Plant Genetics and Genomics: Crops and Models 20

Rebecca Grumet
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Genetics and Genomics of Cucurbitaceae

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Preface

The twenty-first century is a golden age for genetics. Massively increasing DNA sequence information and sophisticated bioinformatic capacity at exponentially decreasing cost allow for a world of knowledge that is no longer limited to model species. Members of the Cucurbitaceae family are among the beneficiaries of these technological gains. The Cucurbitaceae, often referred to as "cucurbits," are probably best known for their large (sometimes extremely large), colorful, and morphologically variable fruits. The most economically important crops are watermelon (*Citrullus lanatus*), melon (*Cucumis melo*), cucumber (*Cucumis sativus*), and various squashes and pumpkins (*Cucurbita pepo, maxima,* and *moschata*), which are produced in widely diverse forms throughout the world. Depending on the specific crop and type, they can be consumed as vegetable or dessert, and in some cases, especially for various squashes and pumpkin, can serve as mainstays of the diet. Additional cultivated crops include bitter, bottle, wax, snake sponge, and ridge gourds, which are primarily cultivated in southern and southeastern Asia. Seeds of cucurbit crops also can be an important source of nutrition. In addition, certain cucurbit species are noted for medicinal properties, and gourd shells have historical uses as containers and musical instruments.

Several genomic initiatives throughout the world are exploring the genetics and genomics of these crops. Genetic features, including diploid genomes and relatively small genome size (~367, 454, 450, and 400 Mbp for cucumber, melon, watermelon, and squash, respectively), facilitate these efforts, and close genetic relationships allow for synergistic approaches. Over the course of the past decade draft genome sequences have been assembled for cucumber, melon, and watermelon; assemblies of *Cucurbita* species are in progress. As would be expected, a major section of *"Genetics and Genomics of the Cucurbitaceae"* is devoted to description of cucurbit genomes and available genomic resources.

Of course genomic information does not exist in a vacuum and must be interpreted within the context of the crop or species and its agronomic, geographic, and evolutionary relationships. The Cucurbitaceae family contains approximately 1000 species, with origins tracing to Southeast Asia prior to subsequent distribution and diversification in Africa and South America. From this great diversity, a small number were domesticated and carried to current crop status. Over the past century, the most extensively cultivated cucurbits have been greatly improved by plant breeders using conventional plant breeding techniques to increase productivity, yield, fruit size, and quality. This volume provides an overview of use of cucurbits and their evolutionary relationships and explores the genetic resources for the cucurbit crops. Much current effort in each of the crops is devoted to incorporation of resistance to critical diseases for which germplasm collections around the world serve as invaluable, critical resources. Looking forward, molecular breeding approaches facilitated by genomic advances are expected to play an increasing role in facilitating crop improvement, including introgression of novel resistance alleles along with other desirable traits.

Finally, the cucurbits are especially noteworthy for several biological features such as unique phloem structure, highly flexible sex expression patterns, extensively diverse fruit size, shape, colors and patterns, and delicious flavors and aromas. Increasing genomic tools and genetic analyses are making major contributions to our understanding of the fundamental bases for these biological phenomena. Thus, collectively, *"Genetics and Genomics of the Cucurbitaceae"* explores the genetic diversity of cucurbit crops, the current state of knowledge of cucurbit genomics, and evolving applications of genetics and genomics for improvement of cucurbit crops and understanding of cucurbit growth, development, and adaptation to their environments.

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Cultivation and Uses of Cucurbits

James D. McCreight

Abstract Cultivated cucurbits have spread through trade and exploration from their respective Old and New World centers of origin to the six arable continents and are important in local, regional and world trade. Cucumber, melon, pumpkin, squash and gourd, and watermelon comprise the major cucurbits. Bitter gourd, bottle gourd, wax gourd, sponge and ridge gourd, and snake gourd are minor cucurbits from a global perspective that are of import to small shareholder farmers, mostly in Asia. Global production of the major cucurbits increased from 1992 through 2013 in terms of area harvested and yield per hectare, and consequently total production. Production per capita, and presumably consumption, increased in parallel with gains in total production. Cucurbits can play an important role in dietary health. They are low in nutritional value, but can be significant dietary sources of vitamins and minerals. Some cucurbits, such as bitter gourd, have medicinal properties. Cucurbits are generally prized for their delicious fruits, which can be sweet, bitter or aromatic, and may be highly perishable or stored for months with little change in quality. The seeds are good sources of vegetable oil and protein. Gourd shells may be used for storage containers, or as musical instruments. The cultivated cucurbits have been greatly improved by plant breeders using conventional plant breeding techniques for more than 100 years; rapidly advancing molecular technologies are being applied to cucurbits to ensure sustainable production, improve fruit quality and shelf life, and develop novel fruit types.

Keywords Cucumber • Melon • Pumpkin • Squash • Gourd • Cucurbit production • Nutritional value • Genetic resources • Disease resistance • Grafting • Plant breeding

Introduction

Cucurbits encompass a diverse group of annual and perennial species, several of which are of commercial importance worldwide. Cucumber (*Cucumis sativus* L.), melon (*Cucumis melo* L.), pumpkin, squash and gourd (*Cucurbita* spp.), and

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Table 1 Number of countries reported by FAO to produce the four major cucurbit crops, 2013

Crop	Species	No. countries
Cucumber & Gherkin[a]	*Cucumis sativus*	142 (72 %)
Melon	*Cucumis melo*	105 (54 %)
Pumpkin, squash & gourd	*Cucurbita* spp.	123 (63 %)
Watermelon	*Citrullus lanatus*	128 (65 %)

FAO. 2015. FAOSTAT http://faostat3.fao.org (Accessed 7 Dec 2015), and percentage of total world countries (www.infoplease.com/ipa/A0932875.html Accessed 7 Dec 2015)

[a]Gherkhin likely refers to small cucumbers rather than to the distantly related, sexually incompatible species, *Cucumis anguria* var. *anguria* (Robinson and Decker-Walters 1997; Whitaker and Davis 1962)

watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] comprise the major cucurbits (Table 1). Members of five additional genera are important to smallholder farmers and home gardens in east, south and southeast Asia: bitter gourd (*Momordica charantia* L.), bottle gourd [*Lagenaria siceraria* (Molina.) Standley], wax gourd [*Benincasa hispida* (Tunb.)], sponge and ridge gourd (*Luffa* ssp.), and snake gourd (*Trichosanthes* ssp.) are minor cucurbits from a global perspective that are of import to small shareholder farmers, mostly in Asia. The current state of the genetics and genomics of the major and minor cultivated cucurbits are reviewed in the following chapters.

Cucurbits have, like many crop species, a long history with human culture (Kistler et al. 2015; Robinson and Decker-Walters 1997; Whitaker and Davis 1962). Low in carbohydrates, they have nevertheless been enjoyed in various forms worldwide; indeed, an Indian tribal person in Madhya Pradesh, India stated, in essence, that “A day without a melon is like a day without the sun.”

A major aspect of cucurbit–human interaction is the movement of cucurbits around the world, far beyond their centers of origin, through exploration and trade. *Cucurbita* ssp. are New World, while the other cucurbits are Old World, either Africa (watermelon) or southern Asia (*Cucumis*, *Momordica charantia, Lagenaria siceraria, Benincasa hispida, Luffa*, and *Trichosanthes*).

Cucurbit Production Worldwide

The four major groups of cucurbits (Table 1) are grown by farmers in 105 (melon) to 142 (cucumber & gherkin) countries across the six hospitable continents (Table 2), among which Asia accounted for 75 % of the area harvested and 83 % of the total production in 2013 (Table 2).

The highest calculated mean yields (tonnes per ha based on FAO statistics for area harvested and total production) were, on average, achieved in Asia (30.7), Australia & New Zealand (23.1), and North America (26.1) (Table 2). Calculated yields varied greatly across the six continents. The range in yields derives from differences in length of growing season, open field *vs.* protected cultivation, and management practices, including irrigation, fertilizer, and pest control.

Table 2 Cucurbit (cucumber, gherkin, gourd, melon, pumpkin, squash, watermelon) cultivation by continent, 2013

Continent	Area harvested (ha)	Production (tonnes)
Africa	856,587 (10.3 %)	11,406,859 (5.0 %)
Asia	6,222,817 (74.8 %)	191,431,365 (83.3 %)
Australia & New Zealand	22,412 (0.3 %)	517,574 (0.2 %)
Europe	746,593 (9.0 %)	16,231,783 (7.1 %)
Northern America	178,478 (2.1 %)	4,651,429 (2.0 %)
South America	294,709 (3.5 %)	5,537,167 (2.4 %)
Total	8,321,596	229,776,177

FAO. 2015. FAOSTAT http://faostat3.fao.org (Accessed 7 Dec 2015)

Table 3 Asia: Cucurbit (cucumber, gherkin, gourd, melon, pumpkin, squash, watermelon) production by region, 2013

Region	Area harvested (ha)	Production (tonnes)
Eastern Asia	3,932,681 (63.2 %)	152,185,158 (79.5 %)
Central Asia	225,939 (3.6 %)	5,348,178 (2.8 %)
Western Asia	635,452 (10.2 %)	13,058,963 (6.8 %)
South-Eastern Asia	281,688 (4.5 %)	4,396,535 (2.3 %)
Southern Asia	1,147,057 (18.4 %)	16,442,531 (8.6 %)
Total	6,222,817	191,431,365

FAO. 2015. FAOSTAT http://faostat3.fao.org (Accessed 7 Dec 2015)

Eastern Asia (China, Japan Korea) accounted for 63 % of the Asian cucurbit production (Table 3). Calculated mean yields (tonnes per ha) ranged from 30.7 (Eastern Asia) to 14.3 (Southern Asia). Detailed statistics are not readily available for the minor cucurbits that are common to Asia, but bitter gourd was reportedly harvested from more than 340 K ha (Dhillon et al. 2016), and bitter gourd was harvested in China from more than 200 K ha of plants grafted onto rootstocks of three cucurbit species (Lee et al. 2010). Thus, minor cucurbits contribute substantially to agricultural production.

North Africa produced 81 % of the total cucurbit production of Africa on 42 % of the area harvested (Table 4). Calculated estimates of mean yields (tonnes per ha) ranged across Africa from a world wide low of 1.6 in the middle of the continent to 25.8 in the north, which is above the world mean of 20.6, where water is more abundant and resources are more readily available for export markets.

Eastern Europe accounted for 69 % of the area harvested but only 51 % of the total production in Europe (Table 5). Northern Europe accounted for 0.4 % and 1.4 % of the area harvested and production, respectively, but its calculated mean yield was 75.4 tonnes per ha; 77 % greater than the mean yield of Europe (42.6). Calculated mean yield for the other parts of Europe ranged from 15.8 (Eastern Europe) to 46.3 (Western Europe).

The USA accounted for approximately 50 % of the area harvested and the total production of North America, followed by Mexico at 30 % for these two measures of productivity (Table 6). The highest calculated mean yields (tonnes per ha) in

Table 4 Africa: cucurbit (cucumber, gherkin, gourd, melon, pumpkin, squash, watermelon) production by region, 2013

Region	Area harvested (ha)	Production (tonnes)
Eastern Africa	61,028 (7.1 %)	434,272 (3.8 %)
Middle Africa	342,738 (40.0 %)	539,583 (4.7 %)
Northern Africa	358,347 (41.8 %)	9,235,405 (81.0 %)
Southern Africa	26,145 (3.1 %)	295,307 (2.6 %)
Western Africa	68,329 (8.0 %)	902,292 (7.9 %)
Total	856,587	11,406,859

FAO. 2015. FAOSTAT http://faostat3.fao.org (Accessed 7 Dec 2015)

Table 5 Europe: cucurbit (cucumber, gherkin, gourd, melon, pumpkin, squash, watermelon) production by region, 2013

Region	Area harvested (ha)	Production (tonnes)
Eastern Europe	519,332 (69.6 %)	8,226,562 (50.7 %)
Northern Europe	2992 (0.4 %)	225,738 (1.4 %)
Southern Europe	194,147 (26.0 %)	6,385,478 (39.3 %)
Western Europe	30,122 (4.0 %)	1,394,005 (8.6 %)
Total	746,593	16,231,783

FAO. 2015. FAOSTAT http://faostat3.fao.org (Accessed 7 Dec 2015)

Table 6 North America: cucurbit (cucumber, gherkin, gourd, melon, pumpkin, squash, watermelon) production by country, 2013

Country	Area harvested (ha)	Production (tonnes)
Canada	8514 (2.5 %)	349,146 (4.0 %)
Costa Rica	6067 (1.8 %)	192,199 (2.2 %)
Guatemala	30,815 (9.1 %)	697,050 (8.0 %)
Honduras	15,074 (4.4 %)	447,025 (5.1 %)
Mexico	104,443 (30.8 %)	2,697,580 (30.9 %)
Panama	4322 (1.3 %)	46,572 (0.5 %)
United States of America	169,964 (50.1 %)	4,302,282 (49.3 %)
Total	339,199	8,731,854

FAO. 2015. FAOSTAT http://faostat3.fao.org (Accessed 7 Dec 2015)

North America were achieved by Canada (41.0) and Costa Rica (31.8), which was followed closely by Honduras (29.6). Calculated mean yield for the USA was 25.3 tonnes per ha.

Brazil accounted for approximately 40 % of the area harvested and the total production of South America (Table 7), while Venezuela was a distant second at 17 % and 19 %, respectively, for these two measures of cucurbit productivity. The highest calculated mean yields (tonnes per ha) in South America were achieved by Peru (24.1) Brazil (24.0), Suriname (21.1) and Venezuela (20.5).

Cucurbit production increased from 1991 through 2013 in terms of area harvested, yield per hectare, and total production (Fig. 1). Watermelon had the largest absolute increase, 1.3 M ha (60 %), compared with cucumber, 0.9 M ha (78 %), melon, 0.3 M ha

Table 7 South America: cucurbit (cucumber, gherkin, gourd, melon, pumpkin, squash, watermelon) production by country, 2013

Country	Area harvested (ha)	Production (tonnes)
Argentina	31,942 (10.8 %)	503,356 (9.1 %)
Bolivia (Plurinational State of)	4311 (1.5 %)	41,030 (0.7 %)
Brazil	114,042 (38.7 %)	2,729,401 (39.3 %)
Chile	11,474 (3.9 %)	224,952 (4.1 %)
Colombia	21,916 (7.4 %)	3,102,86 (5.6 %)
Ecuador	8775 (3.0 %)	107,218 (%)
French Guiana	93 (0.03 %)	1622 (0.03 %)
Guyana	1730 (0.6 %)	14,957 (0.3 %)
Paraguay	30,757 (10.4 %)	145,140 (2.6 %)
Peru	16,232 (5.5 %)	391,092 (7.1 %)
Suriname	130 (0.04 %)	2746 (0.05 %)
Uruguay	2695 (0.9 %)	28,005 (0.5 %)
Venezuela (Bolivarian Republic of)	50,612 (17.2 %)	1,037,360 (18.7 %)
Total	294,709	1,355,075

FAO. 2015. FAOSTAT http://faostat3.fao.org (Accessed 7 Dec 2015)

(32 %), and *Cucurbita*, 0.8 M ha (89 %). Watermelon increased rapidly from the mid-1990s through 2000 and continued to increase at a slower rate (Fig. 1). Cucumber showed a similar trend from 1991 through 2000, but then leveled off. *Cucurbita* steadily increased at a more or less constant rate. Melon increased more gradually starting in 2000, and exhibited greater seasonal variation than the other cucurbits (Fig. 1).

Yields (Hg per ha) of melon and watermelon increased steadily from 1991 through 2013, 97 % and 59 %, respectively (Fig. 1). Cucumber yields increased slightly through 1999 but thereafter increased steadily through 2013, for an increase of 126 %. *Cucurbita* yield increased slightly (20 %) through 2013.

Total production of cucumber and watermelon increased 302 % and 217 %, respectively, from 1991 through 2013 (Fig. 1). Melon and *Cucurbita* production gains were 111 % and 127 %, respectively. Gains in cucurbit production per capita roughly paralleled gains in total production (Fig. 1). Thus, as global cucurbit production increased through a combination of increased area harvested and yield increases, per capita production of major cucurbits increased 141 % overall, and ranged from 69 (melon) to 218 % (cucumber), with increases of 151 % and 80 % for watermelon and Cucurbita, respectively.

Production Methods

Cucurbits may be harvested from monsoon-fed sand dunes of the Thar Desert area of Rajasthan with no other inputs, or they may be grown with modest, e.g., Turkmenistan, or more precise, e.g., lower desert areas of the southwest USA, control of inputs. They may be cultivated under protection with some control of conditions under plastic, e.g., Spain, or more precise control under glass, e.g., The Netherlands.

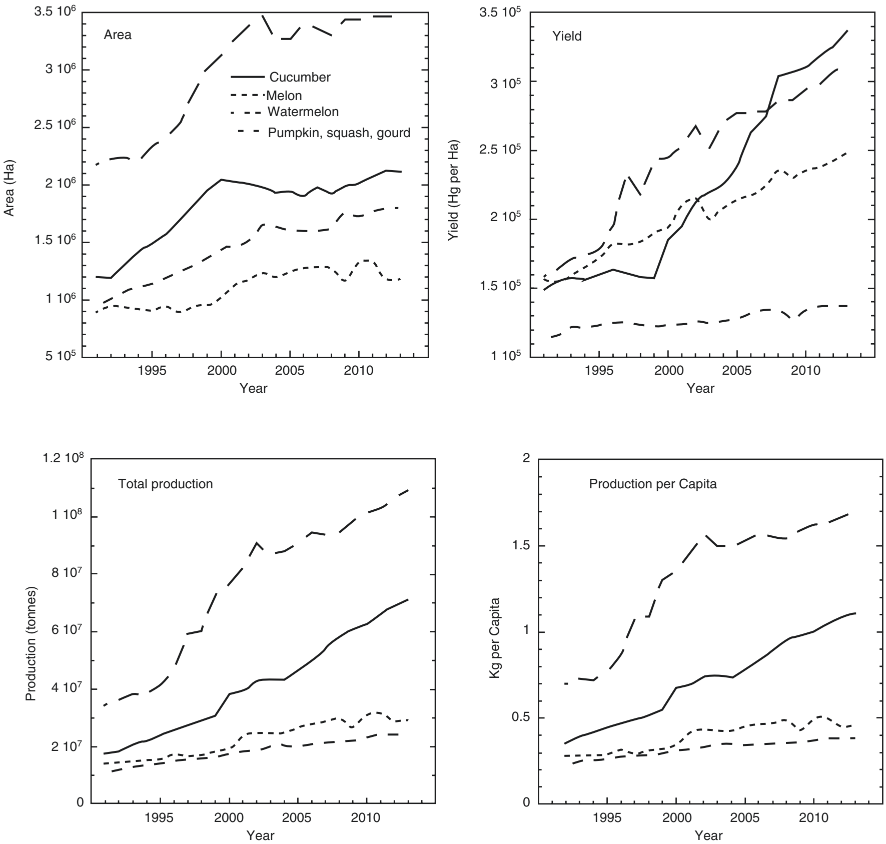

Fig. 1 Trends in area harvested, yield and total production of cucumber, melon, watermelon, and pumpkin, squash and gourd, and their respective production per capita from 1991 through 2013; FAO. 2015. FAOSTAT http://faostat3.fao.org (Area, yield and production-Compare Data link accessed 4 Sept. 2015; Population data for per capita estimate accessed 27 Nov. 2015)

Cucurbits are produced during the dry seasons in areas of abundant rainfall, e.g., south and southeast Asia, and in some of the driest deserts that have external water sources, e.g., Turpan, Xinjiang, China, which is surrounded by the Gobi, Gurbantünggüt and Taklamakan Deserts, or geologic water sources, e.g., Albian Aquifer underlying Algeria, Libya and Tunisia (Foster and Loucks 2006; Mamou et al. 2006; Ouali et al. 2010). Cucurbits are grown in open fields as well under various types of protection, such as wire supported or floating row covers. The plants may be prostrate or trellised. Field cultivation is often done on raised beds for better drainage. Increased soil salinity from surface irrigation in some desert areas must be managed through the use of engineered drainage systems in combination with precision planed (sloped) fields and raised beds, e.g., Imperial Valley, California, USA. Plants in plastic and glass houses may be grown in soil or soilless media, e.g., sand, rockwool, where irrigation and drainage can be precisely managed.

Fig. 2 Irrigated melon in a field claimed from the desert in 2008 by a farmer from the Karakum Desert (in background), Mary, Turkmenistan (Photo courtesy of T.C. Wehner)

The technology used in cucurbit production ranges from low input to maximum input. The native peoples of the Thar Desert area of Rajasthan, India harvest vegetable type melons grown with no other inputs (fertilizer, pesticides) from monsoon-fed sand dunes, as there is no other means of providing water (U. Srivastava, personal communication). In Turkmenistan, farmers are encouraged to expand vegetable production, including watermelon and melon into land newly claimed from the Karakum (Black Sand) Desert that is irrigated with water provided by local irrigation districts and that originated from snowmelt in the mountains of Tajikistan (Fig. 2). Farmers in Ürümqi and Turfan, Xinjiang, China produce watermelon and melons for domestic and export markets using water from the Tian Shan Mountains.

Cucurbits are direct seeded in many areas of the world, but transplants are commonly used for greenhouse production. Grafting is common for stand establishment in Japan, Korea and China, and is expanding to other countries for control of soil-borne diseases, improved vigor, and tolerances to cold temperatures, salinity, drought and flooding (Davis et al. 2008; Lee et al. 2010). Several cucurbit species are suitable as rootstocks.

Cucurbits are subject to many diseases and insect pests. Powdery mildew incited by the two obligate erysiphaceous ectoparasites (*Golovinomyces orontii s.l.*, and *Podosphaera xanthii*) is nearly ubiquitous (Jahn et al. 2002). Many other diseases are also important in one or more regions of the world (Zitter et al. 1996). Their control is not always successful and is done using cultural practices, including chemical protectants or eradicants, and host plant resistance. The succeeding chapters in this review will address host plant resistance, as appropriate.

Consumption and Use of Cucurbits

Increased production per capita likely means increased consumption per capita, assuming other factors constant, e.g., losses due to spoilage, and is likely due to the interplay of factors beyond the scope of this introduction. One factor of note is the educational emphasis by western governments, e.g., 5 A Day for Better Health Program (http://www.fns.usda.gov/5-day), and non-governmental organizations, health care providers and individuals to reverse the trend of increasing obesity and other diseases, e.g., type 2 diabetes, associated with western diets (Taubes 2011).

Cucurbits can play an important role in improved dietary health. They are low in nutritional value, compared with other vegetables, but they provide ranges of sweetness (from subtle, e.g., freshly sliced cucumber, to bold, e.g., watermelon), texture (from crunchy, e.g., Piel de Sapo melons, to stringy, e.g., spaghetti squash, *Cucurbita pepo*), color, and low calorie bulk as fresh alternatives to the proliferating array of readily available, carbohydrate rich, processed foods.

Fruit water content ranges from 86 (winter squash) to 95 % (cucumber), and caloric content per 100 g fresh material ranges from 15 kcal for cucumber to 46 kcal, on average, for winter squash (Ensminger et al. 1983). The minor cucurbits addressed in this volume are comparable to the major cucurbits for water content and caloric value, e.g., bottle gourd (*Lagenaria siceraria* (Molina.) Standley) 92 % water and 26 kcal/100 g fresh fruit wt., and wax gourd (*Benincasa hispida* (Thunb.) Cogn.) 96 % water and 13 kcal/100 g fresh fruit wt (Ensminger et al. 1983).

Sweet or bland, bitter or aromatic, highly perishable or storable for months with little change in quality, cucurbits are, with few exceptions, prized for their delicious fruits that may be consumed immature or mature, and the seeds may be used for vegetable oil and protein (Jacks et al. 1972) (Fig. 3). Cucumbers are enjoyed either fresh or pickled. Watermelon is prized for its sweet crunchy flesh that is typically eaten fresh but which can be prepared into a jam. Leaves may be consumed for food or medicinal purposes: melon in Tanzania (B.D. Jensen, personal communication), *Citrullus* in China (Yang and Walters 1992), and *Cucurbita maxima/moschata* in Zimbabwe (Ndoro et al. 2007), and *Cucumeropsis mannii* Naudinin Benin (Achigan-Dako et al. 2008). Both male and female *Cucurbita pepo* flowers are commonly consumed in Mexico and Italy in soups and other foods (L. Wessel-Beaver, personal communication). Pickled watermelon rinds are commercially available in many countries, and recipes are easily found online. Mature seeds are consumed in numerous countries, e.g., China. Pumpkin seed oil from the Styria region of Austria is a European Union Protected Designation of Origin (PDO) product. "Roaster mixes" of several cucurbit species are common in Asian countries; indeed there were cucumber and melon seeds in one such mix (cucumber PI 175111) purchased at a market in Mussoorie, India. The melon fraction was re-numbered as PI 371795, which after selection for uniform reaction to melon aphid, *Aphis gossypii* gave rise to PI 414723 (Fig. 4), a rich source of genes for host plant resistance to several diseases (Dhillon et al. 2012; McCreight et al. 1992). Fruit of "wild" melons that are small, non-sweet, thin-fleshed and mostly seed are used in Madhya Pradesh, India in cooked dishes and may be dried for use at a later time (Fig. 5).

Winter squashes may be stored for months (Robinson and Decker-Walters 1997). Long season melons grown in the central Asian countries of Uzbekistan and Turkmenistan can be stored for up to 6 months with no loss of quality (14–18 % soluble solids), range in weight from 8 to 35 kg per fruit (Anon 2008; Mavlyanova et al. 2005a), and were prized by European monarchy (Anon 2008).

Fig. 3 Four melon products at a roadside melon market, Tejen, Turkmenistan; background, long season and long shelf-life Vaharman-type fruit with 14–18 % soluble solids; melon seeds in sack, bottled melon seed oil, and cellophane-wrapped "gavun kak," which consists of dried and twisted slices of Vaharman-type fruit (Anon 2008; McCreight et al. 2013. Photo courtesy of J.D. McCreight)

Fig. 4 Sample of fruit diversity of melon; from left to right, Iran H, 'Top Mark', PI 414723, PI 124111, PI 124112, and PI 313970; Imperial Valley, California (Photo courtesy of J.D. McCreight)

Dried gourd shells may be used as ornaments, storage containers, or as musical instruments. Some cucurbits, such as bitter gourd, have medicinal properties (Dhillon et al. 2016). Cucurbits can be used for skin care, e.g., *Luffa cylindrical*

Fig. 5 "Wild" melon fruits split open and drying for later use in soups or stews, Madhya Pradesh, India (Photo courtesy of J.D. McCreight)

used as a sponge, and as extracts in cosmetics (Athar and Nasir 2005). Winter squashes are used in some areas as cattle fodder (Grisales 2015).

See Robinson and Decker-Walters (1997); Whitaker and Davis (1962) for a more thorough overview of cucurbit uses, including many minor species not addressed in this review of major and major-minor cucurbits.

Improvement of Cucurbit Germplasm

The cultivated cucurbits have been improved greatly by plant breeders using conventional plant breeding techniques for more than 100 years. Cucurbit germplasm resources have and will continue to serve as valuable resources for new genes and alleles for important production, e.g., disease resistance, and market traits, including new market types. The USDA, ARS germplasm repositories and associated Germplasm Information Network (GRIN) database (http://ars-grin.gov) serve genetic improvement of cucurbit crops worldwide (Clark et al. 1991; Dhillon et al. 2012). In addition, there are many other cucurbit germplasm repositories/collections worldwide (Esquinas-Alcazar and Gulick 1983), e.g., AVRDC – The World Vegetable Center and Kasetsart University (http://avrdc.org/seed/improved-lines/[accessed 9 Mar 2016]), Centre for Genetic Resources, the Netherlands (http://www.wageningenur.nl/en/[accessed 9 Mar 2016]), Uzbek Research Institute of Plant Industry, Uzbekistan (Mavlyanova et al. 2005a, b).

As we look to the future, rapidly advancing molecular technologies and genomic approaches are being applied to cucurbits to ensure sustainable production, improve fruit quality and shelf life, and develop novel fruit types. The subsequent chapters in this book will describe genetic and genomic resources for the major and minor cucurbit crops and application of those resources to crop improvement and understanding of cucurbit crop biology.

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Phylogeny and Evolution of the Cucurbitaceae

Susanne S. Renner and Hanno Schaefer

Abstract The Cucurbitaceae family contains about 1000 species in 96 genera. Representatives of all genera (except the extinct *Khmeriosicyos*) and a large percentage of the species have been sequenced for the ribosomal RNA transcribed spacer regions and variable regions of the plastid and mitochondrial genome. These data have allowed to infer evolutionary relationships in the family. The major phylogenetic structure of the family is now clear, and this chapter includes an up-to-date phylogenetic scheme with the placement of all genera. The Cucurbitaceae clade originated in mainland Southeast Asia sometime in the Late Cretaceous, and the five deepest evolutionary divergences in the family all date to the Late Cretaceous, 70–80 Ma. Two of these ancient clades, the Gomphogyneae and *Actinostemma*, are now almost restricted to Asia. A third ancient group, the Triceratieae, is mainly Neotropical, except one African genus; other clades and tribes are more widespread. The economically most important genera are concentrated in the Cucurbiteae and Benincaseae, and species of *Cucumis* and *Citrullus*, with well-annotated genomes, therefore have largely comparable (homologous) linkage groups. In contrast to the relatively good data on the family's phylogeny, data on its ecology, physiology and morphological evolution are scarce and collection and study of wild species, many of them in threatened habitats is much needed.

Keywords Collections • Molecular phylogenetics • Molecular clock • Publicly available herbarium specimens • Sister groups • Crop wild relatives

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Introduction

The Cucurbitaceae are a tropical and subtropical family that is related to the Begoniaceae, Datiscaceae, and Tetramelaceae, with which it shares inferior ovaries and parietal placentation (Zhang et al. 2006). The precise relationships among these four families remain unresolved. Their tendrils readily distinguish Cucurbitaceae from their closest relatives, and the family's monophyly is well supported by molecular analyses that have included a dense sampling of both outgroups (potential relatives) and Cucurbitaceae themselves (Kocyan et al. 2007; Schaefer et al. 2009; Schaefer and Renner 2011a, b). Indeed, species from all genera of Cucurbitaceae except *Khmeriosicyos*, a genus only known from the type, a specimen collected in Cambodia in 1873 and now in the Paris herbarium, have been sequenced for at least one nuclear DNA region and one or more plastid regions. Maximum likelihood and Bayesian phylogenies inferred from these large data matrices reveal five statistically well-supported clades. This chapter summarizes the phylogenetic placement of all genera as well as the ages of the family's major clades based on fossils and molecular clock approaches. We conclude with a brief review of morphological trends and historical geographic expansion of the family.

The Main Clades (and Taxonomic Tribes) of the Cucurbitaceae

The most comprehensive molecular phylogenetic analysis of the Cucurbitaceae is that of Schaefer and Renner (2011b) who included ribosomal RNA transcribed spacer regions, two mitochondrial regions, and nine regions of the plastid genome for 664 species of Cucurbitales (most of them Cucurbitaceae, which were represented with 95 genera). Figure 1 shows the placement of all currently recognized genera and is up-dated from the most recent taxonomic classifications of the Cucurbitaceae (Schaefer and Renner 2011a, b). The deepest phylogenetic divergences in the family can be 'captured' in five major groups of genera, namely, (I) a group that includes *Alsomitra*, *Bayabusua*, and *Neoalsomitra*, which corresponds to tribe Gomphogyneae of Bentham & Hooker; (II) a group of one African genus and five Neotropical genera, including *Fevillea* and *Sicydium*, which corresponds to tribe Triceratieae of A. Rich.; (III) a group of four or five genera from Madagascar, continental Africa, Asia, and South America, corresponding to tribe Zanonieae of Bentham and Hooker; (IV) a clade consisting of the Asian *Actinostemma*; and (5) a group of c. 80 genera that has traditionally been ranked as subfamily Cucurbitoideae of Kosteletzky. Before molecular data, the groups (1) to (4) (above) were placed together in a subfamily called Zanonioideae (Benth. & Hook.f.) Luerss. or Nhandiroboideae (Kosteletzky 1833; Jeffrey 1980, 1990, 2005), however, Nhandiroboideae is an illegitimate name, and Zanonioideae is a taxonomic synonym of Fevilleoideae Burnett (Burnett 1835). Neither morphological data nor molecular phylogenetic results support the division of the family Cucurbitaceae into

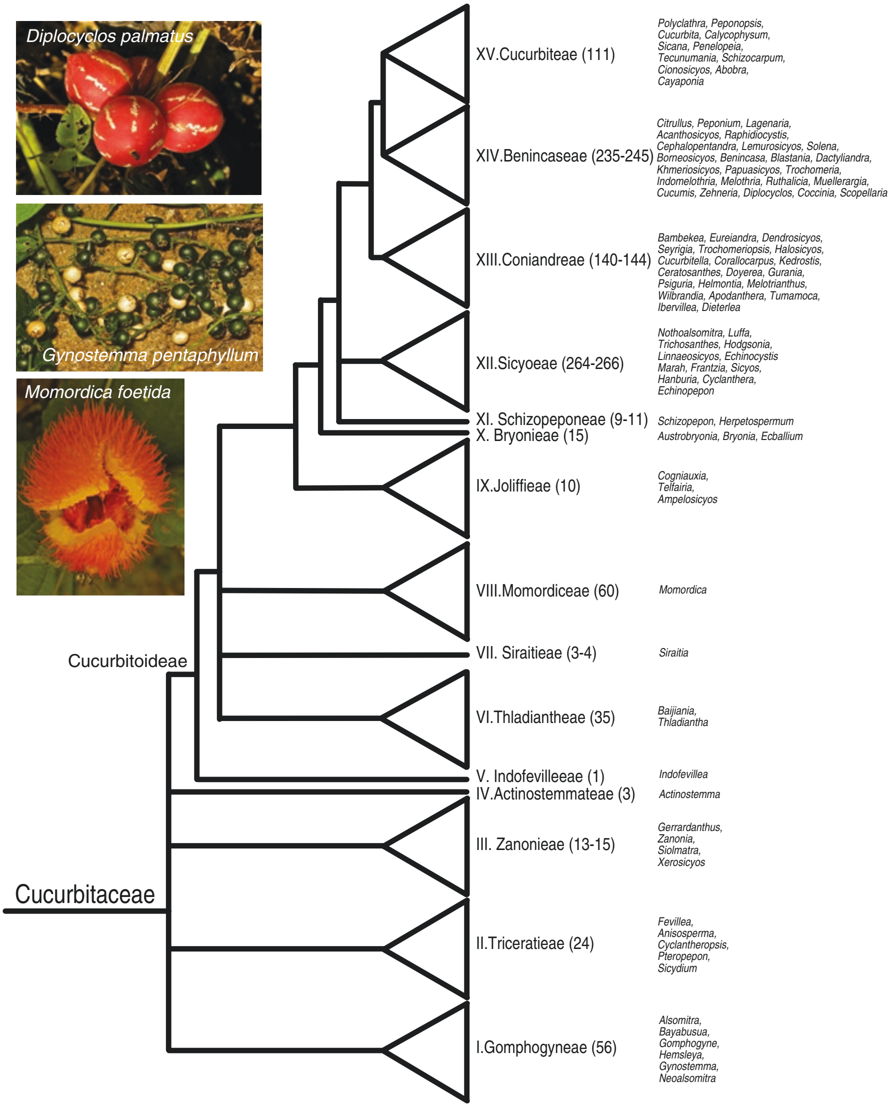

Fig. 1 Cladogram showing the tribal classification of the Cucurbitaceae based on 14 DNA regions from chloroplast, nuclear and mitochondrial DNA sequences. Up-dated from Schaefer and Renner (2011a, b, the latter paper showing the statistical support for this tree). Numbers in parentheses refer to species numbers (Photos by H. Schaefer)

two equal-aged or otherwise equivalent groups, and the morphological characters thought to distinguish Zanonioideae from Cucurbitoideae, namely, striate pollen, winged seeds, and "zanonioid" tendrils (tendrils in which the lower section is capable of curving), all occur also in Cucurbitoideae. We therefore recommend not using any subfamily division in this relatively small family. Brief descriptions of the 15 tribes (Fig. 1), including comments on geographic occurrence, and chromosome numbers are provided in Schaefer and Renner (2011b).

Morphological Evolutionary Trends in the Cucurbitaceae

Sexual Systems

Cucurbitaceae are usually hairy climbers with simple or branched, lateral tendrils (very rarely, the tendrils are lost, e.g. in the cucumber tree, *Dendrosicyos socotranus*), yellow or whitish unisexual flowers, an inferior ovary with parietal placentation and numerous, relatively large seeds. About 50% of their species are monoecious and 50% dioecious; no wild Cucurbitaceae have only bisexual flowers although a few have individuals with bisexual flowers and others with staminate flowers (individuals with bisexual flowers regularly occur in *Schizopepon bryoniifolius* and *Zehneria hermaphrodita*; Schaefer and Renner 2011a). Dioecy appears to be the ancestral condition in the family, with much back and forth between dioecy and monoecy (Zhang et al. 2006; Volz and Renner 2009; Schaefer and Renner 2010), and a dioecious mating system may even go back to the common ancestor of Begoniaceae, Cucurbitaceae, Datiscaceae, and Tetramelaceae, all of which have normally unisexual flowers and are entirely or mostly dioecious (Zhang et al. 2006). Spontaneous mutations that modify flower sex phenotype are common and were favored by breeding targeted towards femaleness (see also The Genomics of Wood Formation in Angiosperm Trees). In *Cucumis*, a genus of 66 species, most of them monoecious but a few dioecious, e.g. *Cucumis hirsutus*, (Sebastian et al. 2010), breeders have selected gynoecious or 'all-female' cultivars of *C. sativus* because of their high fruit yield. Gynoecy, coupled with parthenocarpy, is valued for greenhouse production. Field production of gynoecious varieties requires a few androecious plants (with only male flowers) or monoecious plants with both types of flowers to ensure fertilization. Their sexual lability and economic importance have made cucurbits an important system for the developmental genetics of sex determination (The Genomics of Wood Formation in Angiosperm Trees). The ancient presence of unisexual flowers and dioecious populations in Cucurbitaceae may be the evolutionary 'reason' for the absence of genetic self-incompatibility in this family. All species that have been investigated in this regard are self-compatible. However, the sexual systems of most species are only inferred from a few herbarium specimens rather than field observations of wild populations.

Flower Morphology and Its Evolutionary Trends

Floral symmetry is mostly actinomorphic (radially symmetric), although zygomorphy (mirror symmetry) has evolved in a few species, for example, in *Gerrardanthus* (Fig. 2a), *Xerosicyos,* and a few species of *Momordica.* Male and

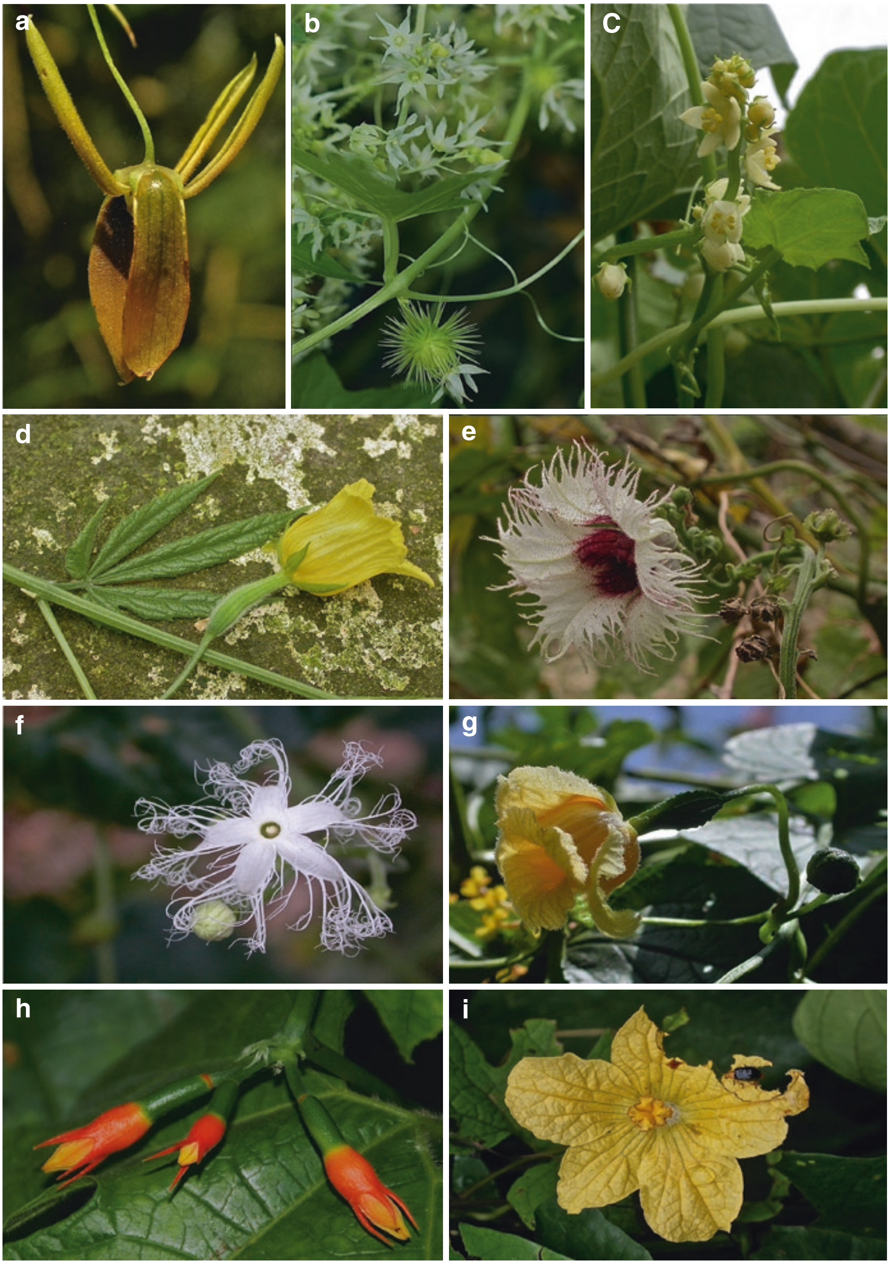

Fig. 2 Diversity of flower morphology in Cucurbitaceae: (**a**) *Gerrardanthus grandiflorus*, male flower (Tanzania); (**b**) *Echinocystis lobata*, male and female flowers (USA); (**c**) *Sicyos edulis* (syn. *Sechium edule*), male flowers (Brazil); (**d**) *Thladiantha hookeri*, female flower (China); (**e**) *Telfairia occidentalis*, male flower (Nigeria); (**f**) *Trichosanthes cucumerina*, male flower (China); (**g**) *Momordica leiocarpa*, female flower (Tanzania); (**h**) *Gurania makoyana*, female flower (Peru); (**i**) *Ruthalicia eglandulosa*, male flower (Sierra Leone); all photographs Hanno Schaefer