Notes on *Lagenaria* and *Cucurbita* (*Cucurbitaceae*) – Review and New Contributions

By

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With 66 Figures

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This paper was prepared in winter 2002/03 as botanical contribution for a book in German language concerning Halloween folklore. Unfortunately, the printing of the book has been delayed; as a consequence of which, the paper was revised, enlarged and rewritten in English. Thus, this is the last and revised version even if it should appear before the German one. The concept of general comprehensibility (not only for botanists) of the first version has not been completely changed in spite of the publication in a botanical journal.

Summary

Teppner H. 2004. Notes on *Lagenaria* and *Cucurbita* (*Cucurbitaceae*) – review and new contributions. – Phyton (Horn, Austria) 44 (2): 245–308, with 66 figures. – English with German summary.

The pollen morphology of *Benincaseae* (tricolporate, reticulate; example *Lagenaria siceraria*, reticulum widened to a perforated tectum) and *Cucurbiteae* (triporate or pantoporate, operculate, echinate; examples *Sicana odorifera* and *Cucurbita pepo*) is discussed. Some characteristics, history and nomenclatural history of *Lagenaria siceraria*, as well as its variability and subspecific differentiation are reviewed. For *Cucurbita*, the nomenclatural history (cucurbits as a homogenous group: Dodonæus 1583 as Pepo, Seringe 1825 as *Cucurbita*; basis for modern species delimitation: Duchesne 1786) and some characteristics are treated. An overview of the genus with special consideration of seed coat characteristics is presented (15 species in 6, hopefully, natural groups). One group (the last) contains *C. ecuador-
ensis, C. moschata, C. argyrosperma and C. pepo; the infraspecific taxonomy of the latter is described (with some emphasis on C. pepo subsp. gumala, which is believed to be related to the evolutionary base of C. pepo subsp. pepo). Five different types of seed coat anatomy of C. pepo are discussed. In Styria the use of pumpkin-seed oil is documented for c. 300 years. Finally, the Vinous Styrian Oil-pumpkin (Cucurbita pepo subsp. pepo var. styriaca), with thin-coated seeds, is treated in respect of its cultivars, history, breeding and importance in Styria (Austria, Europe). All facts indicate the appearance of this segregant in the late 19th century in Western Styria. The term hull-less of plant breeders usually contains not only thin-coated (without any sclerification in the seed coat), but also some more types with different degrees of sclerification in single layers of the seed coat. Two early papers on pumpkin use (Scopoli 1769 and Anonymous 1773) are discussed.

Zusammenfassung


Content

1. Introduction ................................................................. 247
1.1. ............................................................................. 247
1. Introduction

1.1.

The plant family, Cucurbitaceae (the gourd family) is with its c. 120 genera and over 800 species a medium sized, predominantly tropical family. Only few members have been able to adapt themselves to the temperate climate areas (e.g. in Eurasia bryony, Bryonia). The life-form spectrum is very broad; most of them are lianas, which climb (annuals or perennials, herbaceous lianas, also massive, woody lianas for e.g., Alsomitra) with the help of leaf-tendrils (for morphological interpretation comp. Teppner 2000: 3–4). The shoots are popularly referred to as tendrils in German. Tendrils are however the thread-like, sensitive structures, which are capable of catching hold of a support and shorten itself spirally. Moreover tendril-less perennial herbaceous plants (for e.g., squirting cucumber, Ecballium), sub-shrubs, leafless thorny shrubs (the nara-bush from the
Namib, *Acanthosicyos horridus*), leaf- or stem-succulent desert plants, even a thick-stemmed tree (*Dendrosicyos* on the Socotra Island), and many others also exist.

The family as such is part of the *Parietales* or *Violales* in classical systems. In molecular systematics an order *Cucurbitales* (with *Anisophylleaceae*, *Corynocarpaceae*, *Coriariaceae*, *Cucurbitaceae*, *Begoniaceae*, *Tetramelaceae* and *Datiscaceae*), which is believed to be the sister group of *Fagales*, is currently used (comp. for e.g., *Matthews & Endress 2004*).

This paper focuses on botanical facts (morphology, anatomy, systematics etc.) and history of the two title genera while Loy 2004 has published a summary on agricultural traits (physiology, ecology, growth, productivity, yield, quality etc.) for the three most important domesticated *Cucurbita* species.

In the following chapters the pre-Linnean plant names are written in standard letters, scientific plant names *Linne 1753* onwards are set in italics.

### 1.2. Subfamilies

The smaller subfamily (*Zanonioideae*, c. 80 species; styles free, tendril bearers sensitive, with tendril-function, i.e. ability of coiling) is absolutely almost tropical. Readers must be remembering *Alsomitra macrocarpa* (= *Zanonia m.*, *Macrozanonia m.*) of the Southeast Asian Islands, from the first part of the David *Attenborough’s TV-serial “The Private Life of Plants”*, where one of the slightly sickle-formed, c. 10–16 cm wide, thin skinned seeds is shown as it magnificently glides from the canopy of the rainforest. For generations of technicians the seeds served as a model and inspiration for different constructions, e.g. the first air-gliders. *Gynostemma pentaphyllum* (*Jiaogulan, the Chinese immortality herb*) from the mountains of S. China, has gained popularity in the western world, because of its alleged effects on the immune system, the blood circulation etc. It has found so much attention lately, that it is even included in the German cultivar list of medicinal plants (Anonymous 2002: 67–68).

The by far much bigger subfamily, *Cucurbitoideae* [c. 740 species; styles united; tendril bearers not sensitive, without tendril function (only exception: Tribe *Joliffieae*)] can be divided, according to natural relationships, in tribes (*Jeffrey 1990*). Only three of the seven will be mentioned here and members only of two would be discussed in detail.

### 1.3. Tribes and Pollen Characteristics

In the biggest tribe, *Melothrieae* (34 genera, 250 species, *Jeffrey 1990: 457*) (in the traditional sense, i.e., without taking amino acids and
DNA characteristics into consideration) we find the genus *Cucumis* with the table cucumbers (*Cucumis sativus*) and melons (*Cucumis melo*).

What is called „Kürbis“ in German, concerns two different tribes. Although with proper German names „Kürbis“ (*Cucurbita*; engl. pumpkin, squash and ornamental gourds; together: cucurbits) and „Flaschenkürbis“ (*Lagenaria*; engl. bottle gourd), they are often mixed up by laymen. In the tribe Benincaseae (17 genera, 85 species, JEFFREY 1990: 457) belong (without taking the DNA characteristics into consideration) among others, *Lagenaria* (bottle gourd), *Benincasa* (wax gourd), *Citrullus* (with *C. vulgaris*, water melon), *Acanthosicyos* (with *A. horridus*, naras) and – more isolated – *Ecballium* (squirtling cucumber) and *Bryonia* (bryony), remotely isolated also *Luffa* (loofah, sponge gourd). With the exception of some species of *Luffa* and *Lagenaria*, all the genera are native to the Old World.

In the Cucurbiteae belong 13 genera (110 species, JEFFREY 1990: 459), e.g., *Cucurbita* (*Cucurbit*) itself and *Sicana* (with *S. odorifera*, Casabanana, Jamelão, cultivated in the neotropics). With the exception of one of the species of *Cayaponia* (*C. africana* in tropical West Africa and in Mada-

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Fig. 2. *Cucurbita pepo* subsp. *gumala*. Left: general view of a pollen grain with three of the total 10 apertures (pores). Above right: Pollen grain wall fractured, on the nexine big spines and in between dense standing, short spines. Below right: detail of a pore, the exine lid with two big spines sitting on the vaulted intine papilla. – Seeds from Guatemala, 1988, Scheidt, Gießen. – Bot. G. Inst. Bot. Univ. Graz, 15. 8. 2002. – The scale bar on the left equals to 50 µm, the both on the right 10 µm. – Preparation and photos E. Stabentheiner, U. Brosch & G. Prenner.

gascar), the whole tribe is endemic to the New World. Since outward, easily visible, morphological characteristics are under great pressure through adaptation and selection, it is very difficult to find simple and really continuous differentiating characteristics for these two related tribes. But the characteristic pollen viz., the outer wall of the pollen grains, has proved to be a marvellous tool to differentiate these two tribes (Marticorena 1963 and the excellently illustrated work by Khunwasi 1998). Owing to the eternal muddling up of the two genera, it is demonstrated here, that *Lagenaria* and *Cucurbita* are not at all related to each other.

Besides the unstructured inner part of the sporoderm (nexine), the tribe *Cucurbitaceae* has an outer ornamented layer, the sexine, with sculptures in form of single structures: a) big spines, rarely more or less cylindrical structures and b) minute spines, baculae or clavae, which more or less cover the spaces in between (Fig. 2). Apertures are developed as pores, which are closed by an exine lid (with 1–5 big spines). Three (rarely up to 5) pores are distributed regularly around the equatorial plane of the pollen grain [triporate (Fig. 1) to pentaporate; Abrona, Calycophysum, Cayaponia (partly), Cionosicyos, Sicana, Tecunumania]. The pores can also be distributed regularly over the surface of the pollen grain [pantoporate (Fig. 2);
Fig. 3. *Lagenaria siceraria* subsp. *asiatica* 'Kleine Pilgerflasche' ('Small Pilgrim Bottle'). Left two pollen grains with three apertures (colporate) in the equatorial plane. Above polar view, below approximate equatorial view, the pole below, just about visible. – Above right: detail of the surface of the pollen grain with reticulations (network structure), which let only small perforations open. Below right: pollen grain wall fractured, the columellae on the homogenous nexine support the perforated “roof”. – Origin: Tokyo Metropol. medic. Plant Garden 1999: 312 (as *L. leucantha* var. *microcarpa*). – Bot. G. Inst. Bot. Univ. Graz, 13. 8. 2002. – The scale bar on the left equals to 20 μm, above right 5 μm, below right 2 μm. – Preparation and photos E. STABENTHEINER, U. BROSCH & G. PRENNER.

*Cayaponia* (partly), *Cucurbita, Polyclathra, Schizocarpum*. Three apertures around the equator is surely a plesiomorphic character. Moreover the pollen grains are huge, with c. 70–230 μm diameter. The genus *Cucurbita* has pollen grains of 120–200 μm diameter. The ontogeny of the pollen grain wall is well depicted in NEPI & al. 1995 (for e.g., the big spines laid down first, the smaller later and originate from another layer, apertures laid down under spines, etc.).

In the *Benincaseae*, the more or less baculate structures of the sexine are arranged in a grid and are widened at the distal end, so that they fuse there and thus hold up a grid-like roof (sexine reticulate). The meshes can also be broader distally and thus the holes in the roof are smaller than the spaces between the rows of columellae (sexine tectate). The latter is the case for e.g., in *Lagenaria* (Fig. 3). This is a totally different architecture than in *Cucurbiteae*! The pollen grains are tricolporate (Fig. 3). The pollen grains are clearly smaller, and lay in the mean average of the family and have a diameter of c. 40–70 μm usually. *Lagenaria* has pollen grains of diameter c. 60–80 μm, whereas *Luffa* has up to 120 μm.
2. Bottle Gourd or Calabash, *Lagenaria siceraria*  
(Molina) Standley  
(*L. vulgaris* Ser., *Cucurbita lagenaria* L., *C. leucantha* Duch.)

The genus *Lagenaria* covers five perennial wild species in tropical Africa (*L. sphaerica* also in Madagascar and the Comoro Islands) – and in the whole tropics *L. siceraria*, since millenia a widely cultivated annual.

2.1. Characteristics

Some of the important characteristics of *Lagenaria siceraria* are: soft-haired leaves, additionally covered with glandular hairs, foetid, on both sides of the border between the leaf blade and the petiole a nectary, sometimes two [short and thick-stalked bowl with marginal-bulge; the nectar lures mainly ants (Fig. 5) and wasps], tendril bearers with two tendrils (Fig. 4). Male flowers with cylindrical to conical receptacle, on the border of which the sepals and the white, free petals are inserted, whereas the three stamens sit nearly on the base and just about reach the throat with their tips. Female flowers have a short receptacle, which overtops the inferior ovary slightly and bears three small rudimentary stamens. The

![Fig. 4](image1)
![Fig. 5](image2)
![Fig. 6](image3)


Fig. 5. *L. siceraria* subsp. *siceraria* (from Melut, S. Sudan), ant at a nectary at the leaf blade base. – Cult. Graz, Florianig., 11. 6. 1983.

flowers open, depending on the cultivars, around late afternoon, evening or in the early hours of the night and are pollinated by hawkmoths (HEISER 1997) and moths like Autographa gamma (GLADIS 2002: 61, 63) (or by some facultative visitors, e.g. hummingbirds, syrphid flies and Apis, in the evening or in the morning). They whither in the course of the next morning. In the long peduncled, male flowers nectar is secreted at the base, whereas the female ones are deceptive flowers without nectar. In the androecium, the explosive hairs along the thecae ejaculate dark mucilage which apparently functions as an accessory pollen adhesive (at least during hand pollination this slime is always transferred to the stigma). The papillose stigma is covered by stringy mucilage. The ripe fruits show a hard woody fruit wall and are very variable as to their size and structure. The seeds (Fig. 8) are flat, more or less rectangular to narrow trapezidal, whitish to dark brown, at the distal end truncate or emarginate to two-horned, towards the attachment point narrowed and along the sides with more or less marked, marginal- and/or submarginal-bulges.

Elongate bottle gourds (Herkuleskeulen, Hercules’-clubs) and related cultivars with still thinner, nearly cylindrical fruits can reach a length of 1–2 m and are known from the local press as „Riesengurken“ [giant cucumbers] (for e.g., Kleine Zeitung, Graz, 30. 8. 1983 p. 11, 26. 8. 1997 p. 48, 9. 9. 2000 p. 30) and once even as „Neuguinea-Bohnen“ [New Guinea beans] (Kleine Zeitung, Graz, 6. 4. 1996 p. 48). A dipper gourd (‘Weinherber’) type (with a long, thin proximal part and at the floral end bellied) was registered in the Guinness Book of World Records 1988: 72 for its length of 2.375 m. Round fruits are to be found from the size of a fist to a diameter of 50 cm. The first illustration in a herbal (BRUNFELS 1536: 188) shows one of the common fruit forms, the ‘pilgrim bottle’ (Pilgerflasche, Pilgrimsflasche) (Fig. 4). An insight in the diversity of the cultivars in Internet is possible at for e.g., http://www.cucurbit.org/family.html. The cultivar list from DECKER-WALTERS 1999 alone lists 79 cultivars.

2.2. History

In PLINIUS XIX, 69–74 (KÖNIG & al. 1996: 50–55), through the Middle Ages, for e.g., Capitulare de villis Chap. 70 (BRANDSCH 1990: 94) and in the famous, often cited poem from WALAHFRIED STRABO (origin between 842 and 849; PAYNE & BLUNT 1966: 34–37, STOFFLER 1996: 61–64, 130–133) the plant is known as Cucurbita. HILDEGARD VON BINGEN uses the name Cucurbita and Kurbesa, ALBERTUS MAGNUS Cucurbita (comp. FISCHER-BENZON 1894: 91). Even in famous scripts with absolutely beautiful and interesting illustrations, the species in question goes under the name of Cucurbita, for e.g., Historia Plantarum fol. 83r (second half of the 14th century; along with the prevalent curved clubs, four more fruit forms; here also the names carabassa and zucha!) (PANINI & CHIERICI 2001), Tacuinum Sanitatis in Medi-
cina fol. 22v (end of the 14th century; short, fat club forms) (Unterkircher 1967: 50) and Le Livre des Simples Médecines fol. 122r (end of the 15th century; short clubs and pilgrim bottle) (Algas & al. 2001). In the herbals of the 16th century, for e.g., Brunfels 1536: 188, 189, Bock 1539: 71v–72r, 1546: 312r–313r, Fuchs 1542: 367–371 (three cultivars illustrated), 1543: 376–380, Cap. CXXXVII, plates CCVII–CCIX, Dodonaeus 1583: 657–658, Clusius 1583 in Hunger 1927: 425, the name Cucurbita was generally reserved for the bottle gourd, which was named in German mostly as Kürbis, Kürbß, Kürbs or Kurbs; as Spanish names Calabazza or Calabassa are quoted, which were adopted in German and other languages as well. For the fruits introduced after the discovery of the Americas, which were used as vegetables, we find in the above mentioned herbals names like Cucumer, Indianisch öpfel, Summer öpfel, Zucco marin, Plutzer (Dodonaeus 1583: 656), Melopepo, Pepo and others. Under the populace the name Kürbs or Kürbis or similar word formations, in Italy Zucha or zucca, all originally used for Lagenaria, swapped fast over to the yellow-flowered American, which soon ousted the former at least from the kitchen. This name transfer or the problems concerning proper systematic attribution due to the lacking knowledge, mirrors itself in the science as well. The forebodings of which are to be seen for e.g., in the otherwise precise presentation by Dodonaeus 1583: 658–659, whose Cucurbita sylvestris should be having yellow flowers according to the illustrated floral form and thus be an ornamental gourd in the present sense (as interpreted in Teppner 2000: 11, 13). The problems started partly in the mid-16th century already. Eventually Tabernaemontanus 1591: 181–183 united three bottle gourds and three cucurbit-sorts under Cucurbita, while the other cucurbit-sorts are to be found under the names Pepo and Melopepo. Camerarius 1586: 292–293 encompasses both groups under Cucurbita. Bauhin 1671: 311–313 describes cucurbits as Pepo, but others as Cucurbita; on the other hand in Dalechamps 1587: 614–619 and Bauhin & Cherler 1651: 213–231 all bottle gourds and cucurbits are aggregated under Cucurbita. Not everybody followed them. Tournefort 1700: 305–306, plates 33–34, who laid much stress on circumscribing genera on the basis of floral, fruit and seed characters and thus laid down important fundamentals of Botany, stipulated the name Cucurbita clearly and precisely for the bottle gourds and moved the yellow-flowered cucurbits in the genera Pepo and Melopepo. In Morison 1715: Tab. 5, the bottle gourds are clearly attributed to Cucurbita, three cultivars (each with good illustrations of the seeds) are presented. Linné 1753: 1010–1011, in his Species Plantarum, accepts only one genus Cucurbita and the bottle gourd as Cucurbita lagenaria tops the list, three yellow-flowered cucurbits follow it, which he perceives as three different species (today all belonging to the species Cucurbita pepo) and at the tail end even a watermelon! This approach was intolerable for some, thus the very next year
Miller 1754, on the basis of Tournefort, differentiates Cucurbita, Pepo, and Melopepo. This opus was hardly heeded by anybody, most of the botanists followed Linné, for e.g., even Willdenow 1805: 606–610. Thus Seringe 1825 faced the same problems as he started his preparatory work for his monography of the gourd family, i.e., to separate unrelated species and to divide the genus Cucurbita L. He followed the prevailing conventions, to refer cucurbits as Cucurbita (maybe influenced through Linné 1754: 441, Genera Plantarum, where some points of description direct to the effect that Linné could have had mainly the yellow-flowered species in mind ?) and not the original meaning of the name: He separated the bottle gourd and the water melon from the genus Cucurbita L. and created for the former the separate genus Lagenaria. In the same direction goes the proposal of Hitchcock & Green 1929: 190, to fix C. pepo as type for the genus Cucurbita L. A contrary proposal to pick C. lagenaria as the type was made by Britton & Brown 1913: 291, whereby the name Cucurbita would have remained for the bottle gourd and the cucurbits would have to be put in the genus Pepo Miller. To reach stability at last, Nicolson 1992: 562 and Jarvis & al. 1993: 4 proposed C. pepo as lectotype for Cucurbita once more; even if the proceeding is not finished, the decision in this direction should be sure. This is the only sensible way, because for practical reasons it is completely impossible to turn the whole modern nomenclature of cucurbits upside down.

2.3. Variability

Big problems were caused by the wide distribution of Lagenaria siceraria in context of its close contact as a crop plant with the humans. Many speculations as to its transoceanic dispersal through humans have arisen (comp. for e.g., Pickersgill & Bunting 1969, Whitaker 1971, Richardson 1972, Heiser 1979: 99–117). It is through the meritorious work of Kobiakova 1930 and Heiser 1973a, 1979: 92–96, that the many cultivars can be confined to two groups, which were treated as subspecies and can be up to some extent separated from each other by the following characteristics (Heiser 1973a, with additions):

<table>
<thead>
<tr>
<th></th>
<th>Lagenaria siceraria subsp. siceraria</th>
<th>Lagenaria siceraria subsp. asiatica (Kobiak.) Heiser</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves</td>
<td>with smooth or crenate margins, not lobed or with round lobes</td>
<td>serrate margins, sharply 3–5 lobed with pointed, triangular lobes</td>
</tr>
<tr>
<td>Flowers</td>
<td>small to medium, male flowers usually with up to 7 cm diameter</td>
<td>big, male flowers with 7–12 cm diameter</td>
</tr>
<tr>
<td>Sepals of the male flowers</td>
<td>short and broad (2–10 mm long)</td>
<td>longer and narrower (6–20 mm long)</td>
</tr>
<tr>
<td>Seeds</td>
<td>mostly dark, lesser than 2 x long as broad</td>
<td>mostly pale, more than 2 x long as broad</td>
</tr>
<tr>
<td>Distribution</td>
<td>basically in Africa and America</td>
<td>basically in Asia and W. Pacific</td>
</tr>
</tbody>
</table>
The samples from New Guinea, especially the penis-sheaths bottle gourds (Fig. 6), presented a dilemma, which could not be classified definitively (Heiser 1973b). The first DNA analyses (Decker-Walters & al. 2001) have confirmed the classification in two groups and yield, that the New Guinea cultivars are to be assigned to the Asian group. These both subspecies have spread and established themselves in the tropics long before the dispersal of humans. Thus, each culture on different continents had different wild material at their disposal for domestication and thus it does not need enterprising long-distance transport hypotheses; Richardson 1972 came to the same conclusion. The appearance has surely changed secondarily through the exchange between different cultures, especially in the last two centuries through easier transport possibilities and international seed trade.

The difference between both the groups according to its morphological characters alone is not easy in the practice, which is proved by two samples from S. Sudan (Melut, January 1983, leg. H. Neumeister sen.; March 1983, leg. H. Neumeister jun.), apparently subsp. siceraria, which are also interesting due to its differential ways of drying of the pulp (Fig. 7). In the fruit with narrowed ends (broad lemon formed), the placentas dry evenly and remain in contact with the fruit wall. In the totally round fruit, the pulp detaches itself while drying from the fruit wall and lies (with the enclosed seeds) free in the fruit. The form with the lemon-formed fruits have seeds with length-breadth ratio of about 2 (Fig. 8 below) and short sepals, thus seemingly African, while big male flowers (partly up to 9 cm in diameter) and sharp three-lobed serrate leaves point much more in the direc-

Fig. 7. *Lagenaria siceraria* subsp. *siceraria*. Fruits with ripe, firmly bonded (left) and loose placentas (right). – Origin: S. Sudan, Melut, 1983, H. Neumeister sen. & jun.

Fig. 8. *L. siceraria* subsp. *siceraria*. Seeds from the Fig. 7 fruits, with firmly bonded (below) and loose (above) placentas. – 13. 6. 1983.
tion of *asiatica*. The plant with loose placenta had in average narrower (L:B = 1.63–2.22) seeds (Fig. 8 above) in contrast to the flower size (with up to 7 cm diameter) and the leaf form (rounded to shallow lobes, short teeth), which are typically African.

2.4. Use

To name all the uses from vessels of all kinds, a broad spectrum of music instruments and ornaments to masks, buoys, water toys etc. etc. would extend the scope of this publication over its limits. I would recommend the readers Heiser 1979, who has devoted half a book to the bottle gourd. A beautiful folkloristic work on the bottle gourd in Hungary is written by Gunda 1982. On its role in legends, mythology, religion etc. comp. Heiser 1979: 202–228. Two more legends, viz., the survival through the Flood in a bottle gourd and the fast growing shoots as a Jacob’s ladder are sensitively renarrated in Marr & Mei 2001 and Schnebeli-Graf 1995: 69–71 respectively.

It has been often doubted if *Lagenaria siceraria* is indigenous to Latin America (for e.g., de Candolle 1884: 309). From the European point of view and in view of the Near East it has been often postulated that cultivation of grain is a prerequisite for the settling down of the humans and the building of settlements. Therefore I would like to mention the situation of the Peruvian coastal deserts. The local indigenous people there exploited the sea organisms (fish, shellfish, coastal birds, sea lions, seaweeds etc.) for nutrition and lived from c. 2500 B.C. in villages. They practised agriculture and under these circumstances technical plants like cotton (nets, clothes) and bottle gourds (net-floats, vessels) were vitally important plants (Lanning 1965, Pickersgill 1969, Pozorski 1979). The oldest remains from Mexico originate from around the time 4500–4000 B.C. (Prov. Tamaulipas, interpreted as domesticated; Smith 1997b: 372, 373). The oldest findings in S. America (Pikimachay Cave, Ayacucho, S. Peru; Richardson 1972: 267) are clearly older, but since latest datings are not accessible to me, I abstain from naming any numbers.

*Lagenaria siceraria*, before it succumbed to the rivalry of the cucurbits, was cultivated in Central Europe for consumption as well. Pertinent references are to be found already in Plinius (König & al. 1996: 53), who is of the opinion that the long and thinner fruited cultivars are better. With the modern „back to the roots” trends, *Lagenaria* has found its way back to the kitchen (not only fruits, but also leaves and young shoots) and seeds are offered in the trade, for e.g., the cultivar ‘Italian (Edible)’ from the company Willhite, Texas; www.willhite.com; comp. also Gugenhan 2002: 42 for other source of supplies. As a vegetable, only young fruits or only the pulp from the more developed fruits can be considered – and very important, the plants must be free from bitter compounds (careful
taste test!). Strongly poisonous compounds, the cucurbitacins, typical for *Cucurbitaceae*, are to be found in many cultivars of *Lagenaria*. Bitter cultivars are considered often as very poisonous, not only the fruit flesh but also the seeds. According to Lewis & Elvin-Lewis 1977: 36, two children died in Cuba allegedly by the treatment of round worms with *Lagenaria*-pulp. Therefore, caution is recommended, even while scratching dry fruits (do not inhale the dust), and also if using the dried fruits as bottles.

3. Cucurbit, *Cucurbita* Linne emendavit Seringe

Today it is a matter of course, at least for the professional, and at least then, when the whole plant, i.e., with leaves, flowers, fruits and seeds is present, that each cultivar of our cultivated *Cucurbitaceae* can be attributed to a species and that they, with the help of common characters, can be classified to a genus and they in turn to tribes. It is often unfortunately overseen, that it was a stony path, to reach this collection of characters based on a mountain of knowledge, and this was especially difficult in the case of the cultivated *Cucurbitaceae*. From the first herbals to a passable, stable nomenclature and somewhat reasonable grouping based on true relationships, more than 300 years of hard work were required.

3.1. History

The Old World cucumber (Cucumern, Cucumis, Gurchen), melons (Melo, Melopepo, Pepo, Melaun, Melonen, Pfeiden, Pfeben), water melons (Anguria, Citrullen, Melo ?, Pepo ?) and bottle gourds are known in Europe since antiquity. The newcomers from America were treated (as Türckisch Cucumer and Meer Cucumer) by Fuchs 1542: 702–704, plates 697–701, 1543: 692–699, Cap. CCLXVII, plates CCCXCVIII–CCCCII along with cucumbers, melons and water melons in the same chapter (“Von Cucumern”). This unification with the cucumbers was strongly opposed by Bock 1546: 316v and he delimits the cucurbits as Indianisch öpffel from the cucumbers. Furthermore in the herbals of the 16th century, mainly the names Melopepo and Pepo, which were originally used for melons (to some extent also for water melons), were taken up for the cucurbits (and both mixed and exchanged). For e.g., Dodonaeus 1583: 654–656 describes cucurbits, already clearly demarcated, in the chapter Pepo.

On the other hand the eye for the differences between bottle gourds and cucurbits began to darken. (Gessner c. 1560, was most probably one of the earliest, who used the name Cucurbita of the bottle gourds for the cucurbits as well). Around the end of 16th century and early 17th century, a part of the cucurbits, and finally all, were united with the bottle gourds. This regression was facilitated by an other regression: In the herbals, first of all, at least partly the origin of the Cucurbits was given correctly, for e.g., vague and only partially incorrect in Bock 1546: 316v: „Dann war ists
It is said, that they came from West Indies to Italy: that is why they are called by many as Indian". Due to the extremely rapid spread of the cucurbits in the agriculture in different parts of the Old World, they were soon omnipresent. Moreover due to the confusion of West Indies and India, the belief of the Old World origin of the cucurbits emerged (for e.g., WILLDENOW 1805: 609, NAUDIN 1856: 15, 53); which also resulted in the erroneous obsession of searching the cucurbits in the ancient texts, for e.g., PLINIUS. This dogged belief persisted or one declared simply „origin unknown“, so that WITTMACK 1888 and even WHITAKER 1947 had to write essays to prove the New World origin of the cultivated cucurbits.

Although TOURNEFORT 1700: 305–306, plates 33–34 had demarcated the cucurbits from other Cucurbitaceae well, he splitted it into two genera, Pepo and Melopepo. This looks at the first sight quite well, since Pepo has seeds with marginal-bulge (a furrow is present between the marginal-bulge and surface of the seed) (for e.g., in our Cucurbita pepo) and Melopepo without such furrow (today Cucurbita maxima). But on closer examination it turns out that even the Patissons, which surely belong to C. pepo, are listed under Melopepo. Furthermore, the unsound character of number of placentas is used for differentiation (Pepo 3, Melopepo 5). It would be interesting to know if LINNE 1753: 1010 noticed these discrepancies, afterall he united in his opus, which serves as the outset for the present scientific, botanical nomenclature, four TOURNEFORT'S genera under the name Cucurbita and thus didn’t have much luck with them (comp. above the chap. 2.2. on Lagenaria). So it was left to SERINGE 1825 to demarcate the cucurbits as a homogenous group (an inference, which we principally know already from DODONAEUS 1583 under the name Pepo), now under the name Cucurbita, in that, that he assigned the parts of the LINNE'S genus, not belonging there, to other genera.

Other than the genus demarcation, there was still another hitch: the enormous variability of the cucurbits, particularly of the fruits and especially in Cucurbita pepo. When one puts for e.g., the Patisson cucurbit near a big Pumpkin and furthermore one considers the different growth forms (bush form versus vinous), one can hardly understand, that they belong to the one and the same species; it seems to be a matter of course, that all those have received different names. On the other hand, often was the case that, when propagated through seeds, a completely different type arose.
than the one from which the seeds were harvested. What on earth is going
on with the god-created species? Kölreuter 1766 (cited in Teppner 2000: 14–15) described for the first time a prearranged cucurbit cross. He found
fertile progeny of intermediate form and thus concluded that many of the
cucurbits with different fruit forms belong to one and the same species. He
used the character of crossability as a criterium for species delimitation in
his work and thus was far ahead of his times.

The French amateur botanist and gardener Antoine Nicolas Duchesne
wanted to bring order in this chaos and undertook the task to cultivate,
from 1768 to 1774, about hundred cucurbit seed samples, to cross them
manually and to check the progeny. The results were put on record as
water colours and to a smaller extent in sketches (a total of 615 fruits on
258 sheets; now in the Museum National d’Histoire Naturelle, Paris) (Paris
2000 a, b, c). Although Duchesne, like Linne, included in Cucurbita the
bottle gourds and water melons, he managed to split the cucurbits di-
versity in three groups. Whereupon the fertile progeny were to be got only
within the group and not in inter-groups. Thus he could differentiate for
the first time Cucurbita maxima and C. moschata from C. pepo and thus
laid down the foundation for the modern cucurbit systematics. The results
were summarised by Duchesne for the encyclopaedia from Lamarck and
then published as an offprint, as 46-paged script, which remained nearly
unknown and is now a very rare document (Duchesne 1786a, after Paris
2000b). For the famous encyclopaedia the same text from the same block
was used nearly ad verbatim (Duchesne 1786b), but unfortunately not
completely. The most central theme, the taxonomy and the validation of
the taxa, was watered down by Lamarck. Maybe that is the reason why
Duchesne’s outstanding results were hardly accepted and only acknow-
ledged through Naudin 1856. Outstanding successive works like Alefeld
1866: 212–227, Cogniaux 1881: 542–547, Harz 1885: 794–824 and others
have used it as a fundament and thus contributed to the dissemination of
new knowledge.

3.2. Characteristics

The genus Cucurbita consists of c. 15 species, whereof 10 are wild
species and five cultivated species, from which the related wild species are
only partly known. The plants are perennial (some of the wild species, with
fleshy tap root tubers as perennation organs) or annuals, with several ten-
drils per tendril bearer (in wild species sometime only 1–2), with one
flower each (male or female) per leaf axil. Flowers on the base with a bowl-
or cup-shaped structure (the receptacle; in male flowers of cultivated spe-
cies c. 1 cm high), on whose rim the sepals and petals sit, flowers more or
less big, in cultivated species up to 10–13 cm long and up to 20(–22) cm in
diameter. Corolla yellow, funnel- to bell shaped, petals about till half
its length united, with superimposed tips, free lobes have rolled or folded up margins in the bud. Stamens of the male flowers inserted at the base of the receptacle, three, filaments totally or partially free (the slits between them serve as an entrance to the nectar!), anthers united back-to-back. Explosive hairs scattered along the thecae, function not explicitly clear; for a summary on anther hairs see Vogel 1981. The base of the receptacle (within the stamens) lined with a nectary, which ends with a collar-formed raised margin. In the female flowers, the receptacle extends over the inferior ovary only slightly. The nectary surrounds the base of the style as a ring bulge; the outer adjacent, thin margin is the reduced rest of the stamens. Stigma papillose, dry. The inferior ovary (Fig. 24, 26) is made of (5-)3 carpels and gives a hint of the fruit to come. In the course of early ovary ontogeny three septa grow from the carpel borders on the inner side of the ovary wall, the placentas (according to Leins & Galle 1972 and Leins 2000: 110–112 they are in fact folded carpel walls), in the hollow space towards the centre, divide themselves just before the centre, turn around and grow towards the outside, turn again towards the base (insertion) of the placenta; here finally the ovules are developed. The seeds develop then into the placentas (Fig. 50, 51), so that they are enclosed in placenta-pockets. In America pollination is achieved by the indigenous, solitary, oligolectic squash bees (Peponapis and Xenoglossa, e.g., Hurd & al. 1971, Tepedino 1981), otherwise by facultative pollinators (Apis and bumblebees). The fruits, usually named as a pepo, are armour berries, i.e., the outer part of the fruit wall is hard, the inner part and the placentas are, at least in the cultivars, in the ripe stage fleshy. The fruits of the wild species and a part of the ornamentals are bitter (due to cucurbitacins, comp. Lagenaria, end of the chap. 2.4., or for e.g., Teuscher & Lindequist 1987: 146–155, Hegnauer 1964: 611–616, 675, 1989: 346–368, Lavie & Glotter 1971, Tallamy & Kirschik 1989, Metcalf & Rhodes 1990). The seeds are flat, oval and mostly with more or less pronounced marginal-bulge.

In certain species peduncles and fruits are ribbed, whereby the ribs of the peduncle continue as the ribs of the fruit. Primary ribs lie under the calyx lobes or over the vascular bundles supplying the calyx (Fig. 64). Secondary ribs alternating with the primary ones, are often weaker and lie under the corolla lobes or over the vascular bundles supplying the corolla lobes. As an encompassing term for both types the term main-ribs is applicable, which is of interest especially for the cases when all 10 ribs are developed in a similar manner (Fig. 50). Interstitial ribs lie between a primary and a secondary rib each and are often doubled (Fig. 50). In the absence of main ribs interstitial ribs lie on the fruit between the furrows continuing the peduncle ribs (Fig. 20). Interestingly in striped fruits the inheritance of the stripe colour is independent from the characters of main (longitudinal) zone and interstitial zone (Paris 2002).
3.3. Classification

The species can be, on the basis of the presumed relationships, grouped as follows (primarily according to LIRA & al. 1995, WILSON & al. 1992 and PUCHALSKI & ROBINSON 1990 as well as on the basis of the anatomy of the seed coat). The most important cultivated species in Europe are C. pepo, C. maxima and C. moschata; C. argyrosperma and C. ficifolia are less relevant. The seed coat anatomy was investigated with the help of unstained hand sections mounted in glycerine.

Archaeological dating in the following lines refer to macro-remains. With the help of microfossils (phytoliths = silica bodies, which are built up in specific forms in different plant tissues), the history of the cucurbits can be traced back longer, especially in warm-humid climatic-regions with bad conservation conditions for macro-remains (PIPERNO 1989, 2000, PIPERNO & STOTHERT 2003).

3.3.1. Group 1

Perennials with tap root tubers (including the whole hypocotyl) and adventitious root tubers (Rüben), tendril bearers short to reduced, tendril tips a little dilated and secretory at the concave side when the tendril is strongly coiled, seed margin simple, without bulges (Fig. 12, 13).

*C. digitata* A. Gray: leaf lamina very deeply, nearly till the basis incised into narrow parts, tendril bearers very short, 3–5 short tendrils, fruits roundish, c. 6–8 cm, seeds 8–11 mm long, whitish, epidermis as in *C. palmata* (SINGH & DATHAN 1972: 34 Fig. 2L, 40 Fig. 5G, 5H, 43 Fig. 7H). - SE. USA (S. California, New Mexico, Arizona) till NW. Mexico (Baja California, Sonora, Chihuahua), deserts.

*C. palmata* S. Watson (*C. californica* Torrey ex S. Watson): leaf up to the middle incised, the resulting parts triangular, tendril bearer short to reduced, (1–) 2–5 short tendrils (Fig. 11), fruits roundish to somewhat flattened, c. 6–8 cm, seeds 8–11 long, whitish, with placenta epidermis and thin walled epidermis cells which collapse despite sclerified rods (Fig. 12, 13). – SE. USA, NW. Mexico (Baja California), arid bush and deserts.

*C. cordata* S. Watson (*C. cylindrata* L. H. Bailey): leaf deeply incised, the resulting parts lobed, lobes rounded, tendril bearer reduced, 3–5 short tendrils, fruits roundish, c. 6–8 cm, seeds 8–11 mm long, whitish, epidermis apparently as in *C. palmata* (SINGH & DATHAN 1972: 40 Fig. 5C, 43 Fig. 7G). – Mexico (Baja California), deserts.

3.3.2. Group 2

Perennials with tap root tubers (including the whole hypocotyl) and adventitious root tubers (Rüben), tendril bearers well developed, tendrils not secretory.


*C. foetidissima* H.B.K. (Buffalo gourd, Büffel-Kürbis): fleshy tap roots till $2 \times 0.25$ m !, leaf lamina erect, long triangular, unlobed to shallowly lobed, at the base more or less truncate (Fig. 14, 15), silver-grey haired (densely covered by short, soft hairs), 3–7 and more tendrils per tendril bearer, fruits (Fig. 15) round, 5–8 cm, flesh white, fibrous, bitter, seeds 8–12 mm long, bright ochre-coloured, with placenta epidermis and thin walled epidermis cells which collapse despite sclerified rods, with an indistinct marginal-bulge and faint furrows, the epidermis cells elongated inside the furrows (submarginal-bulge), forming marginal-wings, which lay tightly adjacent to the marginal-bulges and somewhat overtopping it,
touching themselves and giving the seed margin an irregular, sharp rim (Fig. 16, 17). – Widely distributed in the SE. USA and in central Mexico up to the outskirts of Mexico City; arid to desert regions. – At the moment under investigation for plant breeding for its starch-containing fleshy tap roots and the oil- and protein-containing seeds (Gathman & Bemis 1990). To be seen in summer in the temperate house of the Botanic Garden of the Institute of Botany (now Plant Sciences) of the University of Graz.

*C. galeottii* Cogniaux 1881: 551 from Oaxaca, Mexico, is interpreted as a synonym of *C. pepo* usually. But from the description this hardly seems to be probable. Thanks to the help of the staff of the herbarium of the National Botanic Garden of Belgium, I had the opportunity to have a look at images of the type specimens. Thus, Bailey 1943: 309, 312 is correct especially concerning the narrow-triangular terminal lobe and the truncate base of the leaf. Therefore new investigations are necessary, if *C. galeottii* can be *C. foetidissima* or a very closely related taxon.

*C. pedatifolia* L. H. Bailey: leaf very deeply lobed, with narrow lobes, white speckled, 3–4 or less tendrils per bearer, fruits spheroidal, 5–8 cm, seeds 10–12 mm long. – C. Mexico; arid regions over 1300 m.

*C. radicans* Naubin: leaf slightly to deeply 3–5 lobed, with broad triangular-pointed lobes, 1–3 short tendrils per bearer, fruits round, 4–7 cm, seeds 7–10 mm long. – C. Mexico; arid regions over 1500 m.

*C. scabridifolia* L. H. Bailey: of hybridogenous origin from *C. foetidissima* and *C. pedatifolia*. – Central Mexico.

3.3.3. Group 3

*C. maxima* Duchesne

*C. maxima* subsp. *andreana* (Naudin) Filov (Zapallito amargo): wild type for the following subspecies. Annual, leaves roundish, moderately soft-haired, fruits longish-oval (Fig. 18), 6.5–16 cm long, fruit peduncle tender, shrinking strongly when ripe, seeds (Fig. 19) 6–8 mm long, whitish to ochre-coloured, with or without placenta epidermis and with thin walled epidermis cells, which collapse largely despite sclerified rods (with splitted distal ends), marginal-bulge broadly rounded, bordered by shallow furrows, within which outwards bent epidermis cells (marginal-wings), which cover the marginal-bulge hardly or up to 1/3rd part. In the plants from Jard. Bot. Fac. Agron. de Azul (Argentina) 1999–2000: 16 the small fruits (6.5–7 × 4.5–6.5 cm, seeds 7–8 mm) were bitter, whereas from another origin (La Plata, Argentina, 18. 11. 1989, Vilma Rosato) with bigger fruits, were not markedly bitter. – N. Argentina, Uruguay (Bolivia ?); fields, ruderal places.

*C. maxima* subsp. *maxima* (giant cucurbit, Riesen-Kürbis, Zentner-Kürbis): annual, leaves roundish to shallowly lobed, with rounded lobes
Fig. 16-17. *Cucurbita foetidissima*, transversal section through the seed margin. – Fig. 16, the margin with projecting rims made up of marginal-wings (R) and covered with placenta epidermis. – Fig. 17, subsequent adjacent right section of the Fig. 16 with submarginal-bulge (SM) and marginal-wing. – Origin is the same as for Fig. 14–15, seeds from own harvest 2002.

(Fig. 20), moderately soft-haired, 3–5 tendrils per bearer, flowers fragrant, corolla-lobes rounded (but with superimposed tip). Fruit peduncle – if long and thin or short and knobby – terete, i.e. in transversal section always round, corky. Fruits in form and colour very diverse. Receptacle often not closed around the style, so that on the fruits the carpel tips are more (turban gourd) or less broadly (corky ring in some distance to the style base, Fig. 20, right) evident. Seeds 13–32 mm long, marginal-bulge broadly rounded, mostly (excl. type 3) separated through simple furrows or rims from the surface (or without furrows), different colour than the surface, surface brownish or white. At least three seed-coat types (Fig. 22): 1. thick-coated: surface brown, epidermis very thick, fracture smooth, walls of the epidermis cells on all sides uniformly thickened (HARZ 1885: 799 Fig. 43). The epidermis cells of the surface build on the margin a rim (Fig. 23), but no marginal-wings and submarginal-bulges, epidermis cells of the marginal-bulge thin-walled with sclerified rods, more or less collapsed. – 2. semithick-coated: surfaces silky-white, epidermis thinner, fracture sur-


face fibrous, otherwise same as above, but the epidermis cells on the surface thin-walled, with sclerified rods splitted at the distal end (HARZ 1885: 803 Fig. 44) (for e.g., partly Hubbard-group, partly ‘Zapallito de Tronco’). – 3. also semithick-coated, whitish to ochre-coloured, but the epidermis cells on the surface more or less collapsed to absent, on the inner side of the marginal furrow through the onset of marginal-wings with narrow but distinct submarginal-bulge, marginal-wings touching or encompassing the marginal-bulge; these seeds (for e.g., in ‘Gelber Zentner’ and related cultivars) thus with the naked eye hardly to be differentiated from *C. pepo*. Intermediary types between 2. and 3. (intact epidermis, white, with more or less distinct marginal-wings) are still to be investigated in detail. – Only in culture, origin S. America (for e.g., PARODI 1935).

Numerous cultivars. Well known is for e.g., ‘Gelber Zentner’. Now also more utilised in Central Europe: cultivar-group ‘Hubbard Squash’ with knobby peduncles, fruits mostly tapering on both ends, with orange, green or blue-green rind; an orange-coloured cucurbit (with green tips and thick-coated seeds) from the group, similar to ‘Uchiki Kuri’, was christened ‘Hokkaido’ at the market at Kaiser-Josef-Platz in Graz, since a woman doctor brought along seeds from the island Hokkaido (Japan) and

Fig. 21. *Cucurbita maxima* subsp. *maxima*. Left from the midpoint of the picture, the worldwide first Hokkaido-cucurbits at the stall of Maria Zeck, a peasant woman from Berndorf near Hausmannstätten, SE. of Graz, at the Kaiser-Josef-Platz in Graz, in front white Patisson-cucurbits (*C. pepo* var. *ovifera*). – 13. 8. 1983.

gave them to a peasant woman for cultivation (Fig. 21); and since then widespread worldwide under this name. Important in the USA: ‘Buttercup’. The cultivar ‘Atlantic Giant’ serves good for attempts at world records (2001: 570.7 kg). Turban- or Turk’s cap-cucurbits (also called Bishop’s cap) are known as ornamentals. For cultivars comp. for e.g., Brancucci & Bänzinger 2000.

3.3.4. Group 4

*C. ficifolia* Bouché (*C. melanosperma* Gasp.) (fig-leaf cucurbit, Feigenblatt-Kürbis): annual, leaves lobed (Fig. 24), 3–4 tendril per bearer, filaments clearly hairy, fruits 15–50 cm long, longish oval to round, fruits of the most cultivars to be found here are green with white marbling, otherwise also white, flesh fibrous, seeds 15–25 mm long, mostly dark brown to nearly black (= colour of the sclerified rods of the epidermis cells and the sclerenchymatic layer; but also cultivars with whitish seeds!), with strong, in transversal section rectangular to trapezial marginal-bulges (with huge hypodermis) and distinct furrow, on whose inner edge on the submarginal-bulge high marginal-wings arise. – Only under cultivation, origin most probably in the mountainous regions from Mexico till the Andes, possibly in northern S. America (Andres 1990). – Used as graft stock for cucumbers.

Fig. 23. *C. maxima* subsp. *maxima*, transversal section through a thick coated seed, border between marginal-bulge (low epidermis cells) and surface of the seeds (high epidermis cells, no marginal-wings). – Peruvian landrace as in Fig. 20 and 22 above.

(e.g. Zwaan Pannevis Katalog Gemüse 1991/92: 24; photo in ROBINSON & DECKER-WALTERS 1997: 131). Once in the European seed trade offered as „Winter- oder Nudelkürbis [Winter- or Noodle-Cucurbit, the most tenable of the edible cucurbits for the winter. The same when cooked, disintegrates to thin, long, as if cut noodles and has a very good taste (KÖLLER 1915: 8)].

3.3.5. Group 5

Seeds greenish-grey, more or less angular.

*C. lundelliana* L. H. BAILEY: annual, leaves light to moderately deep-lobed (Fig. 26), 1–2 tendrils per bearer, fruits (Fig. 27) more or less spheroidal, 8–13 cm long, seeds 6–10 mm long, greenish-grey, with thin-


Walled epidermis cells, which collapse more or less or tilt despite sclerified rods, seeds nearly angular, since the flat, not rounded surface of the marginal-bulge is longitudinal to the seed surface, marginal-bulge very broad, in transversal section rectangular to trapezial, with an extremely strong hypodermis, moreover the margin deeply grooved-wrinkled (Fig. 28), with submarginal-bulges and with tender marginal-wings, which rests against the marginal-bulge (Fig. 29, 30). – Mexico (Yucatán) to Nicaragua; seasonal forests and secondary vegetation.

*C. okeechobeensis* (J. K. Small) L. H. Bailey: annual, leaves 5-7-lobed with triangular lobes, 2-3 tendrils per bearer, fruits roundish, 7-11 cm, seeds 7-12 mm long, greenish-grey, similar to *lundelliana*, but the marginal-bulge is somewhat rounded and wizened, only sporadically weakly grooved, marginal-bulge somewhat lesser pronounced with a weaker hypodermis, with sub-marginal bulge and tender marginal-wings.


Fig. 27. *C. lundelliana*, ripe fruit. Origin as in Fig. 26. – Bot. G. Inst. Bot. Univ. Graz, 23. 11. 2000.

Fig. 28. *C. lundelliana*, the characteristic angled, and at the margin grooved-wrinkled seeds. – Origin as in Fig. 26.

3.3.6. Group 6

Within this group the species usually with soft or less prickly hairs, light to medium yellow flowers, having more or less floral scent, wide, rounded (except for the superimposed tip) corolla lobes widest near the middle (*C. ecuadorensis, C. moschata, C. argyrosperma*) seems to be closer related, whereas *C. pepo* has usually (with exceptions) very stiff and prickly hairs, dark yellow flowers, no scent inside the flower and triangular corolla lobes widest nearer to the base.

*C. ecuadorensis* CUTLER & WHITAKER: annual, stems densely covered by long, soft, patent hairs, leaf 5-lobed (till the middle) with rounded lobes, often white mottled, (1–)2–3 tendrils per bearer (Fig. 31–33), male flowers with broadly rounded receptacle, flowers therefore strict campanulate, medium yellow, with distinct scent, female floral- and fruit-peduncle longitudinally ribbed, slightly dilated at attachment, fruits round, 10–18 cm, sometimes bitter, mostly palatable, seeds 11–15 mm long, ochre to light brown, with distinct marginal-bulge, covered by enormous, more
Fig. 29. *Cucurbita lundelliana*, transversal section through the seed margin with an extremely strong hypodermis; some of the grooves are to be noticed in the section. – Origin as in Fig. 26.

Fig. 30. ditto, with marginal-wings (R).

or less wavy folded marginal-wings, which are darker than the surface of the seed (Fig. 34–36). The species has lately become important as a source of resistance genes. – W. Ecuador; arid bush land in the lowlands, till 400 m, wild, maybe partly semidomesticated.

Authors agree, that *C. ecuadorensis* is related to *C. maxima* (e.g. Puchalski & Robinson 1990, Wilson & al. 1992, Sanjour & al. 2002, Andres & Robinson 2002: 96). I am uncertain about it. It is true, that the bellshaped, scented flowers are in accordance with *C. maxima*. But most of the other characteristics, e.g. the shoot tips growing appressed to the soil, the soft and patent stem hairs, leaf, dilated peduncle at attachment and especially the seeds fit much better with *C. moschata*.

*C. moschata* Duchesne (musk-cucurbit, Moschus-Kürbis): annual, leaves 3–5 lobed, soft-haired, 3–5 tendrils per bearer, sepals often broa-

Fig. 32. ditto, shoot tip. — 8. 8. 2004.

Fig. 33. ditto, leaves, shoot tip and male flower (diameter c. 11 cm). — 6. 9. 2004.

dened like leaves (which is very rare in other species), fruit peduncle 5-ribbed, at attachment on the fruit mostly abruptly pillow-like broadened and the pillow at the margin bulgy (Fig. 38), sometimes flat, then with a narrow cartilaginous border, in some cultivars (e.g., ‘Pawpaw’) though totally without these broadenings), fruits covered by a wipeable waxy layer, in form, size and colour very variable. Seeds 8–21 mm long with rounded marginal-bulge and with submarginal-bulges, margin mostly with a slightly different colour shade than the surface, marginal-wings developed very strongly, which can be lightly appressed or distant, overtopping or encompassing the marginal-bulge, building a folded, fibrous marginal structure (Fig. 39). — Only under cultivation; origin Central America. Oldest archaeological remains in Mexico (Tamaulipas): 800 B. C. (Smith 1997b).

Mostly the cultivar group ‘Butternut’ is available for sale in Europe and USA (fruits beige to orange-brown, at the blossom end swollen, seeds only at this end). Huge fruits (up to 1.2 m long) are to be found from the cultivar ‘Lunga di Napoli’ (‘Pleine de Naples’; Fig. 37) and relatives. For cultivars comp. for e.g., Brancucci & Bänzinger 2000.

*C. argyrosperma* C. Huber

*C. argyrosperma* subsp. *sororia* (L. H. Bailey) Merrick & Bates: Wild type of the following subspecies. Annual, leaves 3–5 lobed, stiff-
Fig. 34. *Cucurbita ecuadorensis*, seeds. – Origin: The same as for Fig. 31. – 7. 6. 2004.

Fig. 35. ditto, transversal section through the marginal-bulge with enormous marginal-wings, one (R) adjacent to the marginal-bulge, the other splitted and epidermal thickenings (rods) separated by cutting. SM = submarginal-bulge.

Fig. 36. ditto, transversal section through the face of a seed. E = embryo.

haired, 3–5 tendrils per bearer, fruit peduncles without thickenings, fruits roundish to pear-shaped, 6–10 cm long, with bitter, white flesh, seeds 7.5–11 mm long, ochre-coloured, with placenta-epidermis and with thin-walled epidermis cells, which collapse extensively despite sclerified rods, with rounded marginal-bulge, which is a shade lighter than the surface, with heavy submarginal-bulges, with marginal-wings, which rest against and encompass the marginal-bulge. – Mexico to Panama; ruderal areas, agricultural land (mainly MERRICK 1990).

*C. argyrosperma* subsp. *argyrosperma* (*C. mixta* PANG.) (ayote, silver-seed cucurbit, Ayote, Silbersamen-Kürbis): annual, soft- or stiff-haired, leaves light to deeply lobed, often white mottled, 2–6 tendrils per bearer, fruit peduncle more or less ribbed longitudinally, often dilated at the point of attachment to the fruit, near the attachment often a little constricted, proximal to the constriction cylindrical to nearly spherical thickened (but also often similar to *C. pepo*), fruits in form, size and colour variable, mostly longitudinally green-white marbled (Fig. 40), fruit flesh whitish to light orange, fibrous to compact, seeds often big to very big [mainly in var. *argyrosperma* (Fig. 41) and var. *callicarpa* MERRICK & BATES; with the exception of var. *palmeri*], (11–)15–35 mm long, with, mainly in var. *argyrosperma*, very broad (till higher than thick), often silver-grey marginal-bulge dominated by hypodermis, with submarginal-bulge and tender marginal-wings, which lay against the marginal-bulge and cover it partly

Fig. 38. ditto, pillowy broadened attachment of the fruit peduncle to the fruit.


to totally, rarely without marginal-bulge, surface whitish, rarely brown. – The weed var. *palmeri* (L. H. BAILEY) MERRICK & BATES in Mexico (mainly in Sierra Madre Occidental), all others under cultivation (MERRICK & BATES 1989, MERRICK 1990). The oldest archaeological remains in Mexico (Tamaulipas): most probably c. 3000 B.C. (SMITH 1997b).

If the seeds are not silver-edged and the other characteristics not typically expressed, the species can be difficult to separate from *C. pepo* (e.g., 'Melonette Jaspee de Vendée' which did not breed with *C. pepo* in our experiment but crossed with silver-seed; silver edged and swollen peduncle were recessive in this cross). Sometimes also confused with *C. moschata* (e.g. 'Cushaw Golden' is *C. moschata*, not *C. argyrosperma*).

*C. pepo* L. (garden-cucurbit, Garten-Kürbis): annual, leaves moderate to deeply lobed, mostly covered with stiff, prickly hairs like the whole plant, 2–7 tendrils per bearer (reduced in bush types), receptacle mostly till the attachment of the style closed, floral- and fruit-peduncle markedly ribbed, towards the attachment mostly somewhat and gradually broadened, if abruptly strongly broadened, then the broadening towards the outside gradually taper off and usually without cartilaginous border, fruits in size, form and colour extremely variable, flesh fibrous, seeds 8–26 mm long, mostly whitish, rarely lightly toned, marginal-bulge rounded, with
submarginal-bulges and marginal-wings, which lie against the marginal-bulge and encompass it. Sometimes the marginal-wings are very high, lying against the marginal-bulge loosely, folded, similar to *C. moschata* (Fig. 47–49, ‘Miniature Ball’ and less expressed in ‘Flat Stiped’) or the marginal-bulge (mainly hypodermis) is very strong, as thick as the seed or thicker, only partly covered by the appressed marginal-wings (‘Citrouille de Touraine’). For thin-coatedness see chap. 4.2. – Wild forms and cultivated forms; details in the next chapter.

4. *Cucurbita pepo* L. (Garden-Cucurbit)

4.1. Classification

The immense magnitude in the cultivar diversity of this species is tried to be coped with botanical methods, which would explain the evolution, and horticultural approaches by delimitating cultivar groups. The botanical classification viz., on the basis of DECKER 1988, DECKER-WALTERS & al. 1993, 2002, is taken here as a framework, to which the cultivar groups (PARIS 1986, 1989) are assigned as usual by contemporary authors. For cultivars comp. for e.g., BRANCUCI & BANZIGER 2000. As to the history of the different cultivars comp. TEPPNER 2000: 6–19 and PARIS 2001.
4.1.1. *C. pepo* subsp. *fraterna* (L. H. Bailey) LIRA, ANDRES & NEE

The formal criteria for to be classified as subspecies from *C. pepo* was fulfilled in LIRA & al. 1995: 77. Small fruited wild type (Fig. 42), with less prickly hairs, well developed leaves deeply lobed, particularly the end lobes lobed again, 3–4 tendrils per bearer, fruits always roundish to somewhat longish-round (not pear-shaped), 7–8 cm, striped, when ripe changing colour from green with brighter stripes to yellow, bitter or not bitter, fruit peduncle usually detaches itself from the fruit after the plant dies off, seeds 9–10 mm long, 4–6 mm broad. –Mexico (Tamaulipas and Nuevo Léon), arid bush and agricultural land. –According to the present state of knowledge most probably without domesticated descendants (DECKER-WALTERS & al. 2002: 23, Fig. 1).

Fruits not ribbed or with interstitial ribs, plants in all parts smaller than subsp. *pepo* and subsp. *gumala* (some cvs. excepted), fruit flesh fibrous (mostly longitudinally in the inner part and transversally in the outer) and usually ± loosened into strands when fully ripe. In wild types and some ornamental gourds fruits often fall easily, before stems are dry.

*C. pepo* subsp. *ovifera* var. *texana* (SCHEELE) DECKER. Small fruited wild type (Fig. 44), fruits mostly pear-shaped, rarely roundish, 5-10 cm, when ripe, ivory-coloured or green-whitish striped, bitter, seeds 9-11,5 mm. – S. USA (Texas). Comp. also BAILEY 1943: 280-285. – According to the present state of knowledge most probably without domesticated descendants (DECKER-WALTERS & al. 1993: 71, 2002: 25).

*C. pepo* subsp. *ovifera* var. *ozarkana* DECKER-WALTERS in DECKER-WALTERS & al. 1993: 69. Small-fruited wild type (Fig. 43), fruits flat-roundish, roundish or pear-shaped, when ripe, ivory-coloured or rarely green-white striped, bitter, c. 4–10 cm long, seeds c. 7–9 mm long. – S. USA [W. Illinois, S. Missouri, Arkansas, E. Oklahoma, Louisiana and Mississippi (also Kentucky and Alabama ?)]; mainly on river banks of the Ozark Plateau and the Ouachita Mountains (also SMITH & al. 1992).

On the basis of morphological characteristics alone, I am not able to follow DECKER-WALTERS and differentiate between a Texas- (var. *texana*) and an Ozark-taxon (var. *ozarkana*) in the material grown to fruit till now (6 populations from Texas, 5 from Mississippi; seeds from USDA) because of the high variability within the two taxa. Also the separation of escapees from cultivation seems sometimes not to be possible without enzyme- and DNA-characteristics.

*C. pepo* subsp. *ovifera* var. *ovifera*. ribs of the fruit peduncle continuing as furrows on the fruit (with interstitial ribs) or the fruit totally smooth, rarely the stripes in the position of the main ribs very weakly projecting near peduncles, fruit forms diverse, surface smooth, ribbed or warty, when ripe unicoloured or striped, colours diverse, white, green, yellow or orange, fruit not bitter (except some ornamentals). – Descending from var. *ozarkana*-type of progenitors (DECKER-WALTERS & al. 2002). The oldest remains from plants allegedly domesticated are seeds from Missouri (Phillips Spring, c. 2500–2300 B.C., COWAN & SMITH 1993).

Cultivar-groups belonging here:

Ornamental gourds [most of the cultivars, incl. ‘Flat Striped’, ‘Miniature Ball’ (Fig. 45–49) and ‘White Egg’].

Acorn squash (Eichel-Kürbis), fruits short, on the peduncle-side truncate, tapering towards the tips, ribbed longitudinally.

Fig. 46. ditto, fruits. – 20. 9. 2000.

Scallop squash (Bishop’s cap; Patisson, Kaisermütze), fruits more or less flat, more or less notched at the edges (Fig. 21). The double-ribs of the crown-Cucurbits (Kronen-Kürbis) and the edges of the patissons are homologous to the double interstitial ribs of subsp. *gumala*.

Crookneck (Drehhals-Kürbis), fruits club-shaped, thin peduncle-side curved.

Straightneck, fruits club-shaped, straight.

4.1.3. *C. pepo* subsp. *gumala* TEPPNER

Strong, big-leaved plants with big flowers (12–13 cm long), ovary with 10 longitudinal ribs, fruit peduncle long (12–20 cm), longitudinally ribbed, fruit peduncle broadened at the point of attachment to the fruit suddenly, gradually levelling towards the edges (or merging into the fruit-ribs). Fruits relatively small, 13–20 cm in diameter, flattish-round, with 10 strong longitudinal ribs (main ribs) in continuation of the fruit peduncle ribs, in between often with additional (mostly two each) interstitial-ribs (Fig. 50), fruits when fully grown dark green, when fully ripe orange-yellow, sometimes green around the point of contact to the peduncle. Receptacle of the fully grown fruits mostly not closed till the style, therefore mostly a corky ring of about 3–8 cm in diameter around the scar of the style (Fig. 50; similar to many *C. maxima* cultivars), hard outer layer of the fruit wall 3–10 mm, light greenish white, of that the actual rind 1.5–4 mm, flesh orange, inner part longitudinally fibrous, outer part compact, seeds (14–)15–21 mm long, mostly with placenta epidermis,
Fig. 47. *Cucurbita pepo* subsp. *ovifera* var. *ovifera* 'Miniature Ball', seeds. - Origin as in Fig. 45. - Bot. G. Inst. Bot. Univ. Graz, harvest 2000.

Fig. 48. ditto, transversal section through the margin of a seed. E = embryo. - Origin as in Fig. 45. - Bot. G. Inst. Bot. Univ. Graz.

Fig. 49. ditto, transversal section through the surface of the seed.

the thin walled epidermis cells largely collapse despite sclerified rods, with submarginal-bulges (Fig. 51) and marginal-wings, which lie closely appressed to the marginal-bulge and largely (2/3 or more) encompass it.

Fig. 52. More illustrations in TEPPNER 2000: Fig. 3, 24, 25, PARIS 2001: pl. 2.3., ANDRES 2002, web site . . . http://www.cucurbit.org/family.html, *C. pepo*, 8th image; all from Guatemala.

Cultivated in Guatemala and seemingly also in the neighbouring Mexico (a part of the cultivars to be found in literature under the name "Mexican landraces", probably belongs here).

*C. p.* subsp. *gumala* has above all with its relatively small fruits and the extremely thick rind of the fruit, wild race characteristics. According to my opinion, the cultivars of the subsp. *gumala* are very close to the erstwhile wild cucurbits, which could be the starting points of the domestication for the subsp. *gumala* and subsp. *pepo*.

In this context the analysis of the *C. pepo*-remains from the B layer of the Guilá Naquitz cave, Oaxaca, S. Mexico, which SMITH 1997a investigated, are specially interesting. On the basis of the fruit rind thickness, fruit peduncle diameter and the seed length (two seeds with 13.2 and 13.8 mm respectively) a part of these is interpreted as domesticated cucurbits. The age of these remains stands at c. 8000–5800 years B.C. The most thrilling fact is the orange coloured fruit wall fragment with pe-
Fig. 50. *C. pepo* subsp. *gumala*. Transversal section of a fruit with 10 main ribs and between them the (mostly) double interstitial ribs; the marked line shows the direction of growth of one of the three placentas (comp. chap. 3.2.). Above a view of the blossom end of the fruit with corky ring around the stylar base. – Origin: Guatemala, comm. SCHEIDT, Gießen, 1988. – Bot. G. Inst. Bot. Univ. Graz, 10. 11. 2002.

Fig. 51. ditto, seeds in a cut fruit showing submarginal-bulges along the marginal-bulge; seeds with placenta epidermis, which is attached to the seed. RW = marginal-bulge, SM = submarginal-bulge.

Fig. 52. ditto, transversal section through the seed, with marginal-bulge, submarginal-bulge (SM), marginal-wings (R) and placenta epidermis. E = embryo.

duncle scar (5800 B.C.; Fig. 2B in SMITH 1997a), which has along with the spoors of 10 (short ?) main-ribs in between partly even spoors of interstitial ribs, which comes close to subsp. *gumala*. The comparison with Zucchiní (*SMITH*) is not appropriate, because this cultivar does not show any interstitial ribs, and is the latest link in the cultivar evolution of *C. pepo* subsp. *pepo* and arose around the end of the 19th century in Italy (PARIS 2001: 148). If one considers *gumala*-sort of wild types as possible, one would have to take a wider fruit peduncle scar into consideration. The seed-length will also have to move away from the presumed not-cultivated: domesticated border of 11–12 mm to c. 15 mm, which is for e.g., to be seen also in *C. ecuadorensis*. Under these circumstances the oldest *C. pepo*-remains of Central America, which has no parallel agriculture traces, could have been collected wild cucurbits. When observed from this perspective, the time span to the *C. pepo* remains from the further northly situated Ocampo caves (Tamaulipas, Mexico) from c. 4500–4000 B.C. which "soon" have other crop-plant companions (incl. maize), becomes more plausible.
4.1.4. *C. pepo* subsp. *pepo*

Fruits round to elongate (cylindrical or towards the blossom end thicker), when fully ripe orange or yellow, rarely white, ribs of the fruit peduncle continue on the fruit as more or less distinct ribs (main ribs) at least in form of short onsets near the fruit peduncle. Flesh whitish to orange, fibrous and sometimes loosened into strands when fully ripe.

According to my opinion originating from subsp. *gumala* or from erstwhile *gumala*-sort of wild type. Maybe the cultivars of *C. pepo* subsp. *ovifera* var. *ovifera* and subsp. *pepo* are more networked than to be presumed. It would be a fascinating idea, that the meeting of the old, agricultural economies of the South Eastern North America (with domesticated var. *ovifera*) and Mexico (with domesticated subsp. *gumala*) triggered off a hybridisation process leading to a morphological explosion of the *C. pepo*-cultivars. Back-crossing series in Mexican culture group could have laid the foundation for the *C. p.* subsp. *pepo*-cultivars and in the region of SE. North America for the *C. p.* subsp. *ovifera*-cultivars.

Going by the diversity, which suddenly appeared in Europe, for e.g., the nearly simultaneous appearance of vinous pumpkins and bushy patissons (inferred from the different herbals), it is impossible that all this could have generated in Europe, the significant basic stock of diversity must have been created by the indigenous people of America.

**Cultivar-groups, which belong here:**

Pumpkin (Plutzer, Herbst-Kürbis), fruits round to somewhat longish, medium to very big fruits (the cultivar ‘Citrouille de Touraine’ is supposed to bear the biggest *C. pepo* fruits, which weigh reportedly 40-45 kg), most of the oil-cucurbits belong here [var. *styriaca* (Fig. 56, 57), var. *georgica*, var. *oleifera* (Fig. 64, 65)] and the typical Halloween-cucurbits (orange, slightly longitudinally ribbed, with dark green, strongly longitudinally furrowed peduncle).

Vegetable marrow (Mark-Kürbis, Spargel-Kürbis; HAAS 1847), fruits nearly cylindrical, towards the peduncle end somewhat narrower, length to breadth ratio 1.5-3.0, here also for e.g., the spaghetti-cucurbits ('Vegetable spaghetti'). Since the character of fruit flesh loosening into strands is to be found in different subsp. *pepo*-cultivar-groups, it is of no use if one creates an own cultivar-group for the spaghetti-cucurbits. – Here also var. *flogra* (Fig. 66).

Zucchini or Courgette (Zuchetti), fruits cylindrical, length to breadth ratio 3.5-5.0, economically an especially important cultivar group.

Cocozelle, fruits long to very long, nearly cylindrical but a little thicker towards the blossom end, length to breadth ratio 3.5 at least, length up to c. 75 cm.

Ornamental gourds (few cultivars, for e.g., 'Small Orange' and 'Orange Ball').
The classification of *C. pepo* presented here is surely a substantial progress in comparison to that what was usual 15 years back. Many things are still unsatisfactory, for e.g., the usage of the category „variety“ in the case of subsp. *ovifera* for a level above the cultivar-group, but for the subsp. *pepo* on the other hand for a level below it. For an alignment inside the whole species *C. pepo* and for a better understanding of the intraspecific phylogeny, many DNA-analyses along with careful morphological documentation of the materials will be necessary.

4.2. Seed Coat

The ovules of the *Cucurbitaceae* have a thick outer and a thin inner integument. The seed coat develops only from the outer integument, while the inner one degenerates, starting from the time of the fertilisation. From the original ovule-epidermis the three outer layers of the seed coat originate in course of the seed development (HÖHNEL 1876, SINGH & DATHAN 1972).

Basically the cultivated cucurbit-species agree among themselves as far as the seed coat structure is concerned. So as not to make it more complicated, here only *C. pepo* and only the surface of the seed is dealt with, and to illustrate it well with an excellent figure from HARZ 1885: 813 (Fig. 53). In normal thick-coated seed, the outer layer is made up of the epidermis (1.), of radially elongated cells with cellulose-thickened rods (two bands on the wall between two adjacent cells form one rod; to be seen in transversal section in BEZOLD & al. 2003: 746 Fig. 1B/E), which branch off at their distal ends. The hypodermis (2.) shows c. 3–5 layers of small, densely packed cells, the cell walls are thickened clearly in the form of a small-meshed net and lignified. The sclerenchyma layer (3.) with the most thickened cell walls consists of one tier (rarely two tiers) and exhibits in transversal section isodiametrical cells, which are, in the plane of the seed, parallel to the longitudinal axis, elongated and tightly interlocked into each other. According to SINGH & DATHAN 1972: 39 only the first formed secondary walls give a positive test for the lignin reaction. Below succeed 1–3 tiers of aerenchyma (4.) out of cells with reticulately thickened cell walls with lignin, big intercellular spaces are to be found between the cells. The innermost layer is the chlorenchyma (5.), a parenchyma, which is above all rich in intercellular spaces and towards the inner side ends with the inner epidermis of the seed coat; it is green in colour due to protochlorophyll (in contrast to chlorophyll a it lacks two hydrogen atoms, which can be added only through a photo-reaction, which is impossible inside the fruit; MUKAIDA & al. 1993). During the seed coat development, the placenta epidermis tightly encompasses the seed; the placenta epidermis cells or at least their outer walls attach themselves on the mature seed and yield through drying, the loose, flimsy silver skin, which is easily

Fig. 53. Cucurbita pepo-seed. Illustration from HARZ 1885: 813 with a transversal section through the seed coat of the normal thick-coated type (detail figure IV). Additional figure is the placenta epidermis (0), which is hinted at and also to the left the used numeration of the different layers of the seed coat: 1 = epidermis, 2 = hypoderma, 3 = sclerenchyma, 4 = aerenchyma, 5 = chlorenchyma.
shaken or rubbed off. The outer wall of the placenta epidermis is hinted at in the Fig. 53 above the original diagram of HARZ and denoted with the symbol 0; it is not an inherent part of the seed coat as in the example of Fig. 53 and therefore in such cases left out in the formulas below.

The destiny of the portrayed layers, if fully developed, not sclerified or completely aborted, can vary independent of each other. In the case of aborted outer epidermis, the placenta epidermis can stick to the seed coat. In this case naturally it becomes a part of the seed mantle (therefore no easily removable silver skin), but can never be such an integral part as the normal epidermis and thus is more or less removable through mechanical manipulations. The symbol 0 is therefore put in such cases in brackets. The layers to be found in the mature seed are denoted with the respective numbers from Fig. 53, if the cell walls are thickened, then the numbers are bold and normal when not thickened. The symbols for the layers not to be found in the mature seeds or for dismantled layers, whose cell structure can not be deciphered are left out. This way the different types of seed

Fig. 54. *Cucurbita pepo* subsp. *pepo* var. *styriaca*. Completely ripe, thin-coated, dried seed, soaked in water, transversal section through the seed coat with well-developed epidermis. – ‘Wies 371’, Origin: LVZ Wies.

Fig. 55. ditto, variant with collapsed epidermis, placenta epidermis lost in this section. – Landrace from Feldbach, E. Styria, received from F. PFEILER, 28. 4. 2000.
coats to be found in mature seeds of *C. pepo* can be portrayed in the following way:

1. **thick-coated** (wild types and the majority of the *C. pepo*-cultivars) (Fig. 53) (incl. variants with collapsed epidermis and in such cases with adhering placenta epidermis)

2. **semithick-coated** (found in the F₂ generation from a cross of thin × semithin)

3. **- (unnamed)** (segregates sometimes from cucurbits of pumpkin type with thick-coated seeds and in progenies of the cross thick- × thin-coated). A variant with epidermis is sometimes to be found in old var. *oleifera*-material

4. **semithin-coated** (*C. p. subsp. pepo var. georgica*)

5. **thin-coated** (*C. p. subsp. pepo var. styriaca, var. oleifera and var. flogra*) (Fig. 54, 55). With variants, for e.g., with more or less collapsed epidermis or with additionally dismantled epidermis [(0).4.5.], in some landraces of var. *styriaca* and in the F₂ of a cross thin × semithin. This variability within thin-coated and the causes (modifications, processing or genetics) are not sufficiently investigated till now

In cucurbit breeding the first case (thick-coated) is usually named hulled (beschält) and all other cases (furthermore including different variants in the character expression in the seed margin) are united under the term hull-less (unbeschalt). The latter term is not exact, because a thin coat is also a hull and the method to unite all what is thinner than thick-coated, veils the genetic diversity involved. Admittedly the consideration of the thin types would be laborious because a correct distinction will be possible only by anatomical means.

Thick-coated is clearly dominant over thin-coated. I was fortunate enough to get some semithin cultivars (*C. p. subsp. pepo var. georgica* TEPPNER 2000) from Dr. R. FRITSCH (Institute for Plant Genetics and Crop Plant Research, Gatersleben, Germany), which made it possible to try out something new and that was to cross thick-coated (*C. p. subsp. pepo var. styriaca* GREB.) × semithin (var. *georgica*). The segregation in the F₂ was so complex, that the independence of the characters of the single layers became clear (TEPPNER 2000: 25–33). The lower limit of the number of genes involved in the seed coat characteristics concerning development, degeneration and lack of layers and degree of sclerification must be 6–9 (with at least 2 alleles each). Under such circumstances there are so many possibilities of combinations, that a constellation of alleles, which would lead to the segregation of thin-coated must be a very rare event. Moreover humans must be present, who observe this and recognise it to be useful and isolate the plant in question and breed it ahead, otherwise the recessive character "thin-coated" would sink in the ocean of the dominant thick-coated again.
It is self-evident that, due to the multi-gene condition, the thin-coatedness occurs in the nature very rarely and has been retained – seen on the worldwide scale – only once, viz., in the 19th century in Styria. Even „semithin-coated” was apparently retained only once and that was in Georgia (Caucasus region).

What are the genetic differences between thick- and thin-coated? SCHÖNINGER came to the conclusion through her analysis of the genetics of the seed coat characters on the basis of the resulting seed coat types from the cross thick × thin, that a major and a secondary sclerifying gene plus some modifier genes are responsible for the differences between thick- and thin-coated. PRYM-VON BECHERER 1955 was for two to three major sclerifying genes and modifiers. GREBENŠČIKOV 1954 was strictly of the opinion that only two alleles of a single gene, plus possible modifiers are responsible. The consequence was that, that this one-gene theory was the only accepted theory for half a century. In my own cross which lead to var. *flogra* (TEPPNER 2000: 23, 25, 35) the quarter of recessives and their progenies contained also individuals with different degrees of sclerification. The cross *C. pepo* subsp. *pepo* var. *styriaca* × subsp. *gumala* was curious in receiving in the *F₂* four individuals with + thick-coated and three with + thin-coated seeds, i.e. also with variants in sclerification. ZRAIDI & al. 2004 interpret the segregation ratio thick-coated : different types all called hull-less 3 : 1 also as the effect of a single major gene with two alleles. This may be sufficient for the praxis of plant breeding. But in my opinion, for a complete understanding of the genetics too little attention has been paid to the different types of more or less thin seed coats till now.

4.3. *Cucurbita pepo* L. subsp. *pepo* var. *styriaca* GREB.,
the Vinous Styrian Oil-pumpkin

4.3.1 Characters and Cultivars

The above name enfolds in it the cucurbits (pumpkins) cultivated in Styria for Kernöl or Kürbiskernöl (name for the exclusive dark-green oil, used mostly as salad oil, extracted from the cucurbit seeds) and snack seeds. These cucurbits comprise of many landraces propagated by the farmers themselves and some commercially bred cultivars.

The significant character, which differentiates all the types of the Styrian Oil-pumpkins (Fig. 54–57) from the others, which are outwardly similar, is the thin seed coat without any thickenings (sclerifications) of the cell walls (the vessels in the vascular bundle excepted; 1.4.5.-type), which lets the protochlorophyll shine through, thus giving the seed a green colour. The protochlorophyll of the seed coat dissolves in the course of the pressing process in the oil from the embryos and thus imparts it (the “black gold” of Styria!) its characteristic colour. All the original races and those
Fig. 56. *Cucurbita pepo* L. subsp. *pepo* var. *styriaca*. Fully ripe fruits in a field on the outskirts of Graz (W. of Florianiberg, Gedersberg), in the background the Koralpe mountains. – 9. 10. 1988.

Fig. 57. *C. pepo* L. subsp. *pepo* var. *styriaca*, transversal section of a fruit with increased number of placentas (4 instead of 3). – Landrace of the family W. Häfeli, Graz-Petersbergen. – 3. 10. 1981.

nearly related to it are vinous. The breeding was moving and moves in the directions, among others, of shortening of the internodes and of increasing seed yield.

In the Austrian cultivar-list (http://www7.ages.at/service/sortenliste/or_sor1f.htm) the following cultivars are registered to date (January 2002).

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Authorised</th>
<th>Breeder</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gleisdorfer Ölkürbis</td>
<td>16. 12. 1969</td>
<td>Saatzucht Gleisdorf</td>
</tr>
<tr>
<td>Sepp</td>
<td>k</td>
<td>Saatzucht Gleisdorf</td>
</tr>
<tr>
<td>Markant</td>
<td>k</td>
<td>Saatzucht Gleisdorf</td>
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<tr>
<td>Steirer</td>
<td>21. 12. 1999</td>
<td>Saatzucht Gleisdorf</td>
</tr>
<tr>
<td>k = short shooted</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

‘Wies 371’ has for e.g., turned to a starting point in oil-cucurbit culture in New Zealand (Burgmans 2000). In the neighbouring nations and many other countries, also in the USA (registred cvs. since 1972, Andres 2000; Cui & Loy 2002, Loy 2004: 358–359) cultivars have been introduced, selected and/or bred by crossing cultivars. According to the cucurbit-specialist Grebenščikov 1954: 165 all crossing experiments over the world for
breeding thin-coated oil-pumpkins trace back to Styrian material, and this situation has remained to date unaltered. Unfortunately, the first appearance of the Vinous Styrian Oil-pumpkin has not been directly documented, or at least no pertinent data have been found as yet.

4.3.2. History of var. *pepo* and var. *styriaca*

Evidences pointing towards the beginnings of the cucurbit-cultivation in Styria with pumpkins with thick coated seeds, which surely dates back in the past, are scarce. Reiterer & Reiterer 1996: 64, 65 presume to see a cucurbit behind the word „Kabaß“ from a menu of the protestant secondary school in Graz from 1596. But considering that time and the Spanish word “cabás”, it is most probably a bottle gourd. For the time being at least the definite proof of cucurbit-cultivation in Styria is from Riegler 2004: 322–323: The legacy of a farm-mistress of a farm in Gleinstätten (S. Western Styria) was taken stock of on 18. February 1697, it contained 54 litres pumpkin seeds. The next evidence comes from Kundegraber 1988: 193. According to it in a farm-handover inventory dating from 26.02.1735 in Ettendorf near Stainz (Western Styria), peeled pumpkin-seeds are mentioned. Four more references of seeds and alternatively, oil, come from the years 1738, 1739 and 1742 (Kundegraber 1988) as well as 1746 (Riegler 2004: 322–325). In the last example purchase and consumption of pumpkin-seed oil in the castle in Gleinstätten is registered. At the same time these are also the first proofs of the exploitation of the oil in Styria and also indications in favour of the opinion, that the cultivation of cucurbits in that time was not a rarity in Styria.

The references to the cucurbit-exploitation from the forgotten script of Scopoli 1769b, deserve to be introduced, even when it does not concern Styria. He furnishes a botanical description, narrates his germination and culture experiments, and also his chemical analyses. Finally he portrays under the title “usus” [uses] his observations in the dukedom of Tyrol. He describes accurately, in his preceding work Iter Tyrolense (1769a: 80–96) the cultivation of the important crop plants (maize, wheat, rye, millet, flax, tobacco, turnips, buckwheat) of his homeland, the Val di Flemme (Fleimstal). Thus it seems his knowledge is from this country. It seems however, that the cucurbits do not form a very important crop, since they are not to be found under the species just mentioned. The “apud nos” [at our place] in the first line must be an allusion to Carniola (Krain), where Scopoli (1723–1788) held the post of a medicus from 1754–(May?)1769 in Idria (Speta 2004: 599). It is for the best if I reproduce in English the in-German translated text by J. Zerobin also containing Scopoli’s own experiments (1769b: 105–106) in full length (latin original in Fig. 58 and 59):

“At our place mainly the sows are fed with fruit of cucurbits, who receive it raw. In the dukedom Tyrol some are accustomed to cook the fruit
flesh with water and then it is popularly eaten together with milk and maize flour. They [the cucurbits] can also be cooked in water with a medium amount of flour, by all means spiced with in-butter roasted onions. In the same region, they are also fed to the pigs, raw as well as cooked with bran and dish-water. Even the cows are offered cucurbits raw for eating.

From one part fruit flesh of cucurbits and two parts wheat flour, I have baked through adding sour dough a gold-yellow, delicious bread of $2\frac{3}{4}$ pounds. With the same amount of flour, sour dough and water, a bread of $2\frac{1}{2}$ pounds resulted with a different baking time. Thus bread can be prepared with the cucurbit, not only without water but also in greater quantity with the same amount of flour.

From the seeds, oil of the very best quality can be pressed, which at night, by candle light shows a reddish colour. From a pound of cucurbit seeds, $\frac{1}{2}$ a pound oil can be got.

The seeds also serve as poor man’s milk. A single, fully mature seed weighs three gran [0.19 g], twenty therefore one drachma [3.75 g]; when the
seed coat is removed, the kernels remain behind, whose weight is about 45 gran [2.8 g]. If therefore a cucurbit fruit of 6 pounds contains 630 seeds, and a single plant can surely bear two such fruits, it is evident, that a huge amount of oil can be produced, if the plants were carefully looked after.

The shoots, pulled out and buried in the earth, serve also as manure”.

A remark to the point, which is translated as poor man’s milk (semina inserviunt pro emulsionibus pauperum). Even Bock 1546: 316v mentions the possibility, to prepare white milk from cucurbit seeds, in a similar way which it is also known from almond seeds. In the anonymous script from 1773a: 6 a refreshing milk is mentioned, which is prescribed to sick people and usually comes from cucurbit seeds. In Anonymous 1773c: 366 one finds, that the seeds “give with water a cooling, moist, soothing and nutritious milk”. The emulsion is prepared by levigating the seeds (with sugar) in a mortar by adding water periodically (Anonymous 1869: 78–79, Geissler & Moeller 1888: 33, 35). The pound specifications can be accepted only as a relative value, since the measuring unit oscillated between
c. 316 and 560 g in different cities and countries (most probably here is the Austrian pound of 560 g or the Austrian pound medicinal weight of 420 g meant). The seed weights indicated are substantially the same as in the present-day’s thick-coated seeds. The statement 1 pound seeds = $\frac{1}{2}$ pound oil makes sense only if dried, peeled seeds are meant. Accordingly 630 seeds from a fruit weigh 88.2 g, which would give about 40 g oil; so one would need – depending on the fruit size and oil content – about 22–28 fruits for 1 kg oil (when 1 gran is calculated as 0.0625 g). This is about the same output dimension from present day’s good (not mediocre) oil-pumpkin fruits (c. 80–130 g dried seeds per fruit).

In the year 1773 the „Vereinigte Böhmisch-Österreichische Hofkanzlei“ (the United Bohemian-Austrian Court Chambers) in Vienna communicated „eine Anzahl Abdrücke von dem Unterricht des Anbaus, und nützlichen Gebrauchs der Kürbis, oder sogenannten Plüzer“ [a number of prints of the instruction for the cultivation and helpful usage of the cucurbit, or the so-called Plüzer] (Anonymous 1773a; type area 23 x 13 cm) along with a decree dated 6. February from Emperor Joseph II to the “Gubernio in denen Inner-Oesterreichischen Fürstenthümern und Landen” in Graz (the highest administration department for Styria, Carinthia, Carniola and other small regions). The commission ordered, this anonymous script be distributed free among the populace and also to publish the text in the newspapers. On 30. March 1773, this script was sent to the “Kreishauptmänner” (governors) and the agriculture society (Steierm. Landesarchiv, R. u. K. 1773-III-145). The aim was apparently to compensate the grain scarcity of that time through forceful and consequent utilisation of the pumpkin fruits (Teppner 1982: 60). In the course of cultivation instructions, even mono-culture is advised (p. 2 below); this however never played a big role in traditional agriculture in Styria, where it was cultivated as intercrop between maize (mainly for own consumption). Mono-culture started playing a bigger role not until 1958, forced with the beginning of the herbicide-usage (active agent Atracin) for maize. For the utilisation of the fruits, the baking of bread ($\frac{2}{3}$ flour, $\frac{1}{3}$ cooked and dripped-off cucurbit-flesh) was stressed upon. The bread-baking is described elaborately and rye-flour is recommended, but otherwise identical to the statement of Scopoli 1769b. Three recipes are given as some examples (p. 6: “one could in fact write half a recipe book.”) for preparation of other food (two of them reproduced in Teppner 1982: 59). Above all the oil is recommended for pharmaceutical use. One can further read out, that lots of experience in cucurbit-utilisation was present, that the cultivation in the monarchy was already widely distributed and the existence of a seed trade (warning against buying seeds “die aus Hungarn kommen” [which come from Hungary] and using them for sowing, p.7). All searches and efforts to clarify details of origin and authorship of this anonymous script
Fig. 60–61. Kurzer Unterricht . . . from 1773, Graz edition, type area 23 x 13 cm. – Fig. 60 Proof (private property). – Fig. 61. First page of the print, at the same time also the title page (library of the Landeskammer für Land- und Forstwirtschaft, Graz).

from 1773 failed till now because relevant parts of the “Allgemeines Verwaltungsarchiv” in Vienna burned down in 1927. An influence of the paper of SCOPOLI 1769b for the 1773 script is of some probability.

There exists a version of this “short instruction” in a private collection, which is apparently a proof and with „Von“ in the title (instead of the correct „Vom“) as well as the upside down catch-letters (Seitenkustode, Reklamant) at the bottom of the first page (Fig. 60; Fig. in WAGNER 1997: 62) makes it easy to recognise as such. These mistakes have been corrected for the print (copies in Steierm. Landesarchiv P. u. K. 1773–III-13 and in the library of the Landeslandwirtschaftskammer) (Fig. 61; Fig. in REITERER & REITERER 1996: 62). The discovery of the apparent proof in Graz and the similarity of the ornamental letters (Zierlettern) and the layout with other
Kurzer Unterricht
vom Anbau und nützlichen
Gebrauche der Kirsfe,
Oder
sogenannte Pfizcr.
Zur weiterer Bekanntschaft von
höchsten Orten zugesandt.
Mit Erlaubnis der Obrern.

Kurzer Unterricht.

Empfangen die bisherige theure
Zeitgen; besonders das arme Volk
auf dem Lande betroffen haben; des
to rühmlicher sind jene Bemühungen zu
schaffen; durch welche Menschenkreus
be den Abgang an Horn durch andere
Gewächse zu stellen zu kommen trach-
ten, welche entweder als schmachhaft
zu sein genonnen; die Brodbäckermühs
unser in hinein verhindern; oder auch gar
wohl vernöthet mit dem gemeinen Reichen
oder rocken Reichte, die Maß des Brodes
sich vermehren; und solches folglich
un ein beträchtlicher wohľeszem machen
konnten, die Kirsfe, ein schon ohnehin
gar bekannte Stängengewächser, dür-
fen sich folgen billich eine der ersten
Stellen verdienen, und die bisherige

---

Fig. 62-63. Kurzer Unterricht ... from 1773, Freising edition, type area 12.6 x 7.6 cm.
- Fig. 62 Title page. - Fig. 63 fol. 2r with the beginning of the text. - Roughwood Collection, Devon, Pennsylvania, USA.

A thrilling surprise was contributed by Mr. W. W. Weaver, who sent me a copy of the „Kurzer Unterricht“ from the Roughwood Collection, Roughwood, Devon, Pennsylvania. The piece in question is a very similar script as far as the text is concerned, also from 1773, but with a smaller format (type area 12.6 x 7.6 cm) and totally different layout (for e.g., no paragraphs) and the other letters it deviates totally. It also has a title page with the imprint of the printer Mößner from Freising (Fig. 62, 63). I presume it is a new print based on the Grazer edition, if not a pirated edition. One finds c. 20-50 small deviations in text per page in the Freising edition,
which are real mistakes even if we take the liberal grammar and orthography of those times into consideration. Serious mistakes are for e.g., fol. 2r “verhindern” [avoid] instead of “vermindern” [decrease], “rocken Mehle” instead of “Roggenmehle” [rye flour] (since 1748 recommended to be written with gg) and “Stangengewächse” [pole plants] instead of “Rankengewächse” [tendril plants] or in fol. 3r “als Berge anziehen” [attract mountains] instead of „als bergan ziehen” [go up-hill]. All these facts, along with the early date of the Grazer script (6. February), strengthen my belief, that the Freising edition is the second print.

It can be concluded from the harvest statistics of the “Steirischer Landbote” that in Styria (incl. former Lower Styria) between the years 1874–1880, cucurbit, grown as intercrop together with beans in the maize field (only in the districts Mureck and Radkersburg also in mono-culture, MüLLER 1879: 7), had c. 2,370 ha as area under cultivation and an annual total yield of fruits between c. 76,000–166,000 tons. During all this time only thick-coated seeds existed. In Styria, the seeds were immersed in hot water before peeling (during which the chlorenchyma adheres to the embryo, thus the oil was green even at that time). Only in the north-eastern parts of Styria and in the neighbouring provinces, the seeds were pounded along with their seed coat and then pressed (comp. TEPPNER 1982, 1999, 2000: 22 and the cited literature there). As far as the appearance of the new character „thin-coated” is concerned, unfortunately only few new information has cropped up, other than the three papers just mentioned. HLUBEK 1860: 171 (reproduced in TEPPNER 1999) mentions in his precise description of the Styrian agriculture, the peeling of the seeds and no thin-coated seeds. In the famous “Landwirthschaftliche Flora” [agricultural flora] from ALEFELD 1866 also no thin-coated cultivar is mentioned. Since both the authors were talented professionals, the only conclusion is that, that at that time no thin-coated cultivar was known. On the other hand we have the research of older cucurbit-breeders, who give the time around 1880 as possible. This coincides well with the few folklore figures. It is to be read in REITTERER 1910: 60, that “Manche haben Kürbisse mit ‘unschoaleten’ Kernen, das heißt Kernen ohne Hülsen” [some have cucurbits with peel-less seeds, that is seeds without a hull]. REITTERER 1919: 25 reports on the Laßnitztal, that there one has nearly only peel-less seeds, which saves the peeling work. After the foreword, p. 4, he started with the material collection 1911 and complains, that the war delayed the publication of the book substantially. One can presume and calculate, that he collected material for the first book before 1910 and for the second one from 1911 to about 1914/15. Till the conditions “nearly nothing but peel-less’ seeds” (REITTERER 1919: 25) existed, for those times and under those circumstances one can easily deduct twenty years. Thus both of these sources point towards the existence of the thin-coated seeds surely since
the end of the 19th century. Fuchs 1930: 34 reports that among the main food for the daily fare from Sulmtal: “Früher hatte man nur Kürbisarten, deren Kerne dicke, weiße Schalen besaßen” [Earlier one had only cur-cubbit-species, whose seeds had thick, white hulls), therefore it is to be concluded that the thin-coated have been dominating here for a long time. So the situation remains constant, that the time between 1870 and 1880 is the most probable for the first appearance of the Vinous Styrian Oil-pumpkin, i.e., for the segregation of the character „thin-coated“ from the normal pumpkins (Plutzer) with thick-coated seeds. When did it appear in the seed trade? An exact answer is impossible because seed-catalogues from the relevant time-span have hardly been retained. The first available record for the local seed trade in Styria is for 1915 in the excellent, richly stocked catalogue of Koller 1915: 51 the entry ,,869 Feldkürbisse, nackte oder schalenlose, zur Ölbereitung ... 1 kg 3,20 Kronen [field-pumpkins, naked or hull-less, for the preparation of oil]. This entry is already a routine-entry and not a new one. In the capital city Vienna, the first record of the Vinous Styrian Oil-pumpkin known till now, is in the “Hauptkatalog 1938”: 36 of the firm P. Hütting: “832 Steirische, schalenlose, reichtragend und hat schalenlose Kerne, wird vielfach zur Oelgewinnung verwendet 1 kg 5,60 Schilling” [Styrian, hull-less, rich-bearing and has hull-less kernels, is often used for the extraction of oil].

4.3.3. Breeding

Naturally, later even the plant breeding embraced the oil-pumpkin. From the older breedings, the Tschermak-cucurbit is the most famous (C. p. subsp. pepo var. oleifera Pietsch, Fig. 64–65). It was registered from 1955–1974 as „Tschermaks Ölkürbis (Kurztriebig, Schalenlos)” in the “Österreichisches Zuchtbuch für Kulturbpflanzen” as a cultivar and was maintained by Probstdorfer Saatzucht in Lower Austria. Tschermak got this short-shooted oil-cucurbit with fruits of pumpkin-type (in the beginning apparently still with a high percent of longish fruits; Tschermak-Seysenegg 1934, Schöniger 1950: 321, 335 Tab. 49) by crossing var. styriaca with a vegetable marrow (‘Mark Marrow’, bush habit). It was however not accepted by the farmers in Styria (due to its smaller and lighter coloured seeds as well as due to the woody margins, which existed at least earlier). But in other regions for e.g., in Germany, it was much more appreciated. The first registered cultivar of Styria was ‘Steirischer Schalenloser Ölkürbis’ [Styrian Hull-less Oil-pumpkin] from the Lambergian manor management in Feistritz near Ilz (1953–1956, was vinous; comp. Buchinger 1950: 217). If after a cross with Zucchini only thin-coated is selected and not back-crossed with var. styriaca, oil-cucurbits with fruits of vegetable marrow type result [C. p. subsp. pepo var. flogra Teppner 2000, incl. alleged Chinese material from trade (Fig. 66)].
With the increase in the importance of Styrian Pumpkin-seed Oil [Steirisches Kürbiskernöl] and snack seeds and as well as use for medical purposes, it is being tried, even within Styria, to improve the yield, quality and other parameters (comp. the already mentioned registered cultivars and WINKLER 1999, 2002, HILLEBRAND & al. 1996). Heterosis breeding was also undertaken for the production of hybrid-(F₁)-cultivars in Styria (‘Steirer’, WINKLER 1999: 40), as well as in the USA (CUI & LOY 2002) and in Vojvodina (BERENJI 2000). Many farmers in Styria, nevertheless have more confidence in their own traditional, private landraces.

There are many researches on the chemical constituents of the seeds and the composition of the oil. Of them, I would like to point out to MURKOVIC & al. 1999 and 2004 and as well as NIKIFOROV & al. 2000. According to them 98% of the fatty acids are palmitic, stearic, oleic and linoleic acids. The content of α- and γ-tocopherol in the seeds is at the average of 37.5 and 383 μg/g dry weight respectively. The main aromatic compounds are pyrazines.

A big slump came in 1997 with the massive occurrence of zucchini yellow mosaic virus (RIEDLE-BAUER 2000, PROVVIDENTI 1990, PFOSSER & BAUMANN 2002). This virus was present for some time, but in this year it resulted in failure of half the Austrian oil-pumpkin production. This has moved to attempts, sort of urgent measure, to cross-in the virus-tolerance
from virus-tolerant zucchini cultivars in the Styrian Oil-pumpkin. The attempts are running positive (LELLEY & al. 2000, 2002, WINKLER 2002, 2004) and from what one hears, the seeds of tolerant cultivars should be available in the trade from 2006 onwards.

A positive improvement and hopefully also an encouragement for the Styrian pumpkin agriculture is the proclamation of “Steirisches Kürbis-Kernöl g.g.A.” [= geschützte geographische Angabe (protected geographical indication)] since 12th of November 1998. This means that Styrian Pumpkin-seed Oil is a protected regional brand, recognised by the European Union (KONRAD 1999, 2000).

For the year 2002 the area under cultivation in Styria was estimated at 13,000–14,000 ha. The percentage on value basis of the pumpkin-seeds from the plant products of Styria lies by 11% (WEBER 2002). The area under cultivation of the cucurbits with thin-coated seeds is said to lie in Europe at about 45,500 ha (KAPAUN 2002).

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