification. Near the hilum, the layer 2 is lignified and here unlignified cells of layer 3 (sclerenchyma) may lie between lignified 2 and 4. Thus I assume that an 'overall lignification gene' (major gene) as gene N should be, is not present in an active, dominant allelic form. Therefore in the whole cross only n must be present. The lignification in the layers 1–4 seems to be independent from each other, thus four genes should be responsible. SCHÖNINGER 1950: 324–325 describes a fifth seed coat type (which I have not in my material), her type 2, in which only the sclerenchymatous layer is lignified. This, as well as lignification only in the sclerenchyma of the margin, also supports the idea of an independent regulation of lignification in the four layers. At least one additional gene seems to be necessary for the decision if the whole layer or only margin or hilum region becomes lignified. These five genes could probably be the 'Nebenverholzungsgen' and the 'Modifikationsgene' of SCHÖNINGER or modifier genes of later authors. (Sum = 6 genes).

From our material it is not possible to conclude if a major degeneration gene exists which is responsible for collapse and resorption of 1–3 or if there are only independent degeneration genes for these layers. In 4 and 5 – very essential – the dead protoplasts with the protochlorophyll were maintained and not completely degraded. Therefore, another type of degeneration gene would be necessary for these layers or an additional gene which stops degradation. For 1–3 also, a modifier seems to be necessary for the surface extent of degradation. Furthermore, protochlorophyll content and number of chlorenchyma cell layers must also need a genetic regulation. (Sum = 6–9 genes).

Another possibility would be, that lignification genes in the classical sense do not exist and only degeneration genes are effective: in this case

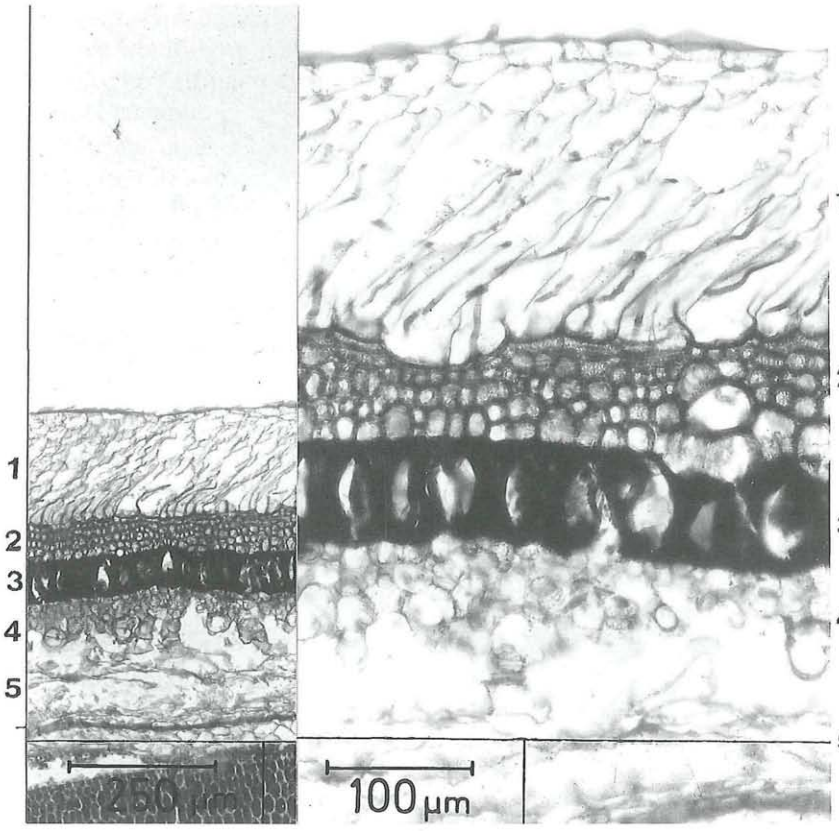

Fig. 45. Thick testa type (transverse section) in a segregant (Fig. 42) of the F_2 from the cross thin × semi-thin (*C. pepo* var. *styriaca* × var. *georgica*). Dry seed, soaked, microtome section, stained (safranine / fast green).

the protoplasts must begin to die at a developmental stage before lignification is possible. This would reduce the number of responsible genes dramatically to ca. 6–9 genes against 12–15 in the first case.

Additionally to the segregation ratio mentioned above (4:4:3:1 for thick : semi-thin : thin : semi-thick) some numbers for singular characteristics of the ripe seeds are presented:

Lignification : no lignification = 11 : 1

Lignification : lignification in margin only : no lignification = 9 : 2 : 1

Epidermis lacking or bad developed : not lignified : lignified = 8 : 1 : 3

Epidermis lacking to not lignified : lignified = 9 : 3

Hypodermis present, lignified : hypodermis lacking = 8 : 4

Aerenchyma lignified : not lignified = 9 : 3

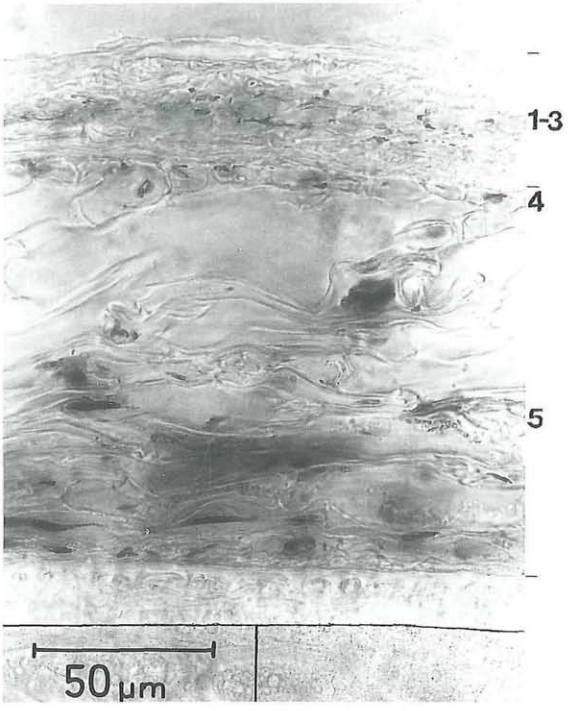

Fig. 46. Thin testa with collapsed epidermis (transverse section) in a segregant (Fig. 43) of the F_2 from the cross thin × semi-thin (*C. pepo* var. *styriaca* × var. *georgica*). – Dry seed, soaked, hand section in glycerine, not stained.

Sclerenchyma lacking : not lignified : partly lignified (scattered or in the margin) : lignified = 2 : 0 : 6 : 4

Sclerenchyma lacking or not lignified : fully or partly lignified = 2 : 10

Most of the above segregation ratios lie near the 3 : 1 and 1 : 1 ratios which are to be expected in the F_2 of dihybridous crosses with dominance and in a backcross of a homozygous recessive with one hetereozygous parent respectively. This strongly support the view that more genes with at least two alleles each are responsbile for the discussed phenotypic seed coat characteristics.

Finally a theoretical consideration. The lowermost estimate was six genes. In a cross in which the dominant and recessive alleles of six genes are homozygously distributed in the parents, there will be 64 genetically different kinds of gametes in the F_1 which lead to 4 096 possible combinations in the F_2 with 729 genotypes and 64 phenotypes. In the case of 9 genes there would be 512 phenotypes, for 12 genes 4 096 phenotypes. The plants with the deviating characteristics, mentioned in the chapter 12.1. in

brackets, may represent most probably own phenotypes. If counted separately we would have just c. 10 phenotypes in our F_2 material up till now. Therefore not all phenotypes which could be expected can be present in this small sample.

Anyhow, such a specialised combination of alleles which lead to no lignification of any seed coat layer, the maintenance of epidermis, the ± complete degeneration of hypodermis and sclerenchyma as in *C. pepo* var. *styriaca* is very, very improbable. And alone the appearance of such an allele combination is not enough. People must be present at that time, who recognize the plant with the new seed type as useful and select, protect and propagate it.

13. Conclusion

A specialist in cucurbits, GREBENŠČIKOV 1954a: 165 (compare also PRYM – VON BECHERER 1955: 11) has written that all crossing experiments over the world for breeding thin coated oil pumpkins trace back to Styrian material. Most probably the today's situation is not quite different. The very complex genetic conditions for thin coatedness may be the reason that a mutant such as the Vinous Styrian Oil Pumpkin is extremely rare and singular.

A lot remains to do for a clarification of the details of the genetics of the seed coat characteristics. This is a difficult task, because of the high number of the phenotypes which are additionally impeded by the often different behaviour of the seed face and the margin.

14. Taxonomic Notes

The scientific names of *Cucurbita* must follow undoubtedly the International Code of Botanical Nomenclature (ICBN) at least up to the subspecies level. For the infrasubspecific classification the International Code of Nomenclature for Cultivated Plants (ICNCP) would be admissible. To the best of my knowledge, cultivar group names in accordance with the conditions of the ICNCP 1995 do not exist. Therefore I'm treating here the taxa under the regulations of the ICBN 1994.

14.1. *Cucurbita pepo* L. subsp. *fraterna* (BAILEY) ANDRES, Cucurb. Genet. Coop. Report 10:71 (1987)

Basionym: *C. fraterna* BAILEY, Gentes Herbarum 6(5):288; Fig. 145 (p. 284) (1943).

Synonyms: *C. pepo* var. *fraterna* (BAILEY) FILOV, in KOROVINA O. N. & FURSA T. B. (Eds.) Fl. Cult. Pl. 21: 188 (1982). – *C. pepo* L. subsp. *pepo* var. *fraterna* (BAILEY) FILOV.

14.2. *Cucurbita pepo* L. subsp. *gumala* TEPPNER, subsp. nova

Diagnosis: *C.pepo*, longicaulis, internodiis longis, foliis magnis, lamina ca. 30–45 × 26–38 cm, profunde lobata, floribus magnis, corolla c. 12–13 cm longa, ca. 13–16 cm diametro, ovario 10-costato, fructibus ca. 17–20 cm diametro, costis primariis 10, valde prominentibus, costis secundariis variabilibus, cortice duro ca. 1 cm crasso vel crassiore, seminibus 18–21 × 8–10 mm, testa crassa.

Holotypus: Steiermark, Graz. – Kultiviert im Bot. Garten des Institutes f. Botanik der Universität Graz. – Herkunft der Samen: Guatemala, comm. SCHEIDT (Gießen, Germany), Sept. 1988. – Anbau 1989, Herb. 8. 8. 1989. – leg. H. TEPPNER (GZU). – Isotypi: GZU and herb. TEPPNER.

Icones: h.l. Fig. 3, 24, 25.

Etymology: artificial adjective, abbreviated from Guatemala.

14.3. *Cucurbita pepo* L. subsp. *pepo* var. *styriaca* GREBENŠČIKOV

Basionym: *C.pepo* L. convar. *citrullinina* GREBENŠČIKOV 1949 var. *styriaca* GREBENŠČIKOV, Züchter 20 (7–8): 199, 201 (1950).

Lectotypus, h.l. design.: Kultiviert in Gatersleben: Nr. PEP 515/49. Herkunft: (Dr. LEMPERG) Hatzendorf, Steiermark. 5. 8. 1949 (GAT).

Horticultural group: pumpkin. – Vernacular names: Langtriebiger Steirischer Ölkürbis, Vinous Styrian Oil Pumpkin.

Reference specimens of the land race used for this study: West-Steiermark, Bezirk Deutschlandsberg, Kraubath in der Weststeiermark, Landsorte der Familie FÜRBASS, feldmäßig gebaut. Herb. 15. 8. 1999, leg. F. STEFFAN (GZU and herb. TEPPNER).

14.4. *Cucurbita pepo* L. subsp. *pepo* var. *oleifera* PIETSCH

Basionym: *C. pepo* L. var. *oleifera* PIETSCH, Landwirtschaftl. Jahrb. 91: 388–389 (1942).

Diagnosis: *C. pepo* subsp. *pepo*, brevicaulis, dumosa, internodiis brevibus, seminibus testa tenui.

Neotypus, h.l. design.: Kultiviert in Gatersleben: Nr. PEP 400/47. Herkunft: Prof. TSCHERMARK-SEYSENEGG. 19. 8. 1947 (GAT). (The herbaria GJO, GZU, LI, W, WHB, WU preserve no material. The Institute of Pflanzenbau in Gießen has not answered as yet).

Note: The degree and location of the partial lignification in the testa of the TSCHERMAK oil pumpkin are variable. In the chosen neotype specimen, sclerenchyma (partly) and aerenchyma are lignified in the margin; on the face of the seed, near the chalazal end, only the sclerenchyma is lignified.

Horticultural group: pumpkin. – Vernacular names: TSCHERMAK-Kürbis, TSCHERMAK-Ölkürbis, TSCHERMAK pumpkin.

14.5. *Cucurbita pepo* L. subsp. *pepo* var. *georgica* TEPPNER, var. nova

Diagnosis: *C. pepo* subsp. *pepo,* longicaulis, internodiis longis, fructibus mediocribus, rotundatis, seminibus ca. (15–)17–19(–20) × (6,5–)8–9 mm, testa semitenui, epidermide, hypodermide et sclerenchymate carenti.

Holotypus: Steiermark, Graz. – Kultiviert im Bot. Garten des Institutes f. Botanik der Universität Graz. – Herkunft der Samen: Landsort. Georg. SSR 1985: 1408. Zanavi, Rayon Borzomi, S-Georgien, 20. 09. 85. Inst. Pflanzengenetik u. Kulturpflanzenf., Gatersleben, Genbank PEP 1540/1986. – Herb. Sept. 1995, leg. H. TEPPNER (GZU).

Habitatio: SW. Asia, Georgia, cult.

Icones: h.l. Fig. 35-38.

Horticultural group: pumpkin.

14.6. *Cucurbita pepo* L. subsp. *pepo* var. *flogra* TEPPNER, var. nova

Diagnosis: *C.pepo* subsp. *pepo,* brevicaulis, dumosa, internodiis brevibus, 1-4 cm longis, cirrhis reductis vel absentibus, foliis lamina ca. 30 × 25 cm, modice lobata, fructibus ca. 20–25 × 11–13 cm, ad apicem dilatatis, seminibus ca. 14–17,5 × 6–9 mm, testa tenui, elignosa.

Holotypus: Steiermark, Graz. – Kultiviert in einem Garten in Graz-Gries, Florianigasse. – Herb. 26. 8. 1999; leg. H. TEPPNER (GZU). – Isotypi: GZU and herb. TEPPNER.

Origin: an artificial cross of an ornamental gourd × Styrian Oil Pumpkin × Zucchini.

Icones: h.l. Fig. 28–30, 33.

Etymology: artificial adjective, formed from Florianigasse Graz, the locality of breeding.

Horticultural group: vegetable marrow.

15. Acknowledgements

For carrying out most of the hand pollinations in the last years and for procuring many of the literature not available at our institute, I am most grateful to Mag. Dr. Ursula BROSCH. Mr. Pramodchandra HARVEY produced not only the microtome sections of the seeds but was also very engaged in preparing the English version of this paper. For advice on my studies of the herbals, I thank Hofrat Dr. Hans ZOTTER (Universitätsbibliothek Graz). I am indebted to the office for the international loan service of the Universitätsbibliothek Graz and to all libraries who sent copies. Without this service this paper would not have been possible. I also wish to thank all persons who supplied seed samples (mentioned at the respective places in the text).

Many thanks to all the gardeners who cultivated the plants during the time, in the last years mainly Mr. Franz STIEBER and Mr. Friedrich STEFFAN. I am grateful to Mr. Peter KOSNIK for the enlargements of the fotos of the testa sections.

Furthermore, I wish to express my gratitude to all institutions and persons who supported me in my interest in cucurbits for the past, now nearly, thirty years in one or the other way: Bibliothek der Bundesanstalt für Alpenländische Landwirtschaft

(Gumpenstein, Styria), Bibliothek der Landeskammer für Land- und Forstwirtschaft (Graz), Österreichische Nationalbibliothek (Wien), Bibliothek des Österreichischen Patentamtes (Wien), Universitätsbibliothek Heidelberg (Germany), Dr. Christian ENICHLMAYR (Oberösterreichische Landesbibliothek, Linz), Mrs. Gerlinde FRANK (Universitätsbibliothek Erlangen-Nürnberg, Germany), Dr. Reinhard FRITSCH (Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany), Dr. Anni GAMERITH † (Graz), Dr. Walter GUTERMANN (Institut für Botanik, Wien), Mrs. Waltraud HOLLERER (Graz), Dr. Erich KLEIN (Purgstall bei Graz), Dr. Peter LASSNIG (Wien), Mrs. Penny LICHTENECKER (Wien), Dr. J. Brent LOY (University of New Hampshire, Durham, USA), Dr. Hermann MANITZ (Herbarium HAUSSKNECHT, Jena, Germany), Dr. Ekkehard MÜLLER (former Landw. Versuchszentrum Wies / now Graz), Mr. Heinz NEUNTEUFL (Graz), Prof. Dr. Timothy J. NG (Cucurbit Genetics Cooperative, University of Maryland, USA), Mr. Harry S. PARIS (Ramat Yishay, Israel), Ing. Helmut PELZMANN (Landwirtschaftliches Versuchszentrum Wies, Styria), Dr. Klaus PISTRICK (Herbarium, Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben), Dr. T. PREUSS (Universität für Bodenkultur, Wien), Mrs. Erika SEIDL (Gleisdorf, Styria), Univ.-Doz. Dr. Franz SPETA (Oberösterreichisches Landesmuseum, Linz), Dr. Robert STANGL (Bibliothek, Institut für Botanik, Wien), Mr. Friedrich STEFFAN (Deutschlandsberg, Styria), Dr. Walter TILL (Herbarium, Institut für Botanik, Wien), Dr. Bruno WALLNÖFER (Bot. Abteilung, Naturhist. Museum, Wien), Mrs. Sylvia WANZ (Bibliothek, Abt. Volkskunde, Joanneum Graz), Ass.-Prof. Dr. Wolfgang WETSCHNIG (Institut für Botanik, Graz), Dr. Alicja ZEMANEK (Jagiellonian University, Cracow, Poland), Prof. Dr. Heinrich ZOLLER (Universität Basel, Switzerland), Dr. Hans-Joachim ZÜNDORF (Herbarium HAUSSKNECHT, Jena, Germany).

Microscopic studies were carried out with a Zeiss Photomicroscope III, generously placed at my disposal by the Austrian Research Foundation (Fonds zur Förderung der Wissenschaftlichen Forschung, FWF).

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