

## DEVELOPMENT OF FLOWER AND FRUIT OF *CAPSICUM ANNUUM* L.

A. J. MUNTING

Afdeling Plantkunde, Landbouwhogeschool, Wageningen

### SUMMARY

The growth and development of buds, flowers and fruits of two varieties of *Capsicum annuum* L. were studied. These two varieties are easily distinguishable by their fruit characteristics. Cell division takes place mainly in the bud stage (pre-anthesis). Cell division takes place at the base of the ovary wall and pericarp during anthesis and post-anthesis.

Shape of the fruit is, especially in one variety, already clearly distinguishable in the pre-anthesis and is predominantly determined by cell division. Size of the fruit is determined by elongation during anthesis and post-anthesis.

### 1. INTRODUCTION

The genus *Capsicum* is a favourable object for anatomical and morphological study, because its species show a great diversity in the shape of their fruits and because the ancestral forms of these species sometimes still exist and changes having taken place by improvement and breeding can be traced back.

Although *Capsicum* is naturalized in many tropical and subtropical areas, it is almost certain that its origin is Central and South America (AUGUSTIN 1907, ERWIN 1929, HEISER & SMITH 1953).

The cultivated types of *Capsicum* are to be found practically throughout the world and are used as food, spice, or as ornamentals.

Since some species of *Capsicum* are very variable, the taxonomy is confused. Initially colour and shape of the fruit were the main characteristics on which the species were classified (MUNTING 1696, FINGERHUTH 1832, VON WETTSTEIN 1897, AUGUSTIN 1907). At the beginning of the 20th century, less variable characteristics were more and more used. Because the shape of the fruit no longer counted as a main characteristic, the number of species decreased sharply in most classifications. ERWIN (1929) took also into account the shape of the calyx. He mentioned that the nomenclature of the genus *Capsicum* was very confused and was based on horticultural needs. SHAW & KHAN (1928) used the characteristics of the flower for the classification of *Capsicum* in India. ODLAND & PORTER (1941) indicated that there is generally a greater degree of variability in both plant and fruit type in peppers than in tomatoes in America. There is a higher degree of crosspollination in the varieties of *Capsicum*. WILSON (1960) also came to this conclusion for *Capsicum* in Africa. SMITH & HEISER (1951) and HEISER & SMITH (1953) used characteristics of the flower to classify the genus. They designed a key to the species of *Capsicum* in which four

species were distinguished. HUNZIKER (1954) used especially characteristics of the androecium in his classification.

Synonyms occur frequently and the place of origin of cultivated types is sometimes no longer traceable. TERPÓ (1966) gave a critical review of the classification of both wild and cultivated types of *Capsicum*. He compared the names used by various investigators and came to the conclusion that in the past different names were used for the same plants. To overcome this, HEISER & PICKERSGILL (1969) made a detailed study of herbarium material in which they tried to find as many flower and fruit characteristics as possible. They distinguished five cultivated species. ROSENGARTEN (1970) adhered to the classification of HEISER & PICKERSGILL (1969) in his book on spices. In their study on the taxonomy and distribution of *Capsicum* in Mexico, MUÑOZ FLORES & PINTO CORTÉS (1967) also arrived at five cultivated species. The distinction in *Capsicum* of five cultivated species is generally accepted at the moment (HEISER 1969).

Literature on anatomy and morphology of flower and fruit of the Solanaceae is scanty. The general structure and development of the fruits of Solanaceae were described by KLEMT (1907). Besides morphological variation, the fruits of Solanaceae show great differences in anatomical and physiological aspects. AUGUSTIN (1907) was one of the first who discussed the anatomy and morphology of flower and fruit of the Hungarian paprika in more detail. In this extensive treatise the difficulty immediately arises that it is not clear which species were examined. This difficulty continues throughout the literature. COCHRAN (1938) studied the morphology of flower and seed of *Capsicum*. MURRAY (1945) investigated the structure of carpels and placentae of Solanaceae in general. The morphology of the fruit of *Capsicum* was studied by KANO et al. (1957) and QUAGLIOTTI (1968). A general review of flower and fruit development was given by NITSCH (1965). FRIDVALSKY & NAGY (1966) examined the pericarp of *Capsicum*. Chloroplasts in the pericarp were examined electron-microscopically by SPURR & HARRIS (1968).

For the present study we chose two varieties of *Capsicum annuum*. Most cultivated varieties in the temperate zone belong to *Capsicum annuum*. The choice fell on two varieties with sharply distinct fruit shapes. We checked at what time the definite fruit shape is recognizable during development of the ovary, what resemblances there are between flower and final fruit shape, where and how long cell division and cell elongation take place during the development of ovary to fruit, and finally what differences there are between the two varieties in initiation and development of flower and fruit.

## 2. MATERIALS AND METHODS

Seeds were obtained from the Department of Agricultural Botany of the University of Reading, England.

The varieties examined were:

*Capsicum annuum* L. var. *minimum* (Mill.) Heiser from Panama

*Capsicum annuum* L. var. *annuum* "Chile cascabel" from Mexico.

The varieties were self-pollinated and therefore cultivated separately in greenhouses to prevent cross-pollination. In winter artificial light was used to maintain flowering and fruit setting. The measurements on buds, flowers and fruits were done with a Vernier caliper. The material was fixed in a solution of formalin-ethanol (96%)-acetic acid 1:18:1 by volume, dehydrated in tertiary butanol and embedded in paraplast (melting point 56–57°C). The material was cut into longitudinal and transverse sections on a Leitz microtome and stained with safranin and fast green by the method of JENSEN (1962). Difficulties arose during sectioning of the fruits because they contain cells with crystal grit or solitary crystals of calcium oxalate which damaged the microtome knife.

Drawings were made with a drawing mirror and a drawing tubus of Wild.

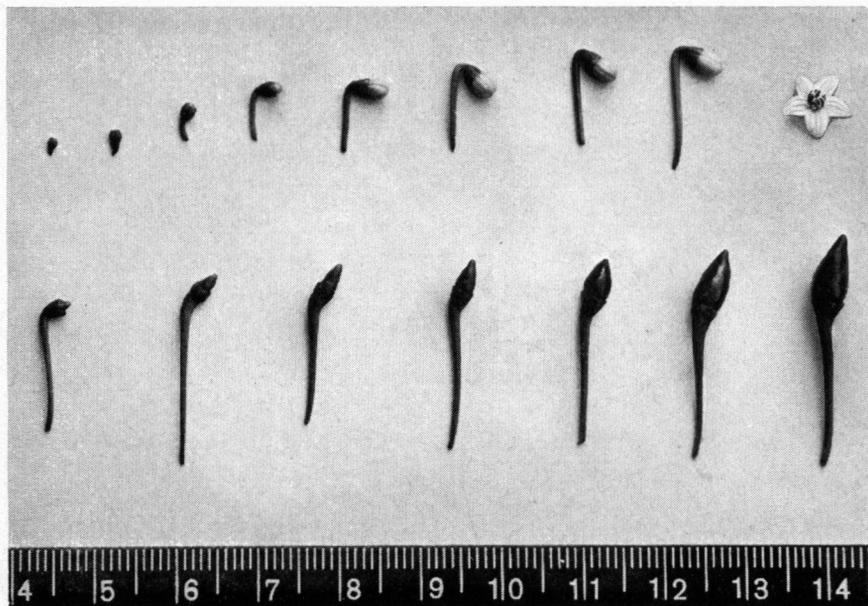
### 3. RESULTS

#### 3.1. Macroscopic morphology

##### 3.1.1. *Capsicum annum* var. *minimum*

*Fig. 1* shows the development of the bud initial to the fruit. In the first stage the pedicel is erect together with the flower primordium. During further development the pedicel curves. This curving starts as soon as the petals close. After pollination the pedicel curves back so that the mature fruit stands upright.

The number of floral parts is constant in this variety, almost without excep-



*Fig. 1.* Development of flower and fruit of *Capsicum annum* var. *minimum*.

tion. The flower is pentamerous, only 5% of the flowers being tetramerous. In both cases the ovary is perfectly or imperfectly bilocular. When the ovary is imperfectly bilocular (60%), the septum is not attached to the top of the ovary. Flowers are solitary or rarely paired. The flower is hypogynous, actinomorphic, hermaphrodite and proterogynous.

In *fig. 2a* length and diameter of a fruit are plotted against time. The maturation of the fruits is not synchronous. The length/diameter quotient is plotted against time in *fig. 2b*. The quotient is 1.3 when the flower has just opened and 2.2 in the full-grown fruit. The average number of ovules was 17 and that of seeds 10. These measurements and numbers are the mean values from some thousands of fruits. The fruit is full-grown about 15 days after pollination.

Drawings of the pistil development are given in *fig. 3*. In *fig. 4* the position of the seeds in the fruit after removal of the pericarp is given.

The septum does not always run right to the top of the fruit. There are two placentae in the whole fruit. Each locule contains two rows with seeds placed below each other. The placental tissue is clearly discernible from the remaining tissue of the septum by a somewhat lighter colour.

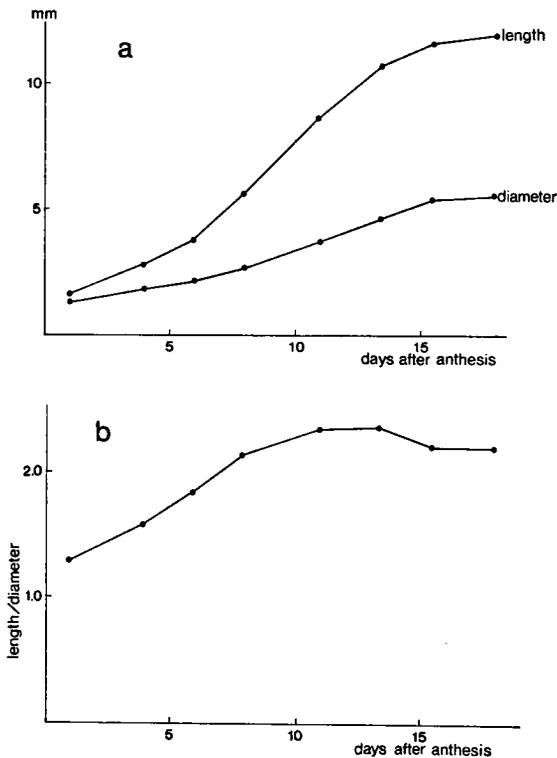


Fig. 2. Growth curve (a) and length/diameter quotient (b) of a fruit of *Capsicum annum* var. *minimum*.

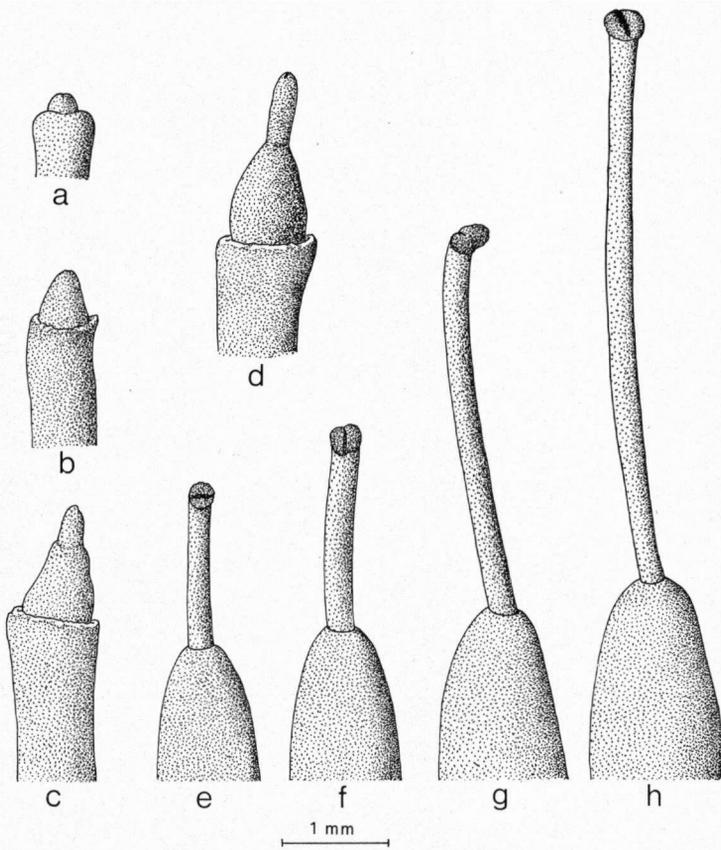


Fig. 3. Growth of a pistil of *Capsicum annum* var. *minimum* in buds 0.7 mm (a), 1.5 mm (b), 2.0 mm (c), 2.5 mm (d), 3.0 mm (e), 4.0 mm (f), 6.0 mm long (g) and in a flower (h).

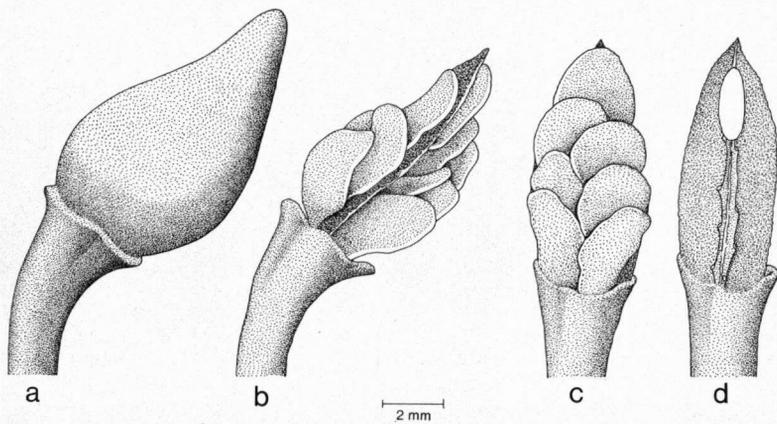


Fig. 4. Fruit (a) and opened fruit of *Capsicum annum* var. *minimum* to show position of seeds (b, c) and incomplete septum after removal of seeds (d).

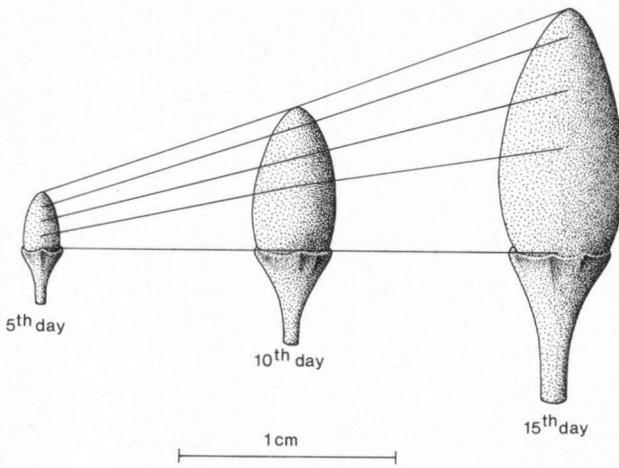


Fig. 5. Localized growth of fruit of *Capsicum annum* var. *minimum*.

By means of ink growth marks it is proved that growth does not take place regularly over the whole length of the fruit. The growth zone is situated at the base of the fruit (fig. 5); if the fruit is injured by marking, growth is disturbed and the fruit becomes deformed.

### 3.1.2. *Capsicum annum* var. *annuum*

Fig. 6 shows the development of the bud initial to the fruit. In the first stage the



Fig. 6. Development of flower and fruit of *Capsicum annum* var. *annuum*.

pedicel is erect together with the flower primordium. The pedicel curves during further development. This curving continues during development of the fruit. Full-grown fruits are on drooping pedicels.

The number of floral parts is variable. The flower is pentamerous (20%), hexamerous (67%), heptamerous (2%) and octamerous (1%). The hexamerous flower is the most frequent. The ovary is bilocular (94%) or trilocular (6%). The septum is always incomplete and not attached to the top of the ovary. Bilocular and trilocular ovaries usually occurs in hexamerous flowers. The distribution and characteristics of the flowers are the same as for the previous variety.

The length and diameter of a fruit are plotted against time (*fig. 7a*). The length/diameter quotient is plotted against time in *fig. 7b*. The quotient is 0.9 when the flower has just opened and 1.1 in the full-grown fruit. The number of

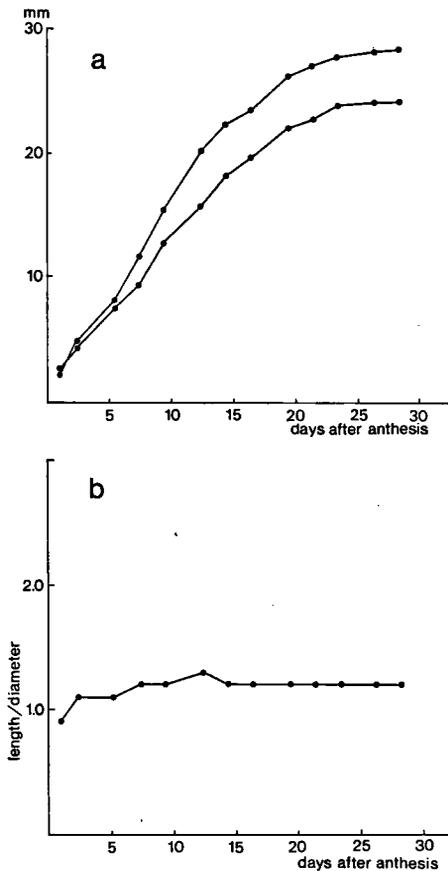


Fig. 7. Growth curve (a) and length/diameter quotient (b) of a fruit of *Capsicum annuum* var *annuum*.

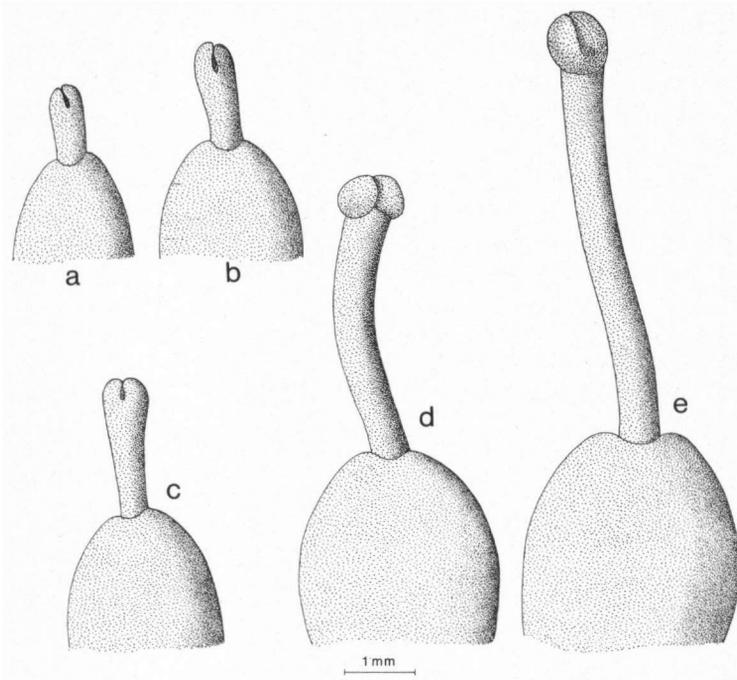


Fig. 8. Growth of a pistil of *Capsicum annuum* var. *annuum* in buds 3.5 mm (a), 5.0 mm (b), 6.0 mm (c), 8.0 mm long (d) and in a flower (e).

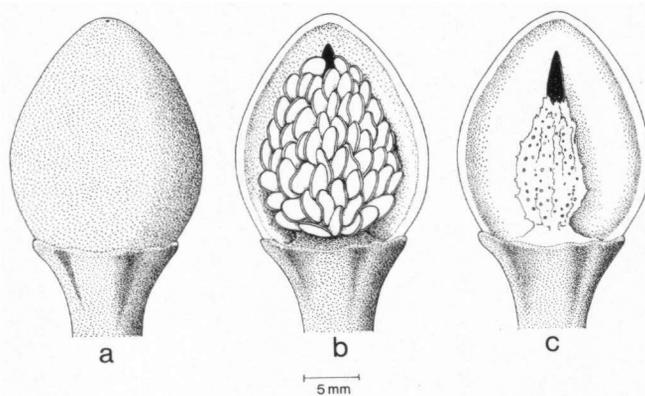


Fig. 9. Fruit (a) and opened fruit of *Capsicum annuum* var. *annuum* to show position of seeds (b) and incomplete septum after removal of seeds (c).

ovules is about 150 and the number of seeds varies and depends on the effect of pollination. The fruit is full-grown about 25 days after pollination.

Drawings of pistil development are given in *fig. 8*. In *fig. 9* the position of the seeds in the fruit after removal of the pericarp is given. The fruit is bilocular or

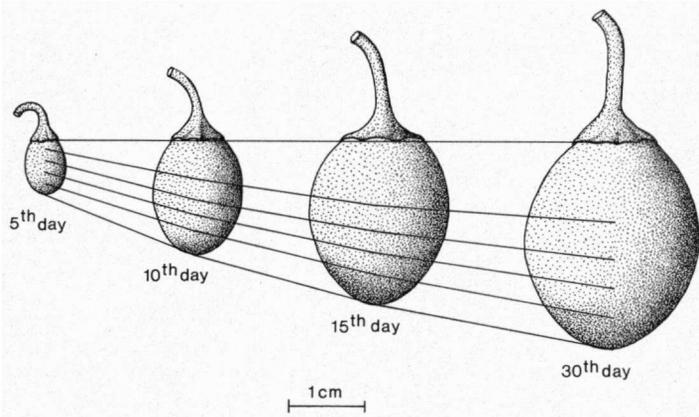


Fig. 10. Localized growth of fruit of *Capsicum annuum* var. *annuum*.

trilocular with two or three placentae and an incomplete septum. The placentae are broad and the attachment of the seeds is random. The placental tissue is distinguished from the remaining tissue by its lighter colour.

By means of ink growth marks it is proved that the growth zone is situated at the base of the fruit (fig. 10).

### 3.2. Microscopic morphology

#### 3.2.1. *Capsicum annuum* var. *minimum*

Fig. 11 shows the development of a flower primordium. When a flower primordium has differentiated the origin of the sepal initials are first perceptible. Papilla-like cells arise at the edges and the calyx closes during development. Petal and anther initials appear successively. The corolla grows in the same manner as the calyx. When the corolla closes and the calyx opens, two carpels are formed out of a ring-shaped meristem and the septum arises from the remaining meristem.

From transverse sections two longitudinal models are drawn of pistil development. In the first model (fig. 12a) two carpels with connate edges are formed out of a ring-shaped meristem. These carpels surround a cavity in which no septum is yet formed. The second one (fig. 12b) is at right angles to the previous model. The first sign of a septum is present here. A suture visible by light microscope can be perceived at the base of the septum. The septum becomes larger and larger through cell division and cell elongation.

The wall of the ovary and the septum are studied at different stages in the development of the ovary (fig. 13a-g). It is notable that the giant cells under the inner epidermis of the wall of the ovary are already perceptible at a very young stage (fig. 13a, b). During development of the ovary these cells enlarge enormously (fig. 13d, f). The number of cell layers increases to about 11. There are crystal grit idioblasts in the wall of the ovary.

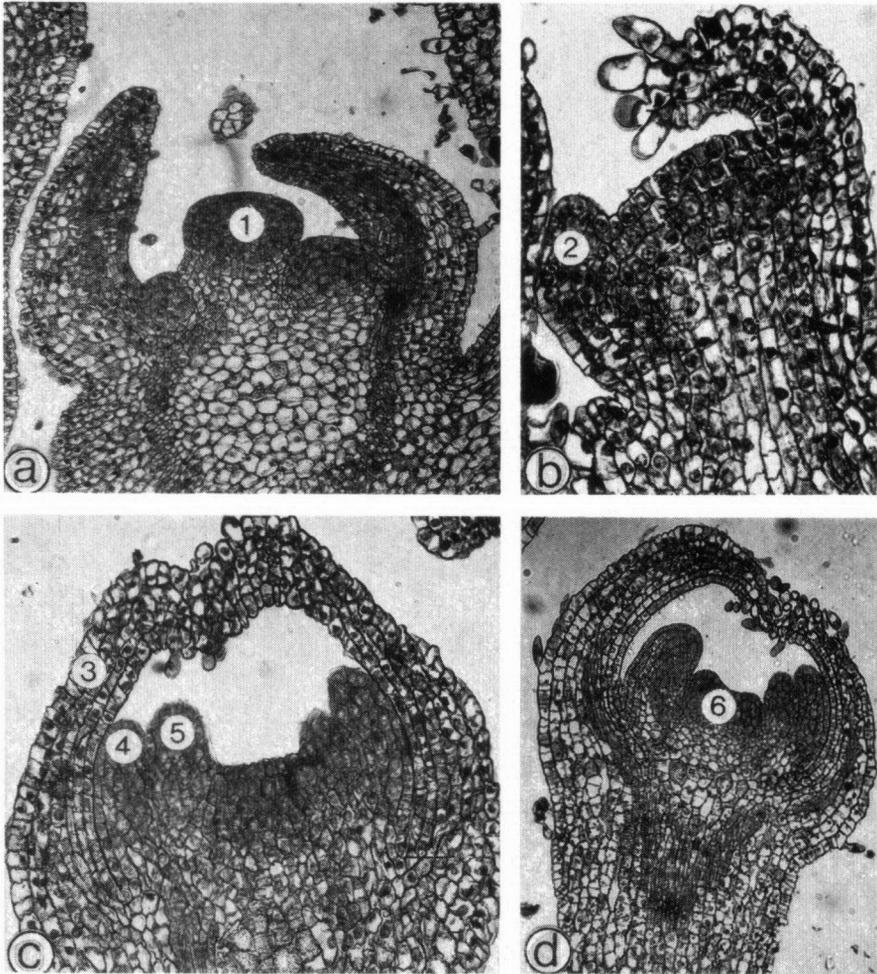


Fig. 11. Development of floral parts of *Capsicum annuum* var. *minimum*.

a. flower primordium,  $\times 125$

b. sepal differentiation,  $\times 310$

c. petal and stamen differentiation,  $\times 190$

d. carpel differentiation,  $\times 100$

1. flower primordium; 2. sepal primordium; 3. sepal; 4. petal primordium; 5. stamen primordium; 6. carpel primordia.

The septum is not perceptible at the youngest stage. Ultimately the septum consists of about 12 cell layers in the ovary (*fig. 13g*).

In the mature ovary the ovules are anatropous. The embryo sac in the ovule is of the *Polygonum* type. The ovules have one integument.

Two zones can be perceived in the pericarp in a longitudinal section of a

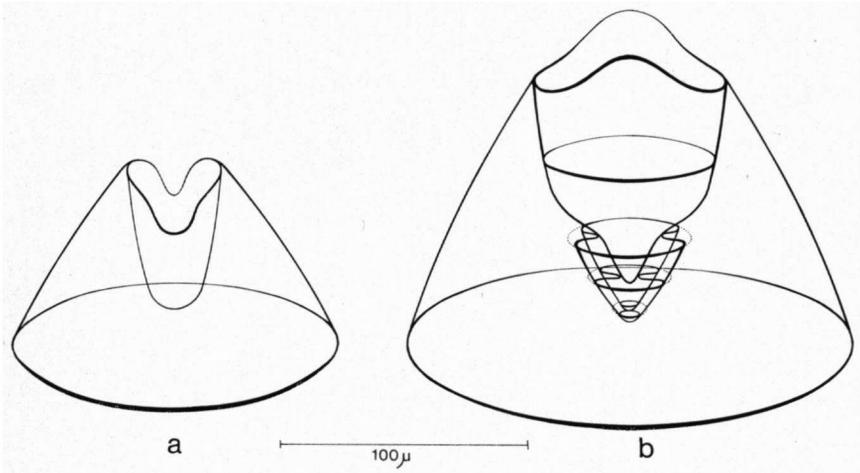


Fig. 12. Models of young pistils. Explanation see text.

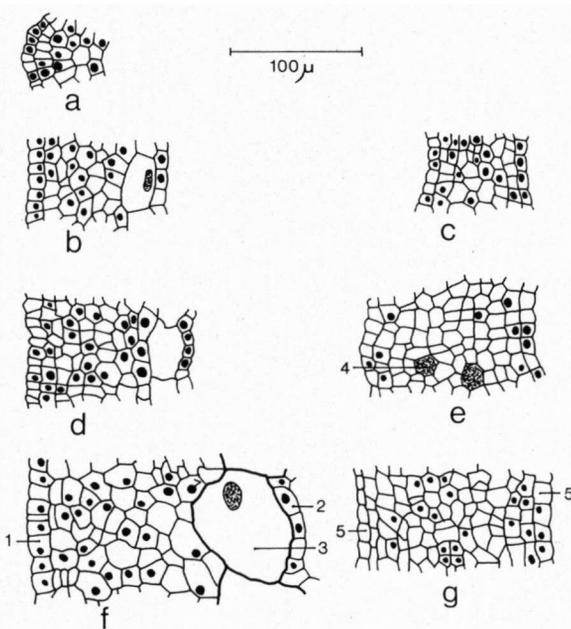


Fig. 13. Transverse sections of ovary wall (a, b, d, f) and septum (c, e, g) of *Capsicum annuum* var. *minimum* in buds 1.2 mm (a), 2.5 mm (b, c), 4.3 mm long (d, e) and in a flower (f, g). 1. outer epidermis; 2. inner epidermis; 3. giant cell; 4. crystal grit idioblast; 5. epidermis of septum.

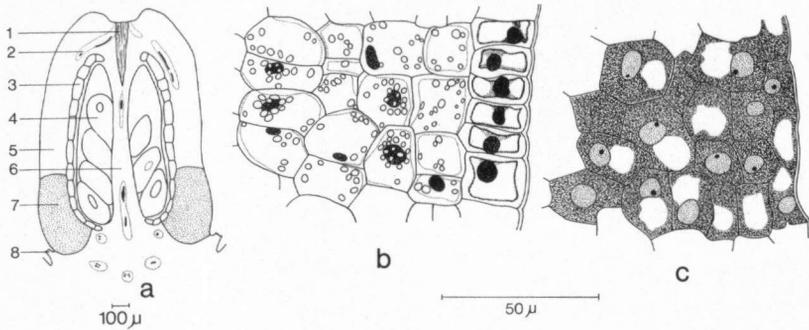


Fig. 14. Longitudinal section of a young fruit (a) and of the pericarp (b, c) of *Capsicum annum* var. *minimum*. 1. conducting tissue; 2. vascular tissue; 3. giant cell; 4. young seed; 5. pericarp (detail see b); 6. septum; 7, pericarp (detail see c); 8. rest of petal.

young fruit (fig. 14a). These zones are present from a bud stage 4.0 mm long to a fruit stage 3.0 mm long. Some of the cells have a parietal cytoplasm and one central vacuole (fig. 14b). This part occupies two-thirds of the pericarp in this longitudinal section measured from the implantation of the style. The remaining part has protoplasma-rich cells with small vacuoles (fig. 14c). Such a subdivision is not present in the septum.

Finally some remarks on the development of the pericarp and septum in diverse fruit stages to a mature fruit (fig. 15a-h). The cuticle of the outer epider-

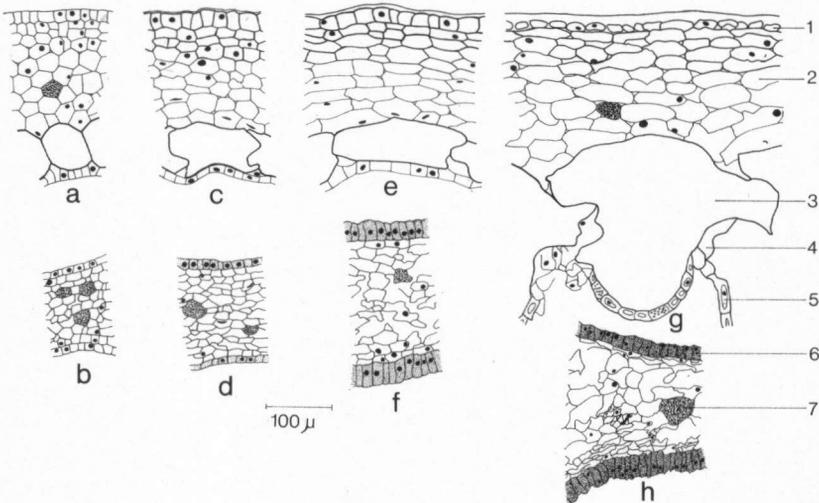


Fig. 15. Transverse sections of pericarp (a, c, e, g) and septum (b, d, f, h) of *Capsicum annum* var. *minimum* in fruits 3.1 mm (a, b), 4.3 mm (c, d), 9.3 mm long (e, f) and mature fruit (g, h). 1. outer epidermis; 2. parenchyma; 3. giant cell; 4. parenchymatic part of inner epidermis; 5. sclerenchymatic part of inner epidermis; 6. epidermis of septum; 7. crystal grit idioblast.

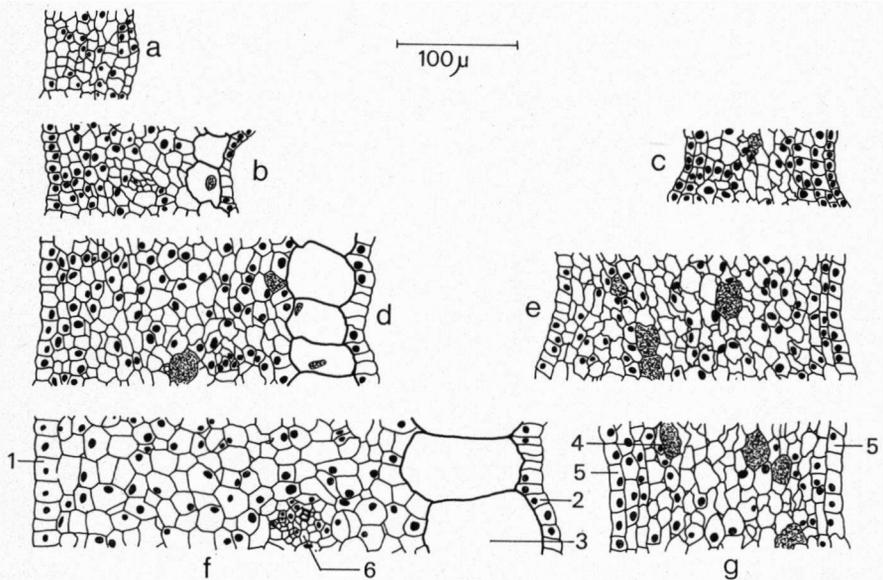


Fig. 16. Transverse sections of ovary wall (a, b, d, f) and septum (c, e, g) of *Capsicum annum* var. *annuum* in buds 1.0 mm (a), 3.5 mm (b, c), 5.7 mm long (d, e) and in a flower (f, g). 1. outer epidermis; 2. inner epidermis; 3. giant cell; 4. crystal grit idioblast; 5. epidermis of septum; 6. vascular bundle.

mis becomes more clearly visible. The subepidermal layers of cells gradually become somewhat collenchymatic. The vascular tissue is embedded in the parenchyma of the pericarp. The giant cells acquire a thicker wall. In the mature fruit (fig. 15g) some cells of the inner epidermis are irregularly thickened. Other cells remain parenchymatic.

In the epidermis of the septum there are some anticlinal divisions. The epidermal cells are rich in cytoplasm and, unlike the other cells of the septum, without a large vacuole (fig. 15d, f, h). Because of the marked elongation of the septum the parenchymatic tissue is provided with large intercellular spaces.

At a certain moment, the full-grown fruit turns deep purple on the side exposed to light through the formation of anthocyanin in the subepidermal cell layers. This colour disappears some days before the fruit matures. The green pigments in the chloroplasts are broken down and light-red chromoplasts are formed.

### 3.2.2. *Capsicum annum* var. *annuum*

The development of the flower is the same as in the previous variety. The wall of the ovary and the septum are studied at different stages in the development of the ovary (fig. 16a-g). The giant cells are distinguishable at a very young stage (fig. 16b). Finally the wall of the ovary consists of 20 cell layers (fig. 16f). There are cells with crystal grit and solitary crystals in the wall of the ovary

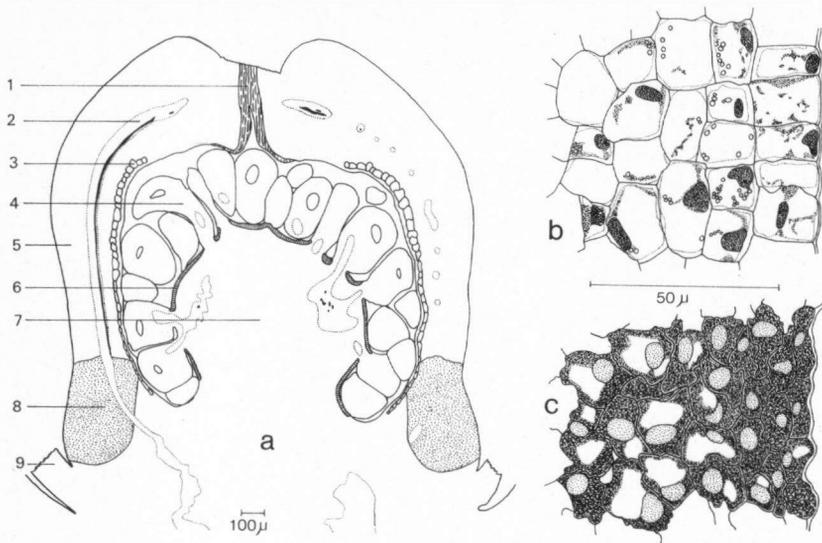


Fig. 17 Longitudinal section of a young fruit (a) and of the pericarp (b, c) of *Capsicum annuum* var. *annuum*. 1. conducting tissue; 2. vascular tissue; 3. giant cell; 4. young seed; 5. pericarp (detail see b); 6. epidermis of septum; 7. septum; 8. pericarp (detail see c); 9. rest of petal.

and in the septum. The septum has about the same number of cell layers as the wall of the ovary. Generally the cells of the septum are smaller. The ovule and the embryo sac are of the same type as in the previous variety.

In the longitudinal section of a young fruit two zones are distinguishable in the pericarp (fig. 17a). During the development of the ovary and the fruit these two zones are present in a bud stage 6.0 mm long to a fruit stage 5.0 mm long. Some cells of the pericarp have parietal cytoplasm and one central vacuole (fig. 17b). This part is about three-quarters of the pericarp in this longitudinal section measured from the implantation of the style. The remaining part has cells that are rich in cytoplasm (fig. 17c). Such a subdivision is not present in the septum.

Finally the development of the pericarp and the septum are studied in the maturing fruit (fig. 18a-c). The outer epidermis of the pericarp is characterized by a well developed cuticle (fig. 18a). There are about 4 layers of collenchyma under the epidermis. The parenchyma consists of about 16 layers in which the vascular tissue is embedded (fig. 18b). The giant cells acquire a thicker wall. The inner epidermis consists of a mixture of cells with thin and thick walls (fig. 18c).

In the epidermis of the septum are the same cells as in the previous variety. In a transverse section the septum consists of about 20 cell layers and the parenchyma has small intercellular spaces.

Formation of anthocyanin was not noted on the fruit. The mature fruit was dark-red by chromoplasts.

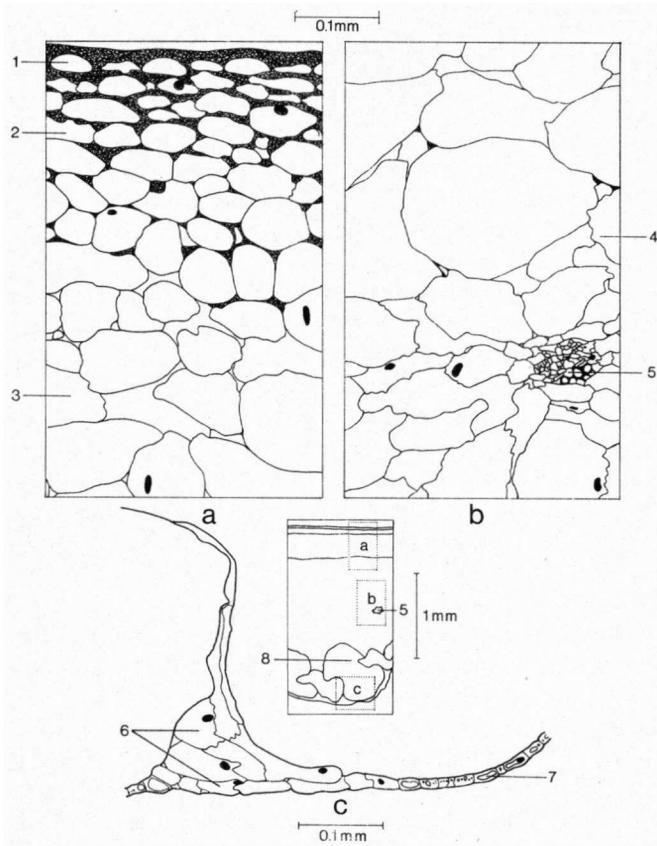


Fig. 18. Transverse section of the pericarp of a mature fruit of *Capsicum annum* var. *annuum*.  
 a. outer part of pericarp  
 b. middle part of pericarp  
 c. inner part of pericarp  
 1. outer epidermis; 2. collenchyma; 3. parenchyma; 4. parenchyma with a vascular bundle (5); 6. parenchymatic part of inner epidermis; 7. sclerenchymatic part of inner epidermis; 8. giant cell.

#### 4. DISCUSSION

In this investigation, resemblances and differences in the development of flower and fruit of two varieties of *Capsicum annum* are studied. For brevity these varieties will be further referred to as *minimum* and *annuum*.

In both varieties the floral parts arise centripetally. AUGUSTIN (1907) proved this for *Capsicum* in general, COCHRAN (1938) for *Capsicum frutescens*, and SMITH (1935) for *Solanum lycopersicum*. The carpels arise in the centre. The number of floral parts of *minimum* is much nearer to constancy than that of *annuum*. The ovary of *annuum* is two or three locular. This locularity does not

show any correlation with the number of floral parts.

The development of ovary and fruit can be classified in four stages as done by NITSCH (1965):

a) pre-anthesis, b) anthesis, c) post-anthesis, d) maturation.

The investigated varieties show very different fruit shapes. *Minimum* has an elongated fruit and *annuum* a more ovoid to spherical fruit. *Capsicum annum* to which *minimum* and *annuum* belong has in fact the most variable fruit shapes and colours of all *Capsicum* species. (HEISER & SMITH 1953).

The growth of the fruit of *Capsicum*, like many others, follows a sigmoid curve (NITSCH 1965; ASAHIRA et al. 1967). The smaller fruit of *minimum* is earlier full-grown than the larger fruit of *annuum* (15 and 25 days, respectively). In *minimum* the length of the fruit increases more than the diameter. The quotient length/diameter is 1.3 for the ovary and 2.2 for the full-grown fruit. The final fruit shape is reached here at the post-anthesis stage.

The length of the fruit of *annuum* increases about as much as the diameter. The quotient length/diameter is 0.9 for the ovary and 1.1 for the full-grown fruit. The final fruit shape is determined at the pre-anthesis stage. According to AUGUSTIN (1907) and KANO et al. (1957) the final fruit shape is only to be seen after anthesis, but according to NITSCH (1965) much earlier.

The growth of the fruit is not uniform over the whole fruit. The developing fruits of *minimum* and *annuum* grow most strongly at the base. KANO et al. (1957) also found this unequal growth in the elongated but not in the ovoid or spherical fruits.

According to NITSCH (1965), cell division generally takes place during pre-anthesis. However, it is remarkable that at the base of the ovary and the fruit a zone in the wall of the ovary and the pericarp remains meristematic during anthesis and part of post-anthesis. Beside this cell division, cell elongation takes place during anthesis and post-anthesis.

This study shows that fruit shape in *annuum* is determined by cell division and in *minimum* by both cell division and cell elongation. Fruit size is determined by cell elongation during post-anthesis in both varieties. KANO et al. (1957) only distinguish between an early stage in the fruit development with mainly cell division and a stage with cell elongation. Cell elongation is of importance here for the final fruit shape.

Anthocyanin is formed in the pericarp of *minimum* just below the outer epidermis of the fruit exposed to light during maturation. There is no anthocyanin formation in the fruit of *annuum*. The formation of anthocyanin has also been noted by AUGUSTIN (1907) in other *Capsicum* fruits.

The shape of the placenta is in accordance with the fruit shape of *minimum* and *annuum*. The septa are incomplete in both varieties but not consistently so in *minimum*.

During the development of ovary and fruit there is one cell layer that is very early noticeable. These cells are called the giant cells which directly adjoin the inner epidermis. There is no cell division in the early development of this cell layer in the ovary (KLEMT 1907, AUGUSTIN 1907, KANO et al. 1957).

In the septum of both varieties, cell division takes place during pre-anthesis and only in the epidermis also during anthesis and post-anthesis. Cell elongation in particular takes place in the septum during anthesis and post-anthesis. Unlike the wall of the ovary and the pericarp, the septum has no zone of cell division during these stages. Because of this, large intercellular spaces arise during the development of the septum. The epidermal cells of the septum are rich in cytoplasm during fruit development. These cells have a glandular function and produce capsaicin (AUGUSTIN 1907, HEISER & SMITH 1953, ROSENGARTEN 1970). Capsaicin gives the strong taste to fruits of both varieties and probably occurs also in other parts of the fruit (AUGUSTIN 1907).

The development of the vascular tissue in the flower and especially in the ovary and fruit are under investigation.

#### ACKNOWLEDGEMENTS

The author wishes to thank Prof. Dr. A. L. Stoffers for his stimulating and helpful discussions and critical revision of the text, and Miss M. A. W. Verheijen for her microtechnical assistance. Mr. J. C. Rigg's correction of the English text is gratefully acknowledged.

#### REFERENCES

- ASAHIRA, T., Y. TAKEDA, T. NISHIO, M. HIRABAYASHI & Y. TSUKAMOTO (1967): Studies on fruit development in tomato I: Ovule development and content of diffusible auxin in synthetic auxin- and gibberellin-induced parthenocarpic tomato fruits in relation to their development. *Mem. Res. Inst. Food Sc. Kyoto University* **28**: 47-74.
- AUGUSTIN, B. (1907): *Historisch-kritische und anatomisch-entwicklungsgeschichtliche Untersuchung über den Paprika*. Thesis, Németbogsán.
- COCHRAN, H. L. (1938): A morphological study of flower and seed development in Pepper. *J. Agr. Res.* **56**: 395-419.
- ERWIN, A. T. (1929): A systematic study of the peppers (*Capsicum frutescens* L.). *Proc. Amer. Soc. Hort. Sci.* **26**: 128-131.
- FINGERHUTH, A. (1832): *Monographia generi Capsici*. Düsseldorfii.
- FRIDVALSZKY, L. & J. NAGY (1966): The differentiation, microscopic and submicroscopic structure of giant cell wall in the pericarp of *Capsicum annum* L. *Acta Agron. Acad. Scient. Hung.* **15**: 69-78.
- HEISER, C. B. (1969): *Nightshades, the paradoxical plants*. W. H. Freeman & Co., San Francisco.
- & B. PICKERSGILL (1969): Names for the cultivated *Capsicum* species (Solanaceae). *Taxon* **18**: 277-283.
- & P. G. SMITH (1953): The cultivated *Capsicum* Peppers. *Economic Botany* **7**: 214-227.
- HUNZIKER, A. T. (1954): Synopsis of the genus *Capsicum*. *Compt. Rend. 8th Internat. Cong. Bot. Paris* Sections 3-6: 73-74.
- JENSEN, W. A. (1962): *Botanical histochemistry*. W. H. Freeman & Co., San Francisco.
- KANO, K., T. FUJIMURA, T. HIROSE & Y. TSUKAMOTO (1957): Studies on the thickening growth of garden fruits. I. On the cushaw, egg-plant and pepper. *Mem. Res. Inst. Food Sc. Kyoto University* **12**: 45-90.
- KLEMT, F. (1907): *Über den Bau und die Entwicklung einiger Solanaceenfrüchte*. Thesis, Berlin.
- MUÑOZ FLORES, L. & B. PINTO CORTÉS (1967): Taxonomy and geographical distribution of peppers grown in Mexico. *Proc. Caribbean Region Amer. Soc. Horticult. Sci.* **10**: 131-147.
- MUNTING, A. (1696): *Nauwkeurige beschryving der aardgewassen*, François Halma & Pieter vander Aa, Utrecht.

- MURRAY, M. A. (1945): Carpellary and placental structure in the Solanaceae. *Bot. Gaz.* **107**: 243–260.
- NITSCH, J. P. (1965): *Physiology of flower and fruit development*. In: W. RUHLAND (ed.) *Encyclopedia of plant physiology* **15**: 1537–1647. Springer, Berlin.
- ODLAND, M. L. & A. M. PORTER (1941): A study of natural crossing in peppers (*Capsicum frutescens*). *Proc. Am. Soc. Hort. Sci.* **38**: 585–588.
- QUAGLIOTTI, L. (1968): Carpological observations on some pepper populations from Piedmont. *Riv. Ortoflorofruttic. Ital.* **52**: 259–268.
- ROSENGARTEN, F. (1970): *The book of spices*. Livingston Publ. Co. Wynnewood, Pa, USA.
- SHAW, F. J. F. & K. S. A. R. KHAN (1928): Studies in Indian chillies. *Mem. Dep. Agr. India Bot. Ser.* **16**: 59–82.
- SMITH, O. (1935): *Pollination and life-history studies of the tomato (*Lycopersicon esculentum* Mill.)*. Thesis, Cornell University, Ithaca, New York.
- SMITH, P. G. & C. B. HEISER (1951): Taxonomic and genetic studies on the cultivated peppers, *Capsicum annuum* L. and *C. frutescens* L. *Amer. J. Bot.* **38**: 362–368.
- SPURR, A. R. & W. M. HARRIS (1968): Ultrastructure of chloroplasts and chromoplasts in *Capsicum annuum* I: Thylakoid membrane changes during fruit ripening. *Amer. J. Bot.* **55**: 1210–1224.
- TERPÓ, A. (1966): Kritische Revision der wildwachsenden Arten und der kultivierten Sorten der Gattung *Capsicum* L. *Feddes Repertorium* **72**: 155–191.
- WETTSTEIN, R. VON (1897): Solanaceae. In: D. ENGLER & K. PRANTL, *Die natürlichen Pflanzenfamilien* IV, 3b. Wilhelm Engelmann, Leipzig.
- WILSON, Y. (1960): The *Capsicum* pepper of West Africa I. The species and range of variation. *J. W. Afr. Sci. Ass.* **6**: 78–95.