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# Molecular basis of cucumber fruit domestication

Gen Che and Xiaolan Zhang

Cucumber (*Cucumis sativus* L.) is an economically important vegetable crop that is cultivated worldwide. Compared to the wild ancestor bearing small, bitter and seedy fruit, domesticated cucumbers exhibit significant variation in fruit appearance, size and flavor. Understanding the molecular basis of domestication related traits can provide insights into fruit evolution and make crop breeding more efficient. Here we review recent advances in relating to the genetic basis of fruit morphological traits (femaleness, fruit spine, wart, size, color and carpel development) and organoleptic features (bitterness) during cucumber domestication.

## Address

Beijing Key Laboratory of Growth and Developmental Regulation for Protected Vegetable Crops, College of Horticulture, China Agricultural University, Beijing 100193, China

Corresponding author: Zhang, Xiaolan ([zhxiaolan@cau.edu.cn](mailto:zhxiaolan@cau.edu.cn))

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## Introduction

Cucumber, *Cucumis sativus* L. ( $2n = 2x = 14$ ) is a major vegetable crop with important economic and biological value. The cucumber fruit is developed from three-syn-carpous gynoecia, and is consumed freshly or as processed pickles 8–18 days after floral anthesis. Fruit appearance varies from a round to cylindrical shape and fruits are 5–40 cm in length [1]. Morphologically, the fruit consists of two parts, the undesirable stalk adjacent to the peduncle and the tasty fruit at the tip. Transversely, the cucumber fruit comprises the epicarp, mesocarp, and endocarp progressing from outer to innermost tissue layers [2]. The epicarp bears spines, warts, and waxes, and becomes yellow or white in color when ripened. The mesocarp is the fruit flesh and is usually white, crisp, and fragrant. The endocarp consists of the placenta and developing ovules in cucumber.

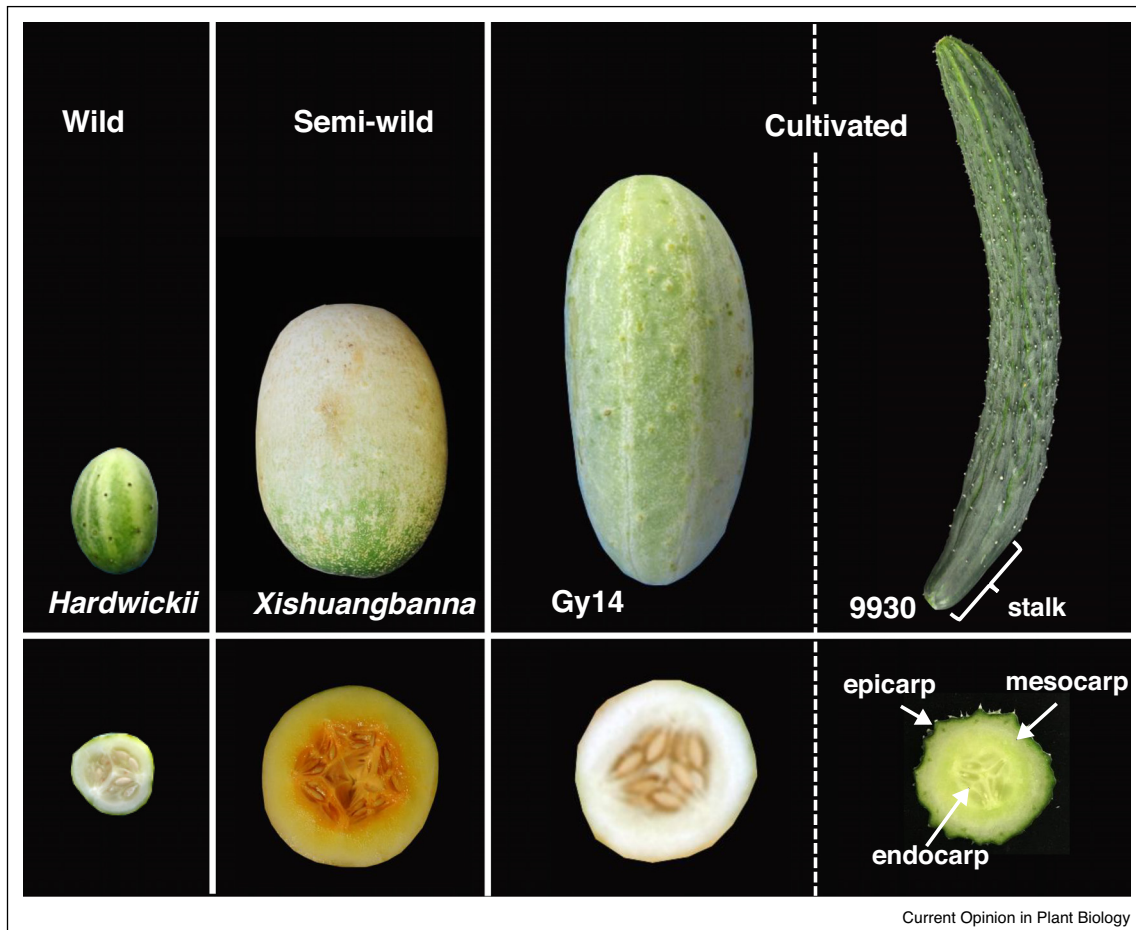
Domestication is a process whereby plants' desirable morphological and physiological traits were deliberately

selected for human consumption and environmental adaptation, such as increased edible part, enhanced robustness, and altered seed dormancy and dispersal [3,4]. Cucumber is indigenous to India and was domesticated in Asia approximately 3000 years ago [5,6,7]. Now, cucumber is cultivated worldwide and its global production was 80.6 million tonnes in 2016 (FAOSTAT), with China being the leading producer followed by Turkey and Iran. Based on the progression of domestication, cucumber can be divided into three types: wild (*C. sativus* L. var. *hardwickii*), semi-wild (*C. sativus* L. var. *xishuangbannanensis*), and cultivated cucumber (*C. sativus* L. var. *sativus*) (Figure 1) [7,8]. The wild cucumber *C. s.* var. *hardwickii* bears small and round fruit with black spines, bitter flesh, and many seeds. The semi-wild cucumber *C. s.* var. *xishuangbannanensis* bears melon-like fruits, with heavy fruit weight and a unique orange endocarp (Figure 1). The cultivated cucumbers exhibit extreme phenotypic variation in fruit size, spines (size, density and color), warts (size and density), wax, fruit skin (colors, ridges, speckling), sex types, and bitterness. Cucumber can also be divided into four geographic groups that exhibit significant genetic variation: Indian, Xishuangbanna, Eurasian and East Asian group [9]. The sequenced pickling cucumber Gy14 is a typical line of the Eurasian group that has sparse warts/spines and a short fruit stalk. The East Asian line 'Chinese Long' 9930 with the cucumber reference genome bears long fruit with high density of warts/spines and an elongated stalk (Figure 1). The remarkable diversity of cucumber horticultural traits contributes to its environmental adaptation and market selection during domestication, and provides a sturdy foundation for future cucumber breeding. Deep resequencing of 115 cucumber lines identified 112 putative domestication sweeps ranging from 50 kb to 780 kb, in which contain genes related to fruit length, bitterness and leaf size [9]. The key genes and molecular mechanisms underlying cucumber domestication-related traits have been intensively explored. In this review, we outline recent advances in the genetic basis of cucumber fruit domestication and discuss future trends and outstanding questions.

## Fruit formation—selection for female flowers in cucumber

The cucumber fruit is developed from the ovary of the female flower, and thus initiation and development of female floral identity preconditions crop production. Cucumber is capable of producing three types of flowers: the male flower, the female flower, and the perfect flower (Figure 2a–c), and exhibits five sexual systems including monoecious (male and female flowers), gynoeccious (female

Figure 1



Cucumber can be divided into wild, semi-wild and cultivated varieties-based on domestication progression, and four geographic groups: Indian, Xishuangbanna, Eurasian and East Asian. From left to right, the wild cucumber *C.s* var. *hardwickii* from the Indian group; the semi-wild *C.s* var. *xishuangbannanensis* cucumber from Xishuangbanna group; the cultivated cucumber Gy14 from Eurasian group and 'Chinese Long' 9930 from East Asian group.

flowers), androecious (male flowers), hermaphroditic (perfect flowers), and andromonoecious (male and perfect flowers) [10]. Most cucumber cultivars, including the wild progenitor, are monoecious. However, gynoeceous cultivars are preferred during cucumber breeding, due to the reduced cost of hybrid seed production, improved earliness, and ease of mechanical harvesting [11].

Flower development in cucumber comprises 12 stages, during which selective arrest of spore-bearing organs at stage 6 gives rise to unisexual flower formation [12]. Ethylene induces female and inhibits male identity in cucumber [13,14]. Four sex-determination genes have been identified in cucumber, including two encoding 1-aminocyclopropane-1-carboxylate (ACC) synthase named *CsACS2* and *CsACS11*, one ACC oxidase (*ACO*, *CsACO2*) that converts ACC into ethylene, and one transcription factor *CsWIP1* [15–17,18\*\*]. *CsACS2* is the

*Monoecious* (*M*) gene acting as staminal inhibitor [16], and *CsACS11* is the *Androeceous* (*A*) gene functioning as a carpel stimulator [17]. *CsWIP1* is the *Gynoeceous* (*G*) gene acting as a carpel inhibitor that is repressed by *CsACS11*, and *CsWIP1* further inhibits the expression of *CsACS2* and *CsACO2* (Figure 2) [17,18\*\*]. The combination of the above four genes governing the selective growth or arrest of reproductive organs leads to the development of different flower sexes (Figure 2) [17,18\*\*].

In addition, the partially dominant *Female* (*F*) locus results from gene duplications of *CsACS1*, and is important for controlling female identity in cucumber [14]. A copy number variation of the *F* locus results in gynoeceous plants bearing only female flowers [19]. The *F* locus was not found in melon, suggesting that it was acquired in cucumber after diverging with melon [17]. *CsGAMYB1*, a positive regulator functioning in the

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