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‘’ORIGIN OF THE DOMESTICATED HUSBANDRY SPECIES AND MOLECULAR-BASES OF FRUIT FORM AND SIZE CHANGES THROUGHOUT THE DOMESTICATION, TAKING TOMATO AS AN EXAMPLE’’

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ABSTRACT:-

The domestication of crop plants is the foundation of modern agriculture, which brings forth desirable changes in cultivated species that distinguish them from their wild relatives. This resulted in the origin of crop species at glorious geographical locations coinciding with the transition of human societies from hunter-gather to agricultural civilizations. Fruit size and shape are very important traits for the horticulture industry, as well as for studying the domestication of the horticultural species. In this review, we have summarized the origin of some widely-grown horticultural crops and also the molecular bases of the fruit size and shape changes of the horticultural crops during the domestication, taking tomato as an example.

Keywords:

Horticultural crops; domestication; fruit size; fruit shape; tomato.

1. Introduction: -

Domestication is a subfield of evolution, in which the selection procedure is brought by humans instead of nature. The domestication processes of most of the crop plants are not restricted in a small area where they originated, such as apple, and the main production area of a certain crop in the modern agriculture industry is often not its origin (Cornille et al., 2014). Thus, it is necessary to trace the origin of the domesticated crops not only for scientific research but also for breeding, because the diversity of every species is often larger within the origin location than different places and it's extremely doable to search out valuable wild species for breeding within the origin website. There are several ways to trace the crop origin site, including analyzing and combining the evidence in the archeological, ecological, linguistic and genetic aspects. With the development of the high-throughput sequencing technology, it is much easier and more accurate to analyze the genomic diversities of a huge number of samples, which gives the researchers the new way to investigate and trace the origin sites of the crops. In the horticulture industry, the fruit is a very important organ for selling and its size and shape are important traits for the determination of its usages, for example, flat and large tomatoes are often used in fast food chains such as in hamburger, while small and pear-shaped tomatoes are popular in making a salad(Fig. 1, A, D). Based on the data we can get, five and three main QTLs are controlling the tomato fruit shape and size, respectively, and most of them have been cloned (Van der Knaap et al.,2014). Although according to the recently published paper, only the fruit size is thought to be selected during the tomato domestication, it is hard to exclude the fruit shape to be selected in the future, because the breeder of processing tomato prefers to select the varieties bearing rectangle-shaped fruits, which are convenient for transport. Therefore, in this review, we summarized the progress in the investigation of the original sites of some key domesticated horticultural crops. At the same time, we also summarized the molecular bases of the genes controlling fruit size and the shape of horticultural plants by taking tomato as an example.

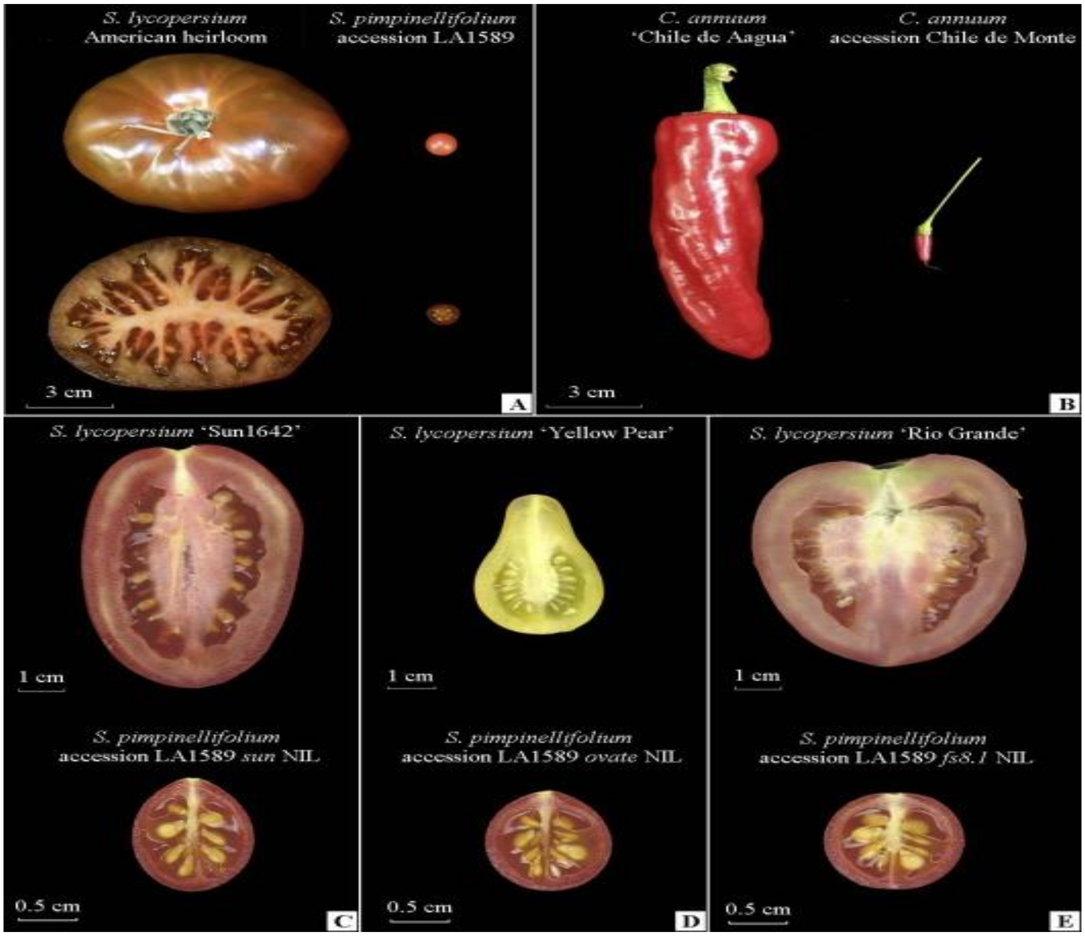

Fig. 1 Fruit size changes in the domestication of tomato and chili

(A) Cultivated tomato (Solanum lycopersicum, American heirloom, left) and wild tomato (S. pimpinellifolium accession LA1589, right) fruits; (B) Cultivated pepper (Capsicum annuum 'Chile de Aagua', left) and wild pepper (C. annuum accession Chile de Monte, right) (C) Fruits harboring the sun locus in 'Sun1642' (upper) and LA1589 background (lower) (D) Fruits harboring the ovate locus in

'Yellow Pear' (upper) and LA1589 background (lower) (E) Fruits harboring the fs8.1 locus in 'Rio Grande' (upper) and LA1589 background (lower).

2. Old World originated horticultural species:-

Tracing the location of domestication and path for subsequent dispersal to other parts of the world is a key step in the evolutionary study of domesticated crops. Besides giving an evolutionary history of domesticated crops, such studies also provide an account of the prevailing genetic diversity of the concerned crop. An integrated approach including archeological evidence, the geographical distribution of wild ancestors, evolutionary genetic studies using molecular markers played a vital role in elucidating the domestication history of crop species (Gepts et al., 2012; Kraft et al., 2014). Recent advancement in high-throughput sequencing has led to the adaption of genomic approaches to study the evolutionary history of horticultural crops (Blanca et al., 2012). Here we will briefly describe the domestication history of some key horticultural plants. Based on the geographical distribution of domestication centers, the crops introduced in this section can be divided into two categories: Old World crops, which were domesticated in Eurasia and Africa, such as grape, apple, melon and Brassica, and New World crops, which were originally domesticated in America, such as tomato and pepper (Zohary et al.,2012). Among the Old World crops, Brassica is a kind of very important vegetable, which is widely grown all over the world and originated and domesticated in Eurasia, especially in the areas around the Mediterranean basin, southwestern Asia and northern Africa (Prakash and Hinata, 1980; Prakash et al., 2011; Al-Shehbaz, 2012). Based on the karyotype, the Brassica crop complex comprises six species, including B. rapa (n = 10, AA), B. nigra (n = 8, BB), B. oleracea (n = 9, CC), B. carinata (n = 17, BBCC), B. juncea (n = 18, AABB) and B. napus (n = 19, AACC). Among them, B. carinata, B. juncea and B. napus are considered to be the high chromosome genomics which was generated from the interspecific hybridization among the low-chromosome monogenic diploids (B. rapa, B. nigra and B. oleracea) (Nagaharu, 1935; Prakash et al., 2009). The evolution and domestication of the Brassica crops are thought to originate from a common ancestor following two pathways: one is the B. nigra pathway, in which the Hirschfeldia incana or a close relative species is considered to be the primary ancestor; the other is the B. oleracea and B. rapa pathway, in which the Diplotaxis erucoides or a close relative is thought to be the primary ancestor (Song et al., 1990). Recent genome sequencing research demonstrated that during the origin and evolution processes, the Brassica genomes underwent a mesohexaploidization and then were shaped by whole-genome triplication followed by extensive diploidization (Wang et al., 2011; Cheng et al., 2013, 2016). Due to the complexity of the Brassica genus, the origin sites of different species of Brassica are not the same. B. nigra probably originated in central and south Europe and has been collected and recorded by the ancients for its medicinal value (Zeven and Zhukovsky, 1975; Prakash et al., 2011). The domestication of B. nigra may be performed by the Mediterranean civilizations, such as Mesopotamia, Egyptian, Greek and Roman, in which it was used not only as a medicinal plant but also as an important condiment (Prakash et al., 2011). B. oleracea is a highly polymorphic species with a huge diversity in the shape of leaf, stem, and inflorescence. Based on the morphology, the B. oleracea complex can be divided into six groups/varieties, including kales (var. acephala), cabbages (var. capitata), kohlrabi (var. gongylodes), inflorescence kales (var. botrytis, var. Italica), branching bush kales (var. fruticosa) and Chinese kale (B. alboglabra) (Dixon, 2007; Prakash et al., 2011). The cultivated B. oleracea crops now are thought to be domesticated from one or several of their wild relative species, which are naturally distributed in the areas of the Mediterranean basin and northwest Europe (Prakash et al., 2011). According to the linguistics research, most of the B. oleracea varieties are considered to be domesticated in Europe, especially in the area around the Mediterranean, with only one exception — the Chinese kale, which is domesticated in southern China (Dixon, 2007). B. rapa is another highly polymorphic species which, based on the usages, can be divided into several different groups or forms, including oleiferous, leafy forms and turnip. Meanwhile, according to the origin or domestication place, B. rapa could also be classified into European, Indian and Chinese forms. On the other hand, by comparison of the morphology and DNA polymorphism, B. rapa can also be divided into two races: the Western race comprising oilseed forms and turnip, and the Eastern race comprising vegetable forms (Denford, 1975; Song et al., 1988; Chen et al., 2000; Guo et al., 2002; He et al., 2003; Zhao et al., 2005; Takuno et al., 2007). The origin and domestication sites of B. rapa now are accepted as two independent centers. Europe is considered to be the primary center for oleiferous forms; then with the spread of the B. rapa, the turnip form might originate in the Middle East; after being spread to the eastward from the Middle East, the oilseed and leafy forms originated in Indian and China, respectively (Prakash et al., 2011). B. juncea, like the two highly polymorphic diploid species mentioned above contains many varieties, which can be classified into different groups based on the morphological characteristics, and in China, according to their usages, the cultivated B. juncea are often divided into five groups: leaf mustard (B. juncea var. multiceps), stem mustard (B. juncea var. tsatsai), root mustard (B. juncea var. megarrhiza), oilseed mustard (B. juncea var. juncea), and seed stalk mustard (B. juncea var. utilis) (Gladis and Hammer, 1992; Fu et al., 2006; Qi et al., 2007, 2008; Wu et al., 2009; Prakash et al., 2011). The domesticated B. juncea now is considered to originate in the region of Middle East from wild B. juncea that today will be found within the upland of Asia Minor and adjoining southern Iran (Mizushima and Tsunoda, 1967; Tsunoda and Nishi, 1968; Tsunoda, 1980). Meanwhile, regions of northwest India and southwest China are thought to be the two important secondary centers for the domestication (Prakash et al., 2011). B. carinata is grown mainly on the East African Plateau, particularly in Ethiopia and in parts of the east and west coasts of the African continent, which is thought to originate in the highlands of Ethiopia and nearby portion of East Africa and the Mediterranean coast (Gómez-Campo and Prakash, 1999). B. napus maybe the latest originated widely-grown Brassica crop which was recorded as a domesticated vegetable in the 15th century. B. napus comprise two cultivated forms: the oilseed rape and the rutabaga, which is now considered to originate from the hybridization between turnips and different B. oleracea forms in the farmers’ field in Europe (Prakash et al., 2011). Besides Brassica, the grape is also an important horticultural crop that is domesticated in Eurasia, especially in Western Asia. The cultivated grape (Vitis vinifera ssp. Sativa Beck.) is considered to be domesticated from its wild ancestor V. vinifera ssp. Silvestris Beck, about 6 000 to 10 000 years ago, primarily in the areas of the southern Caucasus and eastern Anatolia. Moreover, Simple Sequence Repeat (SSR) analysis of local cultivars and wild relatives indicated that Italy is possibly a secondary domestication center of grape (Grassi et al., 2003). In addition to western Asia, central Asia is also a center of domestication of some important horticultural crops, such as apple. Due to the self-incompatibility and vegetative propagation by grafting, the domestication history of apple (Malus × domestica Borkh. or Malus pumila Mill.) is relatively complex and the whole process can be divided into two steps. First, M. × domestica was domesticated from its attainable ancestor rosid dicot genus sieversii (Ldb.) Roem within the space of Tianshan Mountains in central Asia more than 4 000 years ago (Harris et al., 2002; Luby et al., 2002; Velasco et al., 2010; Cornille et al., 2012, 2014). Subsequently, during the dispersal of the domesticated apple to the west of Eurasia along the Silk Route, it was continuously hybridized with other local wild apples, such as M. baccata (L.) Borkh, M. orientalis Uglitz and M. sylvestris Mill, which finally resulted in the generation of the modern cultivated apple species (Cornille et al., 2014). Besides the horticultural crops mentioned above, cultivated melon (Cucumis melo L.) was also domesticated in the Old World possibly from the wild species, Cucumis picrocarpus around 2 000 years ago (Schaefer et al., 2009; Sebastian et al., 2010; Serres-Giardi et al., 2012). However, the exact origin and domestication center for melon are still unclear and eastern Asia, Australia and Africa are all considered as candidate locations for the domestication of melon (Bates and Robinson, 1995; Schaefer et al., 2009; Sebastian et al., 2010; Pitrat et al., 2012).

3. New World originated horticultural species:-

The major cultivated horticultural crop species of the Old World started to change since the great geographical discovery at the end of the 15th century. After the return of Christopher Columbus and other voyagers from the New World, many new species, including tomato and pepper, were taken to Europe and then from there they spread to the other parts of the globe. Cultivated tomato (Solanum lycopersicum) originated and domesticated in areas ranging from northwest of South America to Central America (De Candolle, 1885; Peralta and Spooner, 2006; Bai and Lindhout, 2007; Bauchet and Causse, 2012). Based on the molecular and morphological evidence, Solanum lycopersicum var. cerasiforme (S. l. cerasiforme) or at least a specific group of accessions of S. l. cerasiforme is considered to be the direct progenitor of the cultivated tomato and the domestication process is likely a two step process, which started with the pre-domestication of S. l. cerasiforme from the wild tomato Solanum pimpinellifolium, an indeterminate weedy plant bearing small round fruits, in Ecuador and Northern Peru, followed by migration of S. l. cerasiforme to Mesoamerica, where the true domestication occurred and finally led to the generation of the cultivated tomato bearing big fruits

(Ranc et al., 2008; Blanca et al., 2012; Lin et al., 2014). Chili pepper is considered to be domesticated in the areas from Central America to the west of South America, possibly more than 8 000 years ago (Eshbaugh, 1993; Perry et al., 2007; Kraft et al., 2014). By combining archeological, ecological, linguistic and genetic evidence, Capsicum annuum is now thought to be domesticated from wild ancestors, most likely C. annuum var. glabriusculum, C. annuum minimum and C. annuum aviculare, perennial shrubs bearing many erect, globular, pea-sized fruits, in one or all the areas of northeastern, central-eastern and western Mexico (Loaiza-Figueroa et al.,1989; Kraft et al., 2014).

4. Molecular bases of fruit size of horticultural crops:-

Fruit size is an important trait selected during the domestication of fruit and vegetable crops (Fig. 1, A, B). Until now two fruit size/weight genes have been cloned in vegetable and fruit crops, namely FW2.2/CNR and FW3.2/SlKLUH in tomato (Fig. 1, A, B) (Frary et al., 2000; Chakrabarti et al., 2013). FW2.2/CNR was found to encode a cysteine-rich protein which functions as a negative regulator of cell number (Frary et al., 2000; Guo et al., 2010). The effect of FW2.2 on the regulation of fruit size is based on the modulation of pericarp, placenta and columella size through the regulation of cell proliferation (Liu et al., 2003). The derived allele of FW2.2 possibly arose due to SNPs in the promoter region, which resulted in the lower expression of FW2.2 (Frary et al., 2000; Cong et al., 2002). Additionally, yeast two-hybrid assay revealed that FW2.2 can physically interact with CKII kinase involved in the regulation of the cell cycle (Cong and Tanksley, 2006). Besides tomato, FW2.2 orthologous genes controlling organ size have also been identified in other crops. In maize, 13 CNRs were identified, and overexpression of the CNR1 resulted in reduced plant height, ear length, and biomass, possibly due to the inhibition of cell proliferation (Guo et al., 2010). In avocado, it was observed that an FW2.2-like gene was expressed at a higher level in small fruit accession ‘Hass’ than that of the regular fruit size accession (Dahan et al., 2010). Additionally, in peach, sweet cherry and sour cherry, orthologs of FW2.2 were also identified (De Franceschi et al., 2013). Apart from the fruit size, FW2.2 and its orthologs were also found to regulate fruit numbers and photosynthate distribution in tomato, as well as nodule development in soybean (Nesbitt and Tanksley, 2002; Libault et al., 2010). FW3.2/SlKLUH, the ortholog of KLUH in Arabidopsis, which encodes a cytochrome P450 of the CYP78A subfamily, was the second fruit weight gene cloned in any vegetable and fruit species (Chakrabarti et al., 2013). In tomato, the derived allele of SlKLUH was shown to increase fruit size by regulating the pericarp and septum area through increased cell number. The downregulation of SlKLUH expression in tomato resulted in reduced flower size, seed size, and fruit weight, suggesting that SlKLUH is a positive growth regulator. Association mapping analysis identified an SNP to be significantly associated with the fruit size at the promoter region of SlKLUH. Molecular diversity and phylogenetic analyses revealed that the FW3.2 mutation possibly originated in S. l. cerasiforme background and now widely exist in modern cultivated tomato accessions. Besides tomato, the ortholog of SlKLUH was also found to be associated with fruit weight in chili pepper (Chakrabarti et al., 2013). QTL analysis in sweet cherry (Prunus avium) also indicated that an ortholog of SlKLUH was co-localized with a fruit weight QTL on the linkage group 5 (Campoy et al., 2014). SlKLUH ortholog in grapevine was also found to be colocalized with a major berry weight QTL, signifying a major role of this gene and its orthologs in the regulation of fruit size in diverse vegetable and fruit species (Doligez et al., 2013).

5. Molecular bases of fruit shape of horticultural crops:-

Fruit shape is another important trait selected in vegetable and fruit crops possibly during the crop diversification or improvement process. So far, four fruit shape genes have been cloned in tomato, of which SUN and OVATE control fruit elongation, whereas LC and FAS control locule number and flat shape (Van der Knaap et al., 2014). Fruit shape gene OVATE encodes an OVATE family protein (OFP, Solyc02g085510) (Liu et al., 2002). Tomatoes with obovoid, rectangular, ellipsoid, heart and pear shape often carry the mutant allele of OVATE, which is caused by an SNP in the second exon resulting in a premature stop codon (Liu et al., 2002; Rodríguez et al., 2011). OVATE mutation in tomato is considered to arise in different lineages from LC, FAS, and SUN at the time before the domestication and was introduced to Europe after LC and FAS (Rodríguez et al., 2011). OVATE was shown to affect fruit shape at the early stage of flower development and the effects can be observed in ovaries at an thesis (Liu et al., 2002; Van der Knaap et al., 2014). Yeast two-hybrid screening revealed that in Arabidopsis some OFPs can physically interact with KNOX and BELL transcription factors involved in the maintenance of shoot apical meristem and concomitant regulation of leaf and inflorescence architecture (Hackbusch et al., 2005; Kanrar et al., 2006; Hay and Tsiantis, 2010). In tomato, OVATE can physically interact with the members of TONNEAU1 Recruiting Motif (TRM) superfamily, which was shown to play critical roles in pre-prophase band formation and microtubule array organization (Camilleri et al., 2002; Azimzadeh et al., 2008; Spinner et al., 2010; Drevensek et al., 2012; Van der Knaap et al., 2014). Another major fruit shape gene SUN was shown to encode an IQ67 domain-containing protein (Solyc10g079240) and often leads to extremely elongated fruit shape in some genetic backgrounds in tomato (Rodríguez et al., 2011). Tomatoes with long and oxheart shape often carry the mutant allele of SUN (Fig. 1, C), which originated from an unusual gene duplication event mediated by a long terminal repeat retrotransposon, Rider (Xiao et al., 2008; Rodríguez et al., 2011). SUN mutation is thought to occur after tomato was taken to Europe; thus, it arose much later than that of OVATE, LC and FAS (Rodríguez et al., 2011). The effect of SUN can be observed in ovaries at anthesis, but the major changes of fruit shape occur in the short period after anthesis (Van der Knaap and Tanksley, 2001; Wu et al., 2011). Histological analysis revealed that SUN increases fruit shape by increasing the cell number in the proximal-distal direction but decreases the cell number in the medio-lateral direction, which also leads to an unchanged fruit mass (Wu et al., 2011). At the molecular level, the function of the SUN on modulating fruit shape is not fully understood. In Arabidopsis overexpression of AtIQD1 resulted in increased glucosinolate level, which may be a category of secondary metabolites concerned in plant defense but is absent in the Solanaceae plants (Levy et al., 2005; Xiao et al., 2008). Yeast two-hybrid analysis revealed that AtIQD1 physically interacts with CaM/CMLs (Calmodulin/Calmodulin-like proteins) and kinesin light chain-related protein-1 (KLCR1). KLCR1 was reported to act as a motor in the cellular transport of cargo along the microtubules, such directional transport of cargo may be involved in the regulation of cell division patterns (Hirokawa et al., 2009; Akhmanova and Hammer, 2010;

Verhey et al., 2011). Another fruit shape locus LOCULE NUMBER (LC) was fine mapped to a 1.6 kb region flanked by the ortholog of WUSCHEL (WUS, Solyc02g083950) and a WD40 motif-containing protein (Muños et al., 2011). The presence of LC frequently results in flat shaped tomato fruits by increasing locule number (Rodríguez et al., 2011). A mutant allele of LC exists widely in modern cultivated tomatoes and as well as in some accessions of S. l. cerasiforme, suggesting that LC is an old mutation that arose before the tomato domestication process (Rodríguez et al., 2011). WUS encodes a homeodomain transcription factor which was implicated in the regulation of the stem cell population size in all meristems (Mayer et al., 1998; Clark, 2001). WUS was found to positively regulate the expression of a MADS box transcription factor AGAMOUS (AG), which was reported to play a pivotal role in determining stamen and gynecium identity and also to negatively regulate the WUS Yanofsky et al., 1990; Lenhard et al., 2001; Lohmann et al., 2001). Two SNPs significantly associated with the locule number, located downstream of WUS, were found to overlap with the CArG motif, which is the possible binding site for AG (Van der Knaap et al., 2014). Therefore it is plausible to hypothesize that in the lc mutant failure of AG binding possibly prevents the downregulation of WUS expression, leading to an increased population of stem cells resulting in higher locule number (Van der Knaap et al., 2014). Another major fruit shape gene in tomato is FASCIATED (FAS), which was first reported to encode an ortholog of YABBY gene (Solyc11g071810, SlYABBY2) (Cong et al., 2008). However, based on the newly published paper, SlCLVATA3 (SlCLV3, Solyc11g071380) gene now is strongly considered to underlie the fas locus, of which the a mutation is shown to arise from a 294 kb inversion with one breakpoint on the 1 kb upstream of the SlCLV3 gene resulting in weak expression of the SlCLV3 (Xu et al., 2015). The fas mutation is found to widely present in the US heirloom and Italian lines bearing flat or oxheart shaped fruits and is considered to arise in the LC background before the domestication of tomato (Rodríguez et al., 2011). Compared to LC, a mutant allele of FAS has more pronounced effects on increasing the locule number (Lippman and Tanksley, 2001; Van der Knaap et al., 2014). Genetic analysis has revealed that the loci of lc and fas have significant epistatic interactions, suggesting that these two loci may control tomato fruit locule number through a common pathway (Lippman and Tanksley, 2001; Barrero and Tanksley, 2004). Molecular level investigations indicate that the tomato SlCLV3 gene encodes an ortholog of Arabidopsis CLV3, which is a 13-amino-acid arabinosylated glycopeptide and could bind to the receptor kinase CLAVATA1 (CLV1) (Ohyama et al., 2009). After the binding of CLV3 to CLV1, CLV1, in turn, inhibits the expression of the WUS and prevents stem cell overproliferation (Schoof et al., 2000). Meanwhile, the WUS expression could also promote the transcription of CLV3, which finally makes a CLV3-CLV1- WUS feedback loop in the regulation of the stem cell proliferation (Schoof et al., 2000; Xu et al., 2015). Therefore, the mutation of fas, SlCLV3 lower expression leads to the overexpression of SlWUS which increases the locule number and finally generates a fasciated tomato fruit (Xu et al., 2015).

6. In the future:-

In the past, tracing the origin location of a certain crop can only depend on the archeological, ecological, linguistic and genetic evidence. However, most of the horticultural plants, including their leaves and fruits, are very hard to be preserved in the archeological sites, and digging the information in the tremendous amount of old literature are often not easy, especially when a variety has many different local names or a certain name in different locations is corresponding to varieties of different species. On the genetic aspect, the polymorphism of molecular markers is very important information for clarifying the genetic relationship between cultivated varieties and their wild relatives, as well as tracing the origin site. However, the number of molecular markers used in each research is limited which cannot fully reflect the diversity of the whole genome. Taking the advantages of the second and third generation of sequencing, it is now much easier and cheaper to analyze the genome diversity of a large number of samples in a very short time, which gives the researchers a powerful tool for investigating the domestication of more crops, including the domesticated horticultural species. It is appreciable that more and more investigations, which use the resequencing data for studying the crop domestication, will appear. Regarding the fruit shape, in the past two decades, with the efforts of many researchers, most of the main fruit size and shape controlling loci have been cloned, thus it is hard to find new loci which are more impactive than the fine-mapped fruit size and shape genes.

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