Annals of Botany **85**: 815–830, 2000
doi:10.1006/anbo.2000.1147, available online at http://www.idealibrary.com on IDEAL®

Paintings (1769–1774) by A. N. Duchesne and the History of *Cucurbita pepo*

HARRY S. PARIS

Department of Vegetable Crops, Agricultural Research Organization, Newe Ya'ar Research Center, P.O. Box 1021, Ramat Yishay 30-095, Israel

Received: 25 January 2000 Accepted: 10 February 2000

A. N. Duchesne (1747–1827), a French botanist and horticulturist possessing a keen power of observation for variation in plants, depicted accurately and in painstaking detail the fruits of 98 *Cucurbita* cultivars and their offspring resulting from cross-pollination, between 1769 and 1774. These 364 drawings of *Cucurbita*, most of which are watercolour paintings of *C. pepo*, are preserved in the Central Library of the Muséum National d'Histoire Naturelle in Paris, France, where they are catalogued as manuscript no. 5007. Black-and-white photographs of approximately half of the drawings are housed in the L. H. Bailey Hortorium in Ithaca, New York, USA. The depictions are dated and numbered, with the numbers corresponding to the brief verbal descriptions published in Duchesne's (1786) *Essai sur l'histoire naturelle des courges* (Paris: Panckoucke). Twenty of the drawings of *C. pepo* are reproduced and interpreted herein. They include the earliest known pictures of the economically important cocozelle and straightneck types of squash, as well as the ornamental bicolour and crown gourds. Duchesne's collection of domesticated *C. pepo* contained a far lower proportion of edible-fruited forms than occurs in existing cultigens of this species.

Key words: Pumpkin, squash, gourd, botany, horticulture, crop history, crop evolution, scientific illustration.

INTRODUCTION: THE DISJUNCT HISTORICAL RECORD OF *CUCURBITA PEPO*

Cucurbita pepo L. is perhaps the most variable species in the entire plant kingdom with regard to fruit characteristics (Naudin, 1856). This species encompasses various forms whose fruits are used for culinary purposes, known as pumpkins and squash, as well as various kinds cultivated for ornament, or found growing wild, known as gourds. Originating in North America, *C. pepo* was domesticated thousands of years ago by native populations of that continent (Cutler and Whitaker, 1961). *C. pepo* arrived in Europe within 50 years of European contact with North America. From illustrations published in the botanical herbals of the Renaissance, it can be ascertained that representatives of at least three groups of edible cultivars, the pumpkins, scallop squash, and acorn squash, as well as several kinds of gourds of this species arrived in Europe before 1600. There is evidence suggesting that several groups of edible cultivars subsequently originated in Europe, perhaps by chance crossing of culinary forms with gourds, as early as the 16th century (Paris, 1989).

Most of the early records of *C. pepo* in Europe are illustrations that appeared in the botanical herbals of the Renaissance period. Usually realistic and detailed, most of them are merely black lines on a white background, without shading. Supplementing these are some colour paintings of market scenes by Renaissance artists of northern Europe, in which a variety of different coloured pumpkins can be observed (Zeven and Brandenburg, 1986). The last work of this period to contain information and many illustrations of *C. pepo* is the *Stirpium sciagraphia et icones* of Chabrey (1666), but this is a somewhat modified version of the *Historia plantarum universalis* of J. Bauhin (1651). Whilst nearly all of the illustrations presented in these two works are merely copies from other tomes, many of the descriptions therein are original. From the mid-17th century until the mid-19th, with the publications of Alefeld (1866), Burr (1863), Naudin (1856, 1860) and Vilmorin (1856), there appeared but few original illustrations or original, detailed descriptions of *C. pepo* cultivars or their fruits. For this reason, accurate mid-18th century depictions of the fruits of this species would be invaluable for tracing the history and development of *C. pepo*, its subspecies, and cultivar-groups. This is exactly the legacy of the French horticulturist and botanist, Antoine Nicolas Duchesne (1747–1827), who painted lifelike watercolours of the fruits of dozens of cultivars from 1769 to 1774.

My objectives are to review the background botanical information concerning these paintings, to interpret the numbering system that Duchesne employed for them, and to explain their importance for understanding the history of *C. pepo* under domestication.

BACKGROUND INFORMATION ON A. N. DUCHESNE'S WORK ON *CUCURBITA*

Linné (1753, 1767) listed six species of the genus *Cucurbita*. Two of these six, the watermelon and the bottle gourd, were removed from the genus *Cucurbita* and placed in separate

0305-7364/00/060815+16 $35.00/00

genera, *Citrullus* and *Lagenaria*, respectively, by botanists in the 1830s. Of Linné's other four *Cucurbita* species, *C. pepo* was based on pumpkins, *C. verrucosa* on warted gourds, *C. melopepo* on scallop squash, and *C. ovifera* on smooth, egg-shaped gourds, all of which are recognized today as belonging to the same species, *C. pepo*.

Duchesne was an early follower of the binomial system of species nomenclature established by Linné (Lee, 1964). However, Duchesne insisted that separate binomials be applied to two populations not merely on the basis of divergent phenotype, but rather on the basis of inability to hybridize and produce fertile offspring. Thus, in his idea of what constitutes a species, Duchesne was far ahead of almost all of his contemporaries. He had already applied this concept in the publication, at age 19, of his classic book on the species of the genus of strawberries, *Fragaria* (Duchesne, 1766).

Quite possibly, Duchesne was also familiar with the work of another contemporary, Koelreuter. Koelreuter (1766) reported that the result of his cross-pollinating two forms of *Cucurbita*, one a small gourd and the other a large pumpkin, was a hybrid form intermediate in fruit size and other characteristics.

Duchesne undertook his study of *Cucurbita* in 1768. He explained (1786*a*,*b*) that he chose to work with *Cucurbita* because the great variability that it possessed resulted in its being very confused, to an extent rarely seen in other genera, in botanical texts. He was determined to alleviate the confusion by studying hybridization within the genus. He recorded and documented his results with watercolour paintings, realistic and true to natural colour and to size, of the fruits of dozens of cultivars and their offspring resulting from cross-pollination, for one or more generations.

Several years after completing his work on *Cucurbita*, Duchesne prepared a manuscript which he read before the Académie Royale des Sciences in Paris. Records at the Archives, Académie des Sciences, Institut de France, Paris, indicate that this 'mémoire' was entitled 'Essai d'histoire naturelle des Pépons et sur les variétés produites par la fécondation de l'un, par les poussières de l'autre'. It must have been quite lengthy, as it was read in three instalments, on 28 April, 8 May and 19 May 1779. The reading was accompanied by the paintings, for illustration and documentation. A report summarizing and praising the work was submitted to the Académie on 28 August by de Jussieu and Tillet (1779). Perhaps the first publication mentioning the existence of these paintings by Duchesne was that of Buc'hoz (1777).

According to Lamarck, who was editor of the *Encyclopédie méthodique, botanique* for which Duchesne prepared an article on *Cucurbita* (Duchesne, 1786*a*), the paintings had first been displayed to the king at Versailles in 1779 and then to the Académie des Sciences, before they were retired to the Cabinet des Estampes of the Bibliothèque Royale. In 1793, with the publication of Duchesne's article on *Cucurbita* in the *Encyclopédie méthodique, agriculture* (Duchesne, 1793), the paintings were still referred to as being at the Bibliothèque Royale (which became the Bibliothèque Nationale). It may have been at this time, the darkest days of the French Revolution, that they were moved, for 30 years later, Sageret (1826) and Sylvestre (1827) mentioned that the paintings were at the Bibliothèque Centrale, Muséum National d'Histoire Naturelle, where they are located today. To the best of my knowledge, over a century elapsed before the paintings were referred to again in publications, by Bailey (1948) and Duprat (1964).

The manuscript of Duchesne's mémoire to the Académie Royale des Sciences has been lost; it is not at the Académie nor at the Muséum. Nor is it at the Bibliothèque Nationale, which harbours a number of Duchesne's manuscripts. The Bibliothèque Nationale does contain a manuscript (Duchesne, 1786*c*), a draft which Duchesne prepared for publication in the encyclopedic series of the era, probably at the behest of the publisher, C. J. Panckoucke. From comparison with the notes by de Jussieu and Tillet (1779), it seems that this manuscript must be a very brief summary of the work presented in 1779 by Duchesne before the Académie. After editing, the text was published in two parts, in the *Encyclopédie méthodique, botanique* (Duchesne, 1786*a*) and the *Encyclopédie méthodique, agriculture* (Duchesne, 1793). The text was published in its most complete and least abridged form as a small book, *Essai sur l'histoire naturelle des courges* (Duchesne, 1786*b*). Rare, but known to several historians of botany (Pritzel, 1872; Davy de Virville, 1954; Stafleu, 1964), the *Essai* has escaped the attention of cucurbitologists until now.

Presumably, the lost manuscript of 1779 contained the details of how Duchesne conducted his experiments, including the sources of his seeds and the numbering system he used in designating his watercolour paintings. Based on the existing manuscript and published text, together with the report by de Jussieu and Tillet (1779) on Duchesne's mémoire, the methodology appears to have been as follows: Duchesne interplanted in the same garden, on a small scale in 1768 but on a much larger scale beginning in 1769, one or several seeds from the various *Cucurbita* forms he had obtained. He cross-pollinated the various forms; seeds were saved from the fruits developing from cross-pollination, and several seeds from many of the fruits were planted the following year. This planting of successive offspring from cross-pollination was repeated for several generations (years), until 1773. Mostly during the ensuing winter months, Duchesne carefully observed and drew realistically, at natural size and true to colour, the fruits that he had obtained during the previous summer. By this careful study, he was able to ascertain that while most of the *Cucurbita* forms hybridized freely with one another, there were two small minorities that did not cross with the majority nor with each other. In this fashion, he was able to establish that the various forms of *Cucurbita* in his possession belonged to three species. One of these species was highly polymorphic, encompassing forms which Linné (1753, 1767) had previously designated as four separate species, *C. pepo*, *C. verrucosa*, *C. melopepo* and *C. ovifera*. This polymorphic species was referred to by Duchesne as *C. polymorpha*, but retains today the name *C. pepo* because Linné's designation has precedence. Two species were established by Duchesne through his failed attempts at hybridization with *C. pepo*: *C. maxima* and *C. moschata* (Duchesne, 1786*b*).

Duchesne's species designations within *Cucurbita* were not widely accepted initially. Lamarck did not accept *C. moschata* as being separate from *C. pepo* but rather considered it a subspecific entity of the latter; being editor of the *Encyclopédie méthodique, botanique*, he had it published as such (Duchesne, 1786*a*). De Candolle (1805) and Poiret (1818) added confusion by applying binomial nomenclature to Duchesne's five subspecific groups of *C. pepo*, as if to denote them as species. Spach (1838) may have been the only pre-1850 author to fully adopt the *Cucurbita* species demarcations laid down by Duchesne. Only after Naudin (1856) had thoroughly reviewed the genus were the species of *Cucurbita*, as designated by Duchesne, generally accepted.

Duchesne (1786*b*) designated five subspecific groups for his *Cucurbita polymorpha* (*C. pepo*): the smooth, thin-rinded orange gourd and its relatives, *C. p. Colocyntha*; the smooth, thick-rinded pear gourd and its relatives, *C. p. pyridaris* (misprinted as '*pyxidaris*'); the warted gourd, *C. p. verrucosa*; the pumpkin and its long-fruited relatives, *C. p. oblonga*; and the scallop squash and its relatives, *C. p. Melopepo*. The most recent intraspecific treatment of *C. pepo* (Paris, 2000) is two-tiered, the upper level botanical and the lower level horticultural. Botanically, *C. pepo* consists of three subspecies, *pepo*, *ovifera* and *fraterna*, the latter consisting of wild forms only. These subspecies were defined on the basis of allozyme variation, seed morphology and phenotypic characteristics (Decker, 1988). Horticulturally, *C. pepo* contains eight groups of edible-fruited cultivars: pumpkin, cocozelle (Italian marrow), vegetable marrow, zucchini (courgette), scallop (custard marrow, patisson), acorn, straightneck, and crookneck; the first four belong to ssp. *pepo* and the latter four to ssp. *ovifera*. These groups were defined on the basis of fruit shape (Paris, 1986*b*). *C. pepo* also contains three groups of non-culinary forms: spherical and flattened; warted; and oviform and pyriform gourds; the first two have been placed with ssp. *pepo* and the latter with ssp. *ovifera* (Decker, 1988; Paris, 2000). Duchesne's *C. p. Colocyntha*, *C. p. verrucosa* and *C. p. oblonga* included the spherical and flattened and warted gourds as well as pumpkins, cocozelles and vegetable marrows, all *C. pepo* ssp. *pepo*; his *C. p. pyridaris* and *C. p. Melopepo* included the oviform and pyriform gourds and scallop, acorn and straightneck squash, all *C. pepo* ssp. *ovifera*.

L. H. Bailey (1929), who had been familiar with Duchesne's article in the *Encyclopédie méthodique, botanique* (Duchesne, 1786*a*), wrote that Duchesne's work was 'the foundation of our knowledge of the cultivated cucurbitas'. Upon learning that the paintings referred to in the article were at the Muséum National d'Histoire Naturelle, Bailey corresponded with a Professor H. Humbert of the Muséum in 1946. After considerable effort, the Duchesne drawings were found in the central library of that institution, but were unaccompanied by any written material. Bailey arranged to have photographs taken of the drawings bearing numbers that had been referred to in the article in the *Encyclopédie méthodique, botanique*, of which there were nearly 200. These photographs are now the property of the Hortorium bearing his name. Although he considered Duchesne's work to be 'the real beginning of *Cucurbita* taxonomy', Bailey (1948) wrote that he was unable to elucidate whatever taxonomic significance the drawings might have had. Apparently, he was unable to decipher Duchesne's numbering system.

From the date of my own initial inquiry to the Bibliothèque Centrale, Muséum National d'Histoire Naturelle concerning the drawings, a year and a half passed before they were found. I viewed the paintings at the Muséum in person in July 1997. The collection consists of 364 drawings on 258 plates (Bailey had been told that there were 259; therefore, one might be missing, apparently no. 48) contained in two voluminous portfolios, 64 × 48 cm. Altogether, 615 fruits are illustrated, the majority in watercolour, a small number in pencil (black-and-white). The colour illustrations are indeed lifelike, and do not appear to have faded over the 200 years since they were drawn. The collection is catalogued at the library as manuscript no. 5007, but in fact, as Bailey had been informed, it contains no manuscript. Apparently, this was the missing mémoire; perhaps it was removed by Duchesne himself for reference when he was requested by C. J. Panckoucke, the publisher, to prepare an article on *Cucurbita*.

DUCHESNE'S NUMBERING SYSTEM

Lamarck, in his introductory notes to the Duchesne (1786*a*) article in his *Encyclopédie méthodique, botanique*, wrote: 'On observera que les numéros cités dans les descriptions, indiquent ceux des dessins coloriés que M. Duchesne a faits d'après nature . . . '. By comparing the numbers used in the descriptions in the text with those of the paintings of fruits possessing easily discernable characteristics, such as striping, bicolour pattern, and warts, I was able to verify with certainty that the numbers do indeed correspond exactly.

The numbers can be sorted into three categories. One is the number alone (e.g. 14, 28, 43, 68), another is a number with a letter or letters suffixed (e.g. 43c, 47b, 47ba, 68a), and the last, which appears only in association with no. 14, has a superscript number (14^1, 14^4, etc.).

The *Essai sur l'histoire naturelle des courges* (Duchesne, 1786*b*) is not only more complete than the article in the *Encyclopédie méthodique, botanique* (Duchesne, 1786*a*), it is also more easily understood. It contains, on page 7, a table of Duchesne's classification of the species of *Cucurbita*, unabridged by Lamarck. Under *C. polymorpha* (=*C. pepo*) are listed five subspecific groups. These groups are set off in the text by headings, on pages 22 to 41. The numbers are referred to under these headings. Numbers 1–13 are cultivars of the group of orange and related gourds; nos 14–31 are the smooth, thick-rinded gourds, nos 32–44, 46 and 47 are warted gourds, nos 45 and 48–79 are pumpkins and long-fruited squash; and nos 80–93 are scallop squash and their relatives. That the numbers designate individual cultivars is clear from the text, for example: '. . . les autres numéros de 15 à 28, donnent de véritables variétés qui doivent toutes se rapporter à la race des Cougourdettes . . .'.

The term 'variétés', as used by Duchesne, in some instances refers to what today we would call cultivars or varieties ('véritables variétés') but in most instances it refers to variants produced by a variety. The term 'variantes' was coined later, as can be learned from Sageret (1826). The second category of numbers, that is numbers with a letter or letters suffixed, refers to the variants produced by cultivars. Specifically, each depicted fruit that is labelled with a number having a letter suffixed was from a plant that had been grown from a seed taken from a cross-pollinated fruit of a cultivar. Quite likely, two centuries ago the cultivars were not pure lines. Being heterozygous, the parents would have produced a greater number of variants than if Duchesne's experiment were to be repeated today using extant, modern, more homozygous counterparts. Thus, cultivar no. 37, an orange, warted gourd, produced dissimilar variants: 'J'ai vu le no. 37 produire des variétés assez dissemblables; 37e étoit aussi bien que 39, si abondant en bosselures . . .; 37e avoit la peau très-pâle . . .'. Number 43, an oval, bicolour (orange and green), warted gourd, produced progeny that were quite different from one another ('Le no. 43, qui se trouvoit ovale, chargé de peu de bosselures, mais verd & marqué seulement vers la queue d'un très-grand panache jaune, m'a produit des variétés nombreuses & assez différentes'): one of its offspring, no. 43a, had the same shape, size, and warts but no orange area; another offspring, no. 43b, had the same colouration and warts as no. 43 but was smaller and rounder; 43c was also rounder and green and yellow, but had no warts; 43d had the same type of fruit as the parent but the colour was muted; 43f and 43g were brilliantly coloured with stripes and markings. For two cultivars related to scallop squash, nos 80 and 82, Duchesne obtained 'dans la postérité de ces Pastissons aucun fruit de forme semblable, 80a 80b 82c & 82b, fussent semblables en substance de pulpe & de peau'.

Furthermore, each letter suffixed represents one generation of cross-pollination. For example, both 43a and 43b are from the same cultivar, 43, but were produced by different variant plants that resulted from one generation of cross-pollination on 43. Numbers 43aa and 43ab were produced by saving seeds from plant 43a whereas no. 43ba was produced by saving seeds from plant 43b. Thus, nos 43aa, 43ab, and 43ba all resulted from two generations of cross-pollination, the starting point being cultivar no. 43; 43aa and 43ab are from a family different from that of 43ba, because the progenitor of the first two was 43a and the progenitor of the latter was 43b. Another example: 'En seconde génération, des variations biens plus grandes . . . 82ba étoit devenu une Cougourdette, en Coloquinelle; 82ca au contraire étoit un Giraumon blanc . . .'. Indeed, the second generation of forced cross-pollination would have involved highly heterozygous parents and would be expected to produce much more variation in the progeny.

Many of the drawings bear dates. It can be noticed from the dates that, for a given family, fruits having more letters suffixed are never dated with a year earlier than those having fewer. The fruits that Duchesne obtained from his research plots in the late summer or autumn of each year could be kept for months, or even just over a year but, except for some gourds, it would be highly unlikely that they could be kept for longer than that. In some pictures several fruits are depicted and the suffixes appear as one letter on top of another and the last letter in the suffix appears next to each individual fruit. The fruits in these depictions are from the same generation, and their depiction together was undoubtedly in order to save space, paper, time and effort.

The third category, a number with a superscript number, appears only for no. 14. What Duchesne had in mind was slight variation within the same cultivar or sort, as can be learned from the text: 'Sous le no. 14 se trouvent de légères differences de forme, de grosseur & de panaches, qui ne peuvent porter le nom de variétés . . .'. Interestingly, nos 15–28, which are somewhat similar in shape, size, and colour pattern to no. 14, are given separate numbers by Duchesne because he recognized them as 'véritables variétés'.

The no. 14 series is the most problematic for a complete understanding of Duchesne's numbering system. The painting labelled no. 14 was drawn in February 1770, and fruits labelled 14^1 to 14^{12} were drawn during that same winter, from December 1769 to February 1770. Number 14a, which is one of the progeny, was drawn in April 1770. Evidently, Duchesne had originated his study on the effects of cross-pollination with no. 14 two seasons earlier, in 1768, by growing plants of it and saving its seeds. Thus, he already had seeds of 14a available for sowing in 1769. The fruits for the paintings labelled 14 and 14^1, etc. were perhaps grown in 1769, from remnant seeds of the same cultivar, together with 14a. Or, nos 14^1 to 14^{12} are fruits that had been preserved for over a year, from the 1768 growing season. As the fruits differ in shape from egg to pear, they must be from more than one plant. They also differ in hue, being either green, yellow, or bicolour, green and yellow. In the case of bicolour fruits, the area and distribution of the green and yellow varies among fruits on the same plant! The bicolour variegation in 'Bicolour Pear' and its basis in genetic instability and phenotypic plasticity has been well-documented by Shifriss (1955, 1965, 1966, 1981).

A few of the illustrations bear captions, cited from the Latin designations in the works of Caspar Bauhin (1623) and Jean Bauhin (1651). Duchesne added these captions to forms which he considered to be similar or identical to those described by those botanists.

The numbers of the Duchesne pictures of *C. pepo* fruits range from 1 to 93. Cultivar no. 48 is missing from the collection, although two first-generation offspring, 48a and 48b, are present. Numbers 53 and 55 are pencil sketches only. The remaining 90 depictions of cultivars are watercolour paintings. The overwhelming majority of these cultivars are obsolete. Some 46 of them are orange gourds, pear gourds, warted gourds, and other related ornamental gourds. Of the remainder, only a small minority were specifically mentioned by Duchesne as being well-adapted for culinary use.

Some illustrated fruits bear four-digit numbers. Apparently, the collection of drawings in the Muséum represents but a small part of the thousands of fruits Duchesne illustrated. Furthermore, the numbering system described above must have been a transcription from an earlier numbering system and, given the large number of fruits, it is possible that some errors were made in transcribing.

Below is a presentation of 20 of the 364 drawings and an interpretation of their significance with regard to the history of domesticated *C. pepo*. The depictions are described with their numbers, the date appearing on them (if any), and their actual size. Colour is described verbally and designated numerically according to the colour guide of Kornerup and Wanscher (1963).

SOME OF THE DRAWINGS

Drawing no. 1. (Fig. 1)

Dated February 1770. 6·6 × 7·2 cm. Dark, very intense orange ($6B_8$). This is a gourd known as 'Orange'. Similar cultivars, differing somewhat in shape and intensity of colour, were illustrated as nos 2–5. Similar or identical forms had arrived in Europe by no later than the mid-16th century, having been illustrated by Fuchs (1542). At least two forms, 'Orange' and 'Orange Ball', are still available in the seed trade today.

Drawing no. 7. (Fig. 2)

Dated 26 December 1769. 9·7 × 12·6 cm. Quadricolour, intense and light green ($28F_8/29C_4$) and orange ($5A_8/5A_4$). Longitudinally striped with intensely coloured broad stripes alternating with lightly coloured narrow stripes. Superimposed on this pattern is the latitudinal bicolour variegation. Considered by Duchesne to be closely related to the orange gourds, this is a bicolour, striped version of the gourd known as 'Flat', referred to and illustrated by Shifriss (1965). Bauhin (1651) was probably the first to give a description of the bicolour variegation (Paris, 1986*a*) and Weinmann (1739) was perhaps the first to illustrate it, although poorly. This painting, together with the others of bicolour fruits by Duchesne, is apparently the first to depict the bicolour variegation in *Cucurbita* fruits realistically. Flat gourds without the bicolour variegation had been known in Europe for some time, having been illustrated first by Fuchs (1542).

Drawing no. 14[1] (Fig. 3)

Dated 10 February 1770. 11·0 × 6·4 cm. Quadricolour, intense and pale green ($28E_8/30A_2$) and orange and yellow–orange ($5A_6/4A_2$). The fruit is longitudinally striped with

FIG. 1. Drawing no. 1. Orange gourd.

FIG. 2. Drawing no. 7. Flat bicolour gourd.

FIG. 3. Drawing no. 14[1]. Pear bicolour gourd.

FIG. 4. Drawing no. 14a. Fruits from a single offspring resulting from one generation of cross-pollination of the bicolour pear gourd.

FIG. 5. Drawing no. 17. Egg bicolour gourd.

FIG. 6. Drawing no. 36. Warted orange gourd.

intensely coloured broad stripes alternating with pale-coloured, narrow stripes. This is the bicolour version of the gourd known as 'Pear'. It differs from the green-fruited cultivar 'Pear' by containing the gene for bicolour variegation (Shifriss, 1955). Duchesne did not consider the bicolour form to be a variety distinct from the green form. Green- and bicolour-fruited stocks have been available as separate cultivars, but the bicolour characteristic is genetically unstable; green-fruited plants occur in bicolour-fruited stocks, and green fruits can occur together with bicolour fruits even on the same plant (Shifriss, 1955, 1965, 1981). 'Pear' arrived in Europe at an early date and seems to have been commonly known, with original illustrations of it having been presented by Fuchs (1542), de L'Obel (1576), Besler (1613), and Parkinson (1640).

Drawing no. 14a. (Fig. 4)

Dated 25 April 1770. Largest fruit is approximately 16 × 11 cm. Quadricolour, intense and pale green ($27E_4$/$29A_2$) and yellow–orange ($4B_7$/$4A_2$). These are fruits from a single plant resulting from open-pollination of a plant of no. 14. Shape about midway between egg and short tapered cylinder, rather like a vegetable marrow squash. I have

FIG. 7. Drawing no. 43. Warted bicolour gourd.

FIG. 8. Drawing no. 45. Pale-coloured vegetable marrow squash.

suggested (Paris, 1989) that the pear gourd is involved in the origin of the vegetable marrow group of squash. The cut fruit (left) clearly displays the lignified rind characteristic of the gourd.

Drawing no. 17. (Fig. 5)

Undated. 7·8 × 5·9 cm. Yet another cultivar of quadricolour gourd, intense and light green ($27F_7/30B_4$) and yellow–orange ($5A_7/4A_5$). This one is egg-shaped and quite small. This fruit is unusual in having two separate yellow–orange regions on the otherwise green fruit. Similar to the egg gourd listed by Linné (1767) as *C. ovifera*.

Drawing no. 36. (Fig. 6)

Dated 27 January 1770. 10·8 × 11·0 cm (not including the warty protuberances). Colour: intense orange ($5A_7$). This is a gourd identical or similar to 'Orange Warted'. As Duchesne noted, the warted gourds were larger than the orange gourd and its relatives as well as the other smooth-rinded gourds, even when the protrusion of the warts is not included in the measurement. Numbers 37 and 38 are quite similar to no. 36, differing slightly in fruit shape and size, and density of the warts. Warted gourds are common and orange is the most frequently encountered colour in these, but separate colours are rarely offered for sale today. What is perhaps the earliest depiction of this kind of gourd appeared in the work of Dalechamps (1587).

Drawing no. 43. (Fig. 7)

Dated December 1769. 15·3 × 10·0 cm (not including the warty protuberances). Bicolour, medium-intense orange ($5A_6$) and grey–green ($28D_4$), with the grey–green in the process of changing to orange. This is probably the first record of a bicolour warted gourd.

Drawing no. 45. (Fig. 8)

Dated 30 January 1770. 19·6 × 12·6 cm. Colour: pale grey–yellow ($2A_2$). This is a vegetable marrow type of squash. It is not referred to in the text.

Drawing no. 61. (Fig. 9)

Dated 17 January 1771. 33·9 × 27·5 cm. Colour: grey–green ($26C_4$) turning orange. This is a pumpkin cultivar having oval fruits. Flesh colour is intense orange ($5A_6$), this intensity of flesh colour being quite unusual for *C. pepo*. Besides being intensely coloured, the flesh is thick and the rind is not lignified, clearly indicating that this cultivar was grown for consumption of the mature fruit flesh (Schaffer *et al.*, 1986). This is one of the more unusual but horticulturally valuable forms depicted by Duchesne. Intense orange flesh colour is a highly desirable characteristic, not just for aesthetic value but also because it indicates high carotenoid content (Murphy *et al.*, 1966). It is a rare characteristic of *C. pepo*, but quite common in *C. moschata* and *C. maxima*. It is not known how Duchesne acquired no. 61 or, for that matter, nearly all of the other cultivars in his collection.

Other pumpkins similar to no. 61 in size and shape, but differing in rind colour (and not cut open to show the flesh colour), are presented as no. 62 (alternating broad dark green and narrow dark orange stripes), no. 64 (intense, dark

FIG. 9. Drawing no. 61. Grey–green pumpkin having intense orange flesh.

FIG. 10. Drawing no. 71. Orange pumpkin.

green) and no. 65 (similar to no. 62, but medium rather than dark orange stripes). As the rinds of these pumpkins were slightly ribbed rather than grooved and were completely or striped green rather than completely orange, they were probably European or Asian cultivars, and not North American. The striped-rinded nos 62 and 65 are quite reminiscent of the Styrian oil-seed pumpkins.

Drawing no. 71. (Fig. 10)

Dated 25 December 1769. 22·1 × 14·5 cm. Medium–intense orange ($5A_6$). This is a small, oblong, grooved, orange pumpkin, typical of the pie pumpkins of eastern North America. The reference to it in the text as a 'concombre d'hiver' perhaps alludes to the well-known

FIG. 11. Drawing no. 76. Green and orange striped cocozelle squash.

FIG. 12. Drawing no. 77. Warted, bicolour squash.

ability of these pumpkins to remain in good condition in storage during the winter months.

Drawing no. 76. (Fig. 11)

Dated 12 December 1770. 52·0 × 19·4 cm. Colour: alternating broad dark yellow–green ($30B_7$) stripes with narrow dark yellow–orange ($4A_7$) stripes. This is clearly a cocozelle squash, even though its stylar end is not bulbous. The ribbiness, lopsidedness and lack of swelling of the stylar end could have resulted if there was an abnormally small number of seeds in the fruit. The 52·0 cm length is as measured along the curvature of the axis of the fruit, two-dimensionally; in life the fruit was probably somewhat longer because of three-dimensional curvature. The dark stripes are broad and not highly contrasting with the narrow light stripes, as in the German cultivar 'Cocozelle Tripolis'. Number 73 was a cocozelle cultivar and no. 74 may have been an incipient cocozelle form, because these fruits are clearly bulbous at the stylar end. The sharp ribbiness of no. 74 is reminiscent of 'Romanesco', an extant short cocozelle from Italy. Numbers 74 and 76 were

described together (no. 73 is not mentioned in the text) under the heading of 'Giraumon verd tendre à bandes & mouchetures', with the comment that striping was associated with forms that were the most delicious. The pictures together with the narrative indicate that, even as early as the mid-18th century, the cocozelles were recognized as a group of cultivars to be appreciated and eaten when the fruits were young and tender.

Drawing no. 77. (Fig. 12)

Dated 4 March 1770. 36·5 × 15·3 cm. Bicolour, dark green ($29C_6$) turning orange and dark orange ($5B_7$). This fruit is slightly ribbed, with a uniform short cylindrical shape, somewhat suggestive of a zucchini, but bicolour and warted. Duchesne considered his no. 77 to be a subvariety of 'Giraumon noir'. While one would have hoped to find under this heading a form having uniformly cylindrical, zucchini-type fruits, instead the description is of forms that had black fruits tapered toward the peduncle end or tapered toward the blossom end, or pale-coloured, striped, or yellow fruits. There is no mention of a form having uniformly cylindrical fruits nor is there anything in the description reminiscent of the modern courgette.

Drawing no. 83. (Fig. 13)

Dated 12 January 1770. 32·0 × 14·5 cm. Colour medium-intense yellow–orange ($4A_6$). This fruit is from what was clearly a cultivar of the straightneck group. Described as being yellow in colour and good for eating, this form was classified by Duchesne with the 'Pastissons barbarins', that is, a relative of the scallop squash. It obviously has a constriction or neck and is warted, as are all modern straightneck cultivars. It had been stood upright for the drawing by cutting off the blossom end, which is convex and pointed in straightneck cultivars. Its overall length must have been between 36 and 38 cm, approximately what would be expected for a mature straightneck fruit. This depiction is important because the earliest known straightneck cultivar was previously reported to have been introduced by the seed trade in 1896 (Tapley *et al.*, 1937). Two other distinct forms having fruits that were of medium size, warted, and yellow were depicted and described by Duchesne under the subheading of 'Pastissons barbarines'. One (no. 88) was bottle-shaped in the manner of some *Lagenaria* gourds, but completely covered with warts, and said to have a very thick, durable rind and not to be suitable for culinary purposes. The other (no. 84) was almost lemon-shaped, distinctly pointed at both ends, and edible, matching exactly the description by Naudin (1856) of a cultivar known to him as 'Coloquinte de Liège'. Duchesne did not describe or illustrate a crookneck squash, a group related to the straightneck, but having densely warted, intense orange fruits.

Drawing no. 85. (Fig. 14)

Dated 2 March 1770. 17·5 × 13·6 cm. Colour: medium-intense orange ($5B_6$). This is an acorn squash, although this

FIG. 13. Drawing no. 83. Yellow–orange straightneck squash.

form is not as deeply and regularly furrowed as acorn squash forms illustrated two centuries earlier and presented by Fuchs (1542) and Theodorus (1590). Nearly all modern acorn squash forms are green; this one might have been green at harvest and lost its chlorophyll to become orange after months of storage.

Drawing no. 91. (Fig. 15)

Dated 15 December 1769. 7·7 × 13·6 cm. Colour: alternating broad medium-intense yellow–orange ($4A_6$) and narrow dark green ($28F_7$) stripes, with the dark stripes located between the scallops. This is a striped cultivar of scallop squash. Number 90 is similar, differing somewhat in shape and having intense orange rather than yellow–orange stripes. Both resemble a cultivar illustrated by Naudin (1860) and Vilmorin (1883) known in France as 'Patisson Panaché' and in the USA as 'Variegated Patty Pan'. The striping pattern is clearly different from that of

FIG. 14. Drawing no. 85. Orange acorn squash.

FIG. 15. Drawing no. 91. Yellow–orange and green striped scallop squash.

the cocozelles and the gourds in the other paintings: here, the dark stripes are narrow and the light stripes are broad.

FIG. 16. Drawing no. 92. Yellow–orange and green crown gourd.

FIG. 17. Drawing no. 92a. Flat-fruited offspring from one generation of cross-pollination of 92.

Drawing no. 92. (Fig. 16)

Dated 6 February 1770. 10·7 × 11·1 cm. Colour: broad medium yellow–orange ($4A_5$) stripes alternating with narrow dark green ($28E_7$) stripes, the latter located in the furrows of the fruit, the same striping pattern as in no. 91. This form is very similar to the cultivar known today as 'Striped Crown of Thorns' or one of the colour types available in the colour mixture 'Shenot's Crown of Thorns'. For many years, only a white-fruited form of this shape was available in the seed trade, indeed this form was illustrated by Bailey (1937) who knew it as the 'Finger Gourd'; it was also among the many ornamental gourds in photographs presented by Shifriss (1965). Heiser (1979) also illustrated the white-fruited form but knew of forms of other colours, including what was said to be green-striped white. This form was classified by Duchesne as a 'Pastisson giraumoné', that is, a relative of the scallop squash.

FIG. 18. Drawing no. 92ap, aq, ar, as, at, au. Six offspring from cross-pollination of 92a.

FIG. 19. Drawing no. 93. Light yellow acorn squash.

Drawing no. 92a. (Fig. 17)

Dated 23 February 1771. 9·2 × 11·4 cm. Colour: alternating broad, medium green–yellow ($1B_5$) and narrow dark green ($27E_7$) stripes. This fruit has more distinct and contiguous darker stripes than its parent predecessor. The dark stripes, as in its predecessor, occur in the furrows.

Drawing no. 92ap, aq, ar, as, at, au. (Fig. 18)

Undated. Fruit aq is 38·1 × 15·7 cm. Pencil, uncoloured, except for the three rind portions at the bottom of the picture. All except for fruit au have narrow, contiguous dark stripes, and most of them are nearly cylindrical in shape. Fruits ap and aq are slightly furrowed and closely resemble 'Delicata'. A fruit very much like 'Delicata' was also illustrated by Naudin (1856). 'Delicata' has been available in the seed trade in the United States since 1894, although its origin was stated by Tapley *et al.* (1937) to be unknown. The sequence of no. 92 is suggestive of a possible origin of 'Delicata' by crossing involving 'Striped Crown of Thorns'.

Drawing no. 93. (Fig. 19)

Dated 31 January 1770. 17·2 × 11·2 cm. Colour: light yellow ($3A_4$). Said to be of good culinary quality, this appears to represent another cultivar of acorn squash, but more elongate and not so deeply furrowed as no. 85.

Drawing no. 93n. (Fig. 20)

Undated. 55·9 × 13·7 cm. Colour: alternating broad intense-dark ($26F_8$) and narrow medium-dark ($26D_5$) green stripes. Contains at bottom a caption: Cucurbita aspero folio flore luteo semiarcus in morem intorta J.B. This caption refers to a heading by J. Bauhin (1651, p. 221), under which that botanist described five forms, one of which had narrow, very long (approx. 60 cm), green-marked fruits. This illustration differs from the others by showing a fully grown, but unripe fruit attached to part of the plant. The plant is a short vine, perhaps the F_1 of a viney plant with a bushy one. The fruit is very much like that of existing cocozelle cultivars, being quite long and bulbous at the blossom end. Such long fruits are often curved. Number 93n perhaps resulted from a cross between no. 93 and no. 76. As

FIG. 20. Drawing no. 93n. One of 14 offspring resulting from cross-pollination of 93.

the fruit is so much like modern cocozelles, it also seems possible that its designation as a cross-pollinated derivative of no. 93 may be an error.

DISCUSSION

These drawings of 93 cultivars of *Cucurbita pepo* present a fascinating exhibition of the forms of this species that were in cultivation over two centuries ago. The fruits illustrated range from small gourds less than 10 cm long to pumpkins and squash over 50 cm long; from pumpkins and gourds with round fruits to scallop squash with flat fruits to cocozelle squash with long, narrow fruits. Likewise, all of the colours, colour combinations, and patterns available in extant cultivars are present in the cultivars illustrated in this collection.

However, the collection differs in several ways from the array of *C. pepo* cultivars presently available. Most noticeable is the high proportion of non-culinary forms represented. Besides the 46 paintings of cultivars belonging to the three groups of small-fruited gourds designated by Duchesne, there are examples of non-culinary forms among the two large-fruited groups. Thus, the majority of forms illustrated by Duchesne are gourds, that is, forms ill-adapted for culinary use. At present, many culinary forms of this species are readily available commercially. Few gourds are obtainable, and these are almost always sold as mixtures rather than as individual cultivars.

Even among the pumpkins and squash illustrated by Duchesne, many forms have disappeared. For example, the warted forms, of which no. 77 is only one example, as well as a number of weirdly shaped forms depicted in the collection have no currently existing equivalents. On the other hand, others have greatly proliferated. Summer squash (marrow) is now an important crop and the vegetable marrow, cocozelle and straightneck groups of summer squash, represented by nos 45 (Fig. 8), 76 (Fig. 11) and 83 (Fig. 13), respectively, presently consist of very many cultivars.

Missing from the collection are representatives of two other important groups of summer squash: zucchini (courgette) and crookneck. The zucchini squash, which is today the most economically important group of summer squash, apparently did not originate until a century or more after Duchesne's work (Paris, 2000). On the other hand, what appears to be an illustration of the crookneck squash had been published two centuries earlier (Camerarius, 1586; Mattioli, 1586).

North American stocks are poorly represented in the Duchesne collection. Most of his pumpkins have green or green-striped fruits typical of modern cultivars from Europe and Asia. The orange-fruited pumpkins, so common in eastern North America, are depicted in one or perhaps two drawings. The crookneck squash, used for culinary purposes in North America but not in Europe or Asia, is entirely absent from the collection.

The Duchesne depictions show how profoundly cultigens of *C. pepo* could be altered by cross-pollination (compare Figs 3 and 4, and Figs 16, 17 and 18). Until approximately 1930, *C. pepo* cultivars were highly heterozygous (Sinnott and Durham, 1922), and maintenance of uniform stocks was quite difficult because of the outcrossing tendency of this species. The difficulties encountered in maintaining

horticulturally superior stocks of *C. pepo* have been well described by Sabine (1816) and others. Lack of adequate isolation may have hampered efforts to maintain such uniquely shaped stocks as the crooknecks, accounting in part for there being only one pre-19th century illustration of this group of squash. Duchesne's acorn squash, nos 85 and 93 (Figs 14 and 19) are not as deeply and regularly ten-furrowed as those depicted in 16th-century herbals (Fuchs, 1542; Theodorus, 1590), which is suggestive of contamination. Heterozygosity may well have made an important contribution to the bewildering array of fruit forms Duchesne observed as resulting from cross-pollination.

Duchesne carefully studied fruit colour in relation to fruit development, anatomy and shape, and enumerated 14 general observations (Duchesne 1786*b*, pp. 17–22). Among them was that fruit colour is a function of its stage of development; it is not static but instead changes with development, a concept developed, described in great detail, and illustrated by Shifriss (1949). Furthermore, fruits which are most intensely coloured prior to ripening have the most intense colour when ripe, even if they change in hue, an observation whose genetic basis is, at least in part, now known (Paris and Nerson, 1986).

Another of the more important observations was the recognition of the position of the ten nutrient vessels, or main carpellary vein tracts, in relation to the striping and shape of the fruit. Five of these tracts, which can be stronger than the other five alternating tracts, pass from the five main ribs of the peduncle to the sepals. The other five pass from the intermediate region between the five main ribs of the peduncle to the central, main vein of each petal of the corolla. The ten main carpellary tracts can be discerned in the fruit in cross-section. If, instead of being round in cross-section, the fruits are decagonal or ribbed, as in many cultivars of pumpkins and vegetable marrow, cocozelle and zucchini squash, the vein tracts occur in the ribs (protrusions) of the decagon; alternatively, if the fruits are furrowed in cross-section, as in the acorn and scallop squash, the veins occur in the furrows, as illustrated by Bailey (1937). For striped fruits, the position of the vein tracts is readily recognized: the narrower stripes, whether light- or intense-coloured, occur over and adjacent to the vein tracts and the alternating, broader stripes occur in the areas between the vein tracts.

Duchesne discussed the bicolour characteristic at greater length than any other. He noticed that the yellow and/or orange area always occurs in the medial region of the fruit and usually nearer the peduncle end rather than the stylar end. When the yellow area of a bicolour fruit is extensive, it may leave only a green ring or almost no green at all around the peduncle and a larger green area nearer the distal end. Often the yellow area extends around only two-thirds or three-quarters of the circumference of the fruit, leaving a zone of green connecting the proximal and distal green regions of the fruit. The yellow area was observed to be most extensive in the narrower portions of the fruit. Many years later, these observations were confirmed and illustrated and their genetic basis, in part, illuminated (Shifriss, 1955, 1965, 1966, 1981; Shifriss and Paris, 1981).

Most of the bicolour cultivars illustrated by Duchesne were gourds. Four of the 13 cultivars of orange gourd relatives were in fact bicolour, for example, no. 7 (Fig. 2). Of the 18 smooth, thick-rinded, gourds, five were bicolour, such as no. 14[1] (Fig. 3) and no. 17 (Fig. 5). Of the 15 warted gourds, only no. 43 (Fig. 7) was bicolour. Of the 33 pumpkins and their relatives, only three were bicolour; interestingly all three, like no. 77 (Fig. 12), had warts. Of the 14 scallop squash and relatives, none was bicolour. Bicolour variants of various sizes and shapes resulted from cross-pollination. The earliest unquestionable recorded case of a bicolour cultivar grown for culinary use is that of an American cultivar known as 'Cocoanut', which entered commercial channels in 1868 (Gregory *et al.*, 1869; Paris, 1986*a*). Little is known of the origin of 'Cocoanut', but it was originally, in 1869, an acorn squash. Round-fruited variants that had been selected from it by 1883 acquired the name 'Cocoanut', but the original form reappeared soon after under the name 'Golden Heart' (Tapley *et al.*, 1937). Apparently the bicolour variegation originated in the gourds (Shifriss, 1955) and was introgressed into edible-fruited cultivars from them. The origin of some edible-fruited forms from crosses involving gourds seems to be suggested in the drawings of the no. 14 and no. 92 series (Figs 3, 4, 16, 17 and 18), too.

Domesticated *C. pepo* has undergone considerable changes since Duchesne studied this species. What was once considered a minor crop at best, or used as an ornament or for animal food at worst, has become one of the most important vegetable crop species. The *C. pepo* fruits depicted by Duchesne, when compared with their modern counterparts, indicate that there has been a considerable turnover in the cultigens toward kinds fit for human consumption. In spite of this radical change in the constitution of cultivated *C. pepo* over the past 200 years, Duchesne's treatment of the genus *Cucurbita* and of *C. pepo* in particular are consistent with the most recent considerations of these taxa. As Duchesne's observations were unaided by knowledge of modern concepts of genetics and molecular biology, his insight was truly remarkable.

ACKNOWLEDGEMENTS

The 20 Duchesne drawings are presented here with permission of the Bibliothèque Centrale, Muséum National d'Histoire Naturelle, Paris, France. I express my deepest appreciation to Pascale Heurtel of that institution for locating the Duchesne paintings for me and handling my request for their reproduction; to Robert Dirig of the Liberty Hyde Bailey Hortorium, Cornell University, Ithaca, New York, for handling my requests for photocopies and photographs of the Duchesne paintings in the Hortorium; to Madeleine Pinault-Sørensen, Département des Arts Graphiques, Musée du Louvre, Paris and M. C. Miessner of the Département des Estampes of the Bibliothèque Nationale, Paris, for their help in attempting to locate the Duchesne drawings; to Eric de Lussy of the Bibliothèque de l'Institut de France, Paris, for the prompt handling of my request for photocopies of Duchesne's *Essai* and his

biography by Sylvestre; to Claudine Pouret of the Archives, Académie des Sciences, Institut de France, for locating the records of Duchesne's memoir to the Academy; to Monique Refouil of the Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, and P. Ojalvo of the Bibliothèque Sainte Geneviève, Paris, for helping to locate Duchesne's article in the *Encyclopédie méthodique, agriculture*; and to Shemu'el Golan of the Newe Ya'ar Research Center, Israel, for the photography. Contribution no. 102/00 from the Agricultural Research Organization, Bet Dagan, Israel.

LITERATURE CITED

Alefeld F. 1866. *Landwirtschaftliche Flora*. Berlin: Wiegandt and Hempel, 212–227.

Bailey LH. 1929. The domesticated Cucurbitas. *Gentes Herbarum* **2**: 62–115.

Bailey LH. 1937. *The garden of gourds*. New York: Macmillan.

Bailey LH. 1948. Jottings in the Cucurbitas. *Gentes Herbarum* **7**: 447–477.

Bauhin C. 1623. *Pinax theatri botanici*. Basel: Regis, 310–313.

Bauhin J. 1651. *Historia plantarum universalis* **2**: 218–232. Yverdon: Graffenried.

Besler B. 1613. *Hortus eystettensis*. Collectarum plantarum, tertius ordo autumnalium. Nuremburg, plate 2.

Buc'hoz PJ. 1777. *Histoire universelle du regne végétal* **7**(text): 88–91.

Burr F Jr. 1863. *The field and garden vegetables of America*. Boston: Crosby and Nichols, 200–228.

Camerarius J. 1586. *Kreutterbuch*. Frankfurt-on-Main: Feyerabends, 155–157.

de Candolle AP. 1805. *Flore Française* **3**: 691–694. Paris: Agasse.

Chabrey D. 1666. *Stirpium sciagraphia et icones*. Geneva: Gamoneti and de la Pierre, 129–135.

Cutler HC, Whitaker TW. 1961. History and distribution of the cultivated cucurbits in the Americas. *American Antiquity* **26**: 469–485.

Dalechamps J. 1587. *Historia generalis plantarum* **1**: 616–626. Leiden: G. Rovillium.

Davy de Virville A. 1954. *Histoire de la botanique en France*. Paris: Société d'édition d'enseignement supérieur, 78.

Decker DS. 1988. Origin(s), evolution, and systematics of *Cucurbita pepo* (Cucurbitaceae). *Economic Botany* **42**: 4–15.

Duchesne AN. 1766. *Histoire naturelle des fraisiers*. Paris: Didot.

Duchesne AN. 1786*a*. Courge, *Cucurbita*. In: M de Lamarck JBPA, ed. *Encyclopédie méthodique, botanique* **2**: 148–159. Paris: Panckoucke.

Duchesne AN. 1786*b*. *Essai sur l'histoire naturelle des courges*. Paris: Panckoucke.

Duchesne AN. 1786*c*. *Mélanges agronomiques. Plan d'un article pépon pour l'encyclopédie de. . . .* Paris: Bibliothèque Nationale. Manuscript no. 12333.

Duchesne AN. 1793. Courge, *Cucurbita*. In: Tessier AH, Thouin A, eds. *Encyclopédie méthodique, agriculture* **3**: 605–614. Paris: Panckoucke.

Duprat G. 1964. Les dessinateurs d'histoire naturelle, en France au 18e siècle. In: Adanson M, ed. *The bicentennial of Michel Adanson's 'Familles des plantes'*. Part 2. Pittsburgh: Hunt Botanical Library, 451–470.

Fuchs L. 1542. *Vienna Codex 11* **120**: 467–479, **124**: 119–135. Vienna: Austrian National Library.

Gregory JJH, Henderson P, Others. 1869. Notes on new or noteworthy vegetables in 1868. *American horticultural annual 1869*. New York: Orange Judd, 132–142.

Heiser CB Jr. 1979. *The gourd book*. Norman: University of Oklahoma Press, 38–41.

de Jussieu AL, Tillet M. 1779. *H. naturelle des pépons. M. Duchesne*. Paris. Archives, Académie des Sciences, Institut de France, pochette de la séance 28 August.

Koelreuter JG. 1766. *Dritte Fortsetzung der vorläufigen Nachricht, no. 63*. Leipzig: Gleditschischen, 118–119.

Kornerup A, Wanscher JH. 1963. *Taschenlexikon der Farben*. Zurich: Musterschmidt.

Lee V. 1964. Antoine Nicolas Duchesne—first strawberry hybridist. *American Horticultural Magazine* **43**: 80–88.

von Linné C. 1753. *Species plantarum* **2**: 1010–1011. Stockholm: Salvii.

von Linné C. 1767. *Mantissa plantarum* **1**: 126. Stockholm: Salvii.

de l'Obel M. 1576. *Sev stripium histoira* **1**: 641–645. Antwerp: Plantin.

Mattioli PA. 1586. *De plantis epitome utilissima*. Frankfurt-on-Main: Calceolario, 292–297.

Murphy EF, Hepler PR, True RH. 1966. An evaluation of the sensory qualities of inbred lines of squash (*Cucurbita maxima*). *Proceedings of the American Society for Horticultural Science* **89**: 483–490.

Naudin C. 1856. Nouvelles recherches sur les caractères spécifiques et les variétés des plantes du genre *Cucurbita*. *Annales de Sciences Naturelles, botanique, IV* **6**: 5–73, 3 plates.

Naudin C. 1860. Les courges: leurs espèces et leurs variétés. *Flores Serres des Jardins de l'Europe* **12**(1858): 113–125.

Paris HS. 1986*a*. Origin of the edible bicolour-fruited cultivars of *Cucurbita pepo*. *Phytologia* **60**: 447–452.

Paris HS. 1986*b*. A proposed subspecific classification for *Cucurbita pepo*. *Phytologia* **61**: 133–138.

Paris HS. 1989. Historical records, origins, and development of the edible cultivar groups of *Cucurbita pepo* (Cucurbitaceae). *Economic Botany* **43**: 423–443.

Paris HS. 2000. History of the cultivar-groups of *Cucurbita pepo*. *Horticultural Reviews* **25** (in press).

Paris HS, Nerson H. 1986. Genes for intense fruit pigmentation of squash. *Journal of Heredity* **77**: 403–409.

Parkinson J. 1640. *Theatricum botanicum*. London: Cotes, 768–771.

Poiret JLM. 1818. Courge. *Dictionnaire des Sciences Naturelles* **11**: 231–243.

Pritzel GA. 1872. *Thesaurus literaturae botanicae*, new edn. Leipzig: Brockhaus, 92, no. 2441.

Sabine J. 1816. A description and account of the cultivation of a variety of gourd called vegetable marrow. *Transactions of the Horticultural Society of London* **2**: 255–257.

Sageret A. 1826. Considérations sur la production des hybrides des variantes et des variétés en général et sur celles de la famille des Cucurbitacées en particulier. *Annales des Sciences Naturelles, Botanique* I, **8**: 294–314.

Schaffer AA, Boyer CD, Paris HS. 1986. Inheritance of rind lignification and warts in *Cucurbita pepo* L. and a role for phenylalanine ammonia lyase in their control. *Zeitschrift für Pflanzenzüchtung* **96**: 147–153.

Shifriss O. 1949. A developmental approach to the genetics of fruit colour in *Cucurbita pepo* L. *Journal of Heredity* **40**: 232–241.

Shifriss O. 1955. Genetics and origin of the bicolour gourds. *Journal of Heredity* **46**: 213–222.

Shifriss O. 1965. The unpredictable gourds. *American Horticultural Magazine* **44**: 184–201.

Shifriss O. 1966. Behavior of gene *B* in *Cucurbita*. *Vegetable Improvement Newsletter* **8**: 7–8.

Shifriss O. 1981. Origin, expression, and significance of gene *B* in *Cucurbita pepo* L. *Journal of the American Society for Horticultural Science* **106**: 220–232.

Shifriss O, Paris HS. 1981. Identification of modifier genes affecting the extent of precocious fruit pigmentation in *Cucurbita pepo* L. *Journal of the American Society for Horticultural Science* **106**: 653–660.

Sinnott EW, Durham GB. 1922. Inheritance in the summer squash. *Journal of Heredity* **13**: 177–186.

Spach E. 1838. Histoire naturelle des végétaux. *Phanérogames* **6**: 197–203. Paris: Roret.

Stafleu FA. 1964. Introduction to Jussieu's genera plantarum. In: de Jussieu AL, ed. *Genera Plantarum*. Weinheim: Cramer.

de Sylvestre AF. 1827. *Notice biographique sur M. Ant.-Nicolas Duchesne*. Paris: Huzard.

Tapley WT, Enzie WD, van Eseltine GP. 1937. *The vegetables of New York*, Vol. 1. Part 4. Albany: Lyon, 33–50.

Theodorus J. 1590. *Icones plantarum*. Frankfurt-on-Main: Bassé, 470–479.

Vilmorin A. 1856. *Description des plantes potagères*. Paris: Vilmorin, 105–119.

Vilmorin A. 1883. *Les plantes potagères*. Paris: Vilmorin, 169–191.

Weinmann JW. 1739. *Phytanthoza iconographia* **2**: 284–289, pl. 443–446.

Zeven AC, Brandenburg WA. 1986. Use of paintings from the 16th to 19th centuries to study the history of domesticated plants. *Economic Botany* **40**: 397–408.