

From Ancestors to Modern Cultivars: Tracing the Origin, Evolution, and Genetic Progress in Cucurbitaceae

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Abstract The Cucurbitaceae family, encompassing a wide array of economically significant species, has undergone extensive evolutionary diversification since its origin in the Late Cretaceous period. This systematic review synthesizes the current understanding of the genetic and evolutionary trajectories within the Cucurbitaceae, tracing the lineage from ancestral forms to modern cultivars. We integrate findings from whole-genome analyses, phylogenetic studies, and gene family evolution research to construct a comprehensive picture of the genetic progress in this family. The review highlights the whole-genome duplication event in the *Cucurbita* genus approximately 30 million years ago, which has led to a rapid turnover and neofunctionalization of protein-coding and long noncoding RNA genes, particularly in *Cucurbita argyrosperma*. Additionally, the evolution of *Benincasa hispida* is examined, revealing its unique phylogenetic position and significant gene loss from its common ancestor, alongside the conservation of the phenylalanine ammonia-lyase gene family across six Cucurbitaceae species. The phylogenetic relationships within the family are clarified, with an emphasis on the major clades and their geographical distributions, as well as the need for further ecological and morphological studies. This review provides valuable insights into the genetic mechanisms underlying the diversity and adaptation of Cucurbitaceae species, offering a foundation for future research and breeding programs.

Keywords Cucurbitaceae; Evolution; Genome duplication; Gene turnover; Neofunctionalization; Phylogenetics; Phenylalanine ammonia-lyase; *Cucurbita argyrosperma*; *Benincasa hispida*; Genetic diversity

1 Introduction

The Cucurbitaceae family, encompassing a wide array of economically and nutritionally significant crops, is pivotal to both agriculture and dietary regimes across the globe. This family includes a variety of species such as watermelon, honey melon, cucumber, squash, zucchini, and pumpkin, which are integral to human consumption and cultural practices. The systematic review titled “From Ancestors to Modern Cultivars: Tracing the Origin, Evolution, and Genetic Progress in Cucurbitaceae” aims to delve into the rich tapestry of this plant family’s history, examining its evolutionary trajectory and the genetic advancements that have been achieved through selective breeding practices.

Cucurbitaceae crops are some of the world’s most valuable, with their domestication dating back to at least 11 000 years ago in various regions including the New World, Asia, and more recently, Africa (Chomicki et al., 2019). The significance of these crops extends beyond their economic value, as they have played a crucial role in the development of human civilizations, providing sustenance and hydration, especially in arid regions where watermelons were cultivated as a source of fresh water (Paris, 2016).

The diversity within the Cucurbitaceae family is remarkable, with a history of widespread dispersal and adaptation. Phylogenetic studies have traced the family’s origin to Asia in the Late Cretaceous, followed by numerous transoceanic dispersal events that have led to their current global distribution (Schaefer et al., 2009). This genetic diversity is not only of academic interest but also has practical implications for breeding programs aimed at improving crop resilience and nutritional content (Velkov and Petkova, 2014).

This systematic review will provide a detailed account of the Cucurbitaceae family’s journey from wild ancestors to the diverse and essential cultivars of today, offering insights into the genetic progress that has shaped these crops and setting the stage for future innovations in cucurbit research and cultivation.

2 Origin and Early Evolution of Cucurbitaceae

The origin and early evolution of Cucurbitaceae are characterized by an Asian origin, multiple long-distance dispersal events, and significant genomic changes, including polyploidization. These factors have collectively shaped the wide diversity and global distribution of the family.

2.1 Geological and fossil evidence of early Cucurbitaceae

The Cucurbitaceae family, with its significant economic and biological importance, has a deep evolutionary history that can be traced back to the Late Cretaceous period. Geological and fossil records, combined with phylogenetic studies, suggest that the family originated in mainland Southeast Asia during this era. The earliest divergences within the family date back to 70–80 million years ago, indicating an ancient lineage that has since diversified into a wide array of genera and species (Renner and Schaefer, 2016).

Historical records, including archaeobotanical finds, iconography, and literature, have provided evidence of the use of cucurbits by humans. For instance, *Cucurbita* spp. were first cultivated in the Americas over 10 000 years ago, with indigenous American peoples developing various cultivar-groups of pumpkins and squash by 1492 CE. Watermelons have a history of cultivation in northeastern Africa dating back at least 4 000 years, initially valued for their water content. Melons and cucumbers, native to Asia, were likely first cultivated for their young fruits as vegetables. Melons spread to eastern Africa early on, while cucumbers, a more recent domesticate, spread westwards to Europe in early medieval times (Paris, 2016).

2.2 Theories on the geographical origin of the family

Theories on the geographical origin of Cucurbitaceae have been shaped by extensive phylogenetic research. A comprehensive multigene phylogeny, which included a wide sampling of species from herbarium collections, points to an Asian origin of the family. This is supported by the fact that two of the oldest clades within the family are now almost exclusively found in Asia. The family's spread to other continents, such as Africa, the Americas, and Australia, is attributed to numerous long-distance dispersal events, which have been a significant factor in the family's global distribution (Schaefer et al., 2009).

2.3 Domestication history and phenotypic evolution of Cucurbitaceae crops

A comprehensive phylogenetic analysis has provided insights into the domestication of these crops, suggesting that an annual life cycle may have been a contributing factor. The domestication of these species is believed to have begun around 11 000 years ago in the New World and Asia, with some evidence of more recent domestication in Africa. Notably, certain crops like melon were domesticated multiple times from different populations in Asia and Africa (Figure 1) (Chomicki et al, 2019).

The study by Chomicki et al. (2019) offers a valuable perspective on the domestication syndrome within the Cucurbitaceae family, examining how selective breeding has altered key phenotypic traits such as size, shape, and taste of fruits from their wild ancestors. Understanding these transformations is crucial for appreciating the impact of human agriculture on plant biodiversity and for guiding future breeding strategies aimed at improving crop yield, resistance, and nutritional content. The use of visual comparisons between wild and domesticated forms provides a clear and immediate understanding of the extent of changes induced by selective breeding. Such insights are essential for geneticists and breeders who aim to harness the genetic potential of wild progenitors to introduce desired traits into modern cultivars, thereby enhancing genetic diversity and crop resilience.

The domestication of Cucurbitaceae crops has been characterized by the selection of non-bitter and palatable fruit, a trait that was favored early in the process. Genomic studies have shed light on how the loss of bitterness was achieved through convergent evolution. Additionally, the genetic pathways involved in the accumulation of lycopene, which contributes to the red or orange color of the pulp, as well as the determination of fruit size and shape, are beginning to be elucidated (Chomicki et al., 2019).



Figure 1 Illustration of domestication syndrome in Cucurbitaceae crops (Adopted from Chomicki et al., 2019)

Image caption: This figure contrasts the phenotypic characteristics of wild progenitors with their domesticated descendants within the Cucurbitaceae family. (a, b) Display honey melon (*Cucumis melo*) with (a) showing the wild melon progenitor, Asian agrestis (*Cucumis melo* subsp. *melo* f. *agrestis*), and (b) the domesticated melon from the Asian lineage. (c, d) Watermelon (*Citrullus lanatus*) with (c) depicting the wild watermelon progenitor, Kordofan melon (*Citrullus lanatus* subsp. *cordophanus*), and (d) the domesticated watermelon. (e, f) Cucumber (*Cucumis sativus*) with (e) the wild cucumber progenitor (*C. sativus* f. *hardwickii*) and (f) the domesticated cucumber. This visual comparison underscores the significant morphological changes resulting from domestication processes (Adapted from Chomicki et al., 2019)

2.4 Phylogenetic studies and genetic data supporting evolutionary pathways

Phylogenetic studies using molecular data, such as the internal transcribed spacer regions (ITS1 and ITS2) of nuclear ribosomal RNA genes, have provided insights into the relationships among different members of the Cucurbitaceae family. These studies have revealed a polyphyletic origin for New World species and have highlighted the role of introgression and polyploidization events in the evolution of the family (Jobst et al., 1998). Additionally, chloroplast DNA sequences have been used to infer phylogenies, which have helped clarify the classification of the family and the evolution of key characters such as flower and fruit morphology (Kocyan et al., 2007).

Whole-genome duplications have also been identified as pivotal events in the family's evolution. The discovery of an overlooked paleotetraploidization event suggests that genome duplications have played a crucial role in the establishment of the Cucurbitaceae family (Wang et al., 2017). Furthermore, phylotranscriptomic analyses have revealed multiple whole-genome duplications that coincide with bursts of diversification and morphological innovations, supporting the hypothesis that genetic diversity following polyploidizations has driven the adaptive evolution of the family (Figure 2) (Alverson et al., 2010; Guo et al., 2020).

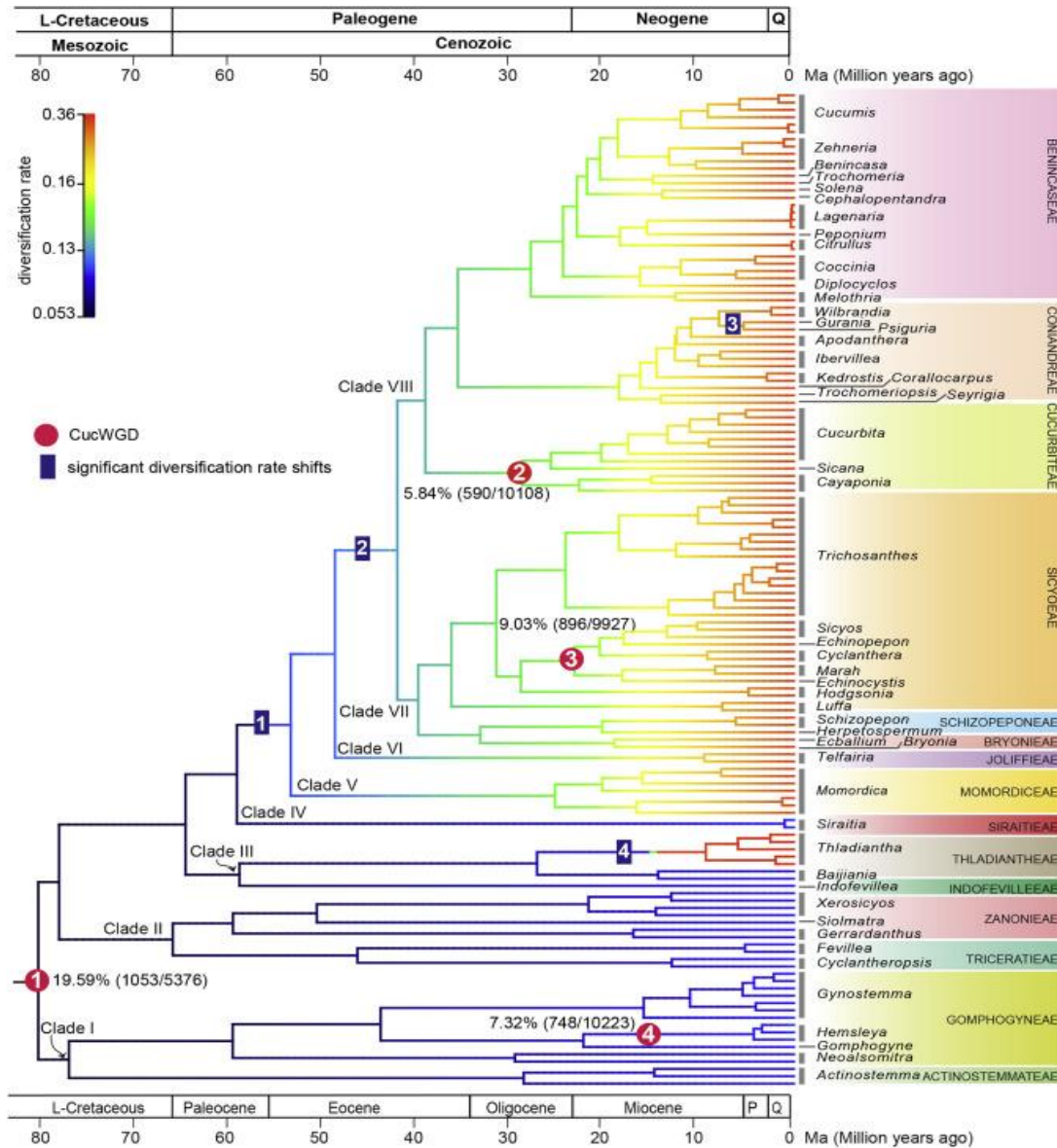


Figure 2 Diversification rate shifts and large-scale gene duplications in Cucurbitaceae (Adopted from Guo et al., 2020)

Image caption: This phylogenetic tree illustrates the historical diversification rate shifts and large-scale gene duplications across the Cucurbitaceae family. Dark blue bars indicate species diversification rate shifts estimated by BAMM and MEDUSA, with branch colors representing the mean diversification rate (species/million years). Red dots numbered 1 to 4 mark the locations of four significant whole genome duplications (CucWGD1 to CucWGD4), with the percentages and numbers of duplicated gene families displayed adjacent to each dot. The right side lists the relevant genera and tribes, aligning with the branches they correspond to. The geological timeline is shown at the top and bottom of the figure, providing a temporal context for these evolutionary events (Adapted from Guo et al., 2020)

This study by Guo et al. (2020) presents compelling evidence of whole genome duplications within the Cucurbitaceae family, which have played a pivotal role in the evolutionary history and diversification of this group. The identification of four major WGD events (CucWGD1 to CucWGD4) across different clades and tribes

signifies key evolutionary moments that likely contributed to the adaptive success and phenotypic diversity observed among the cucurbit species today. The integration of diversification rate analysis with genomic evidence provides a nuanced understanding of how gene duplications have influenced both the genetic architecture and ecological adaptations of the family. Such insights are crucial for further research into the functional implications of these genomic changes, potentially informing breeding strategies and conservation efforts for cucurbit species. The study underscores the importance of genomic studies in revealing the underlying mechanisms of plant evolution and diversification.

3 Diversification and Speciation in Cucurbitaceae

3.1 Role of environmental factors and geographical expansion

The Cucurbitaceae family, with its significant genetic diversity, has been subject to extensive research to understand the role of environmental factors and geographical expansion in its diversification. The family's origin in Asia during the Late Cretaceous period and subsequent spread across continents through long-distance dispersal events have been well-documented (Schaefer et al., 2009). The successful colonization of new territories, such as North America, Madagascar, and Australia, by Cucurbitaceae species is attributed to at least 43 long-distance dispersal events over the past 60 million years (Schaefer et al., 2009). This geographical expansion has been facilitated by the family's ability to adapt to various environmental conditions, leading to a wide distribution of cucurbit crops worldwide (Ma et al., 2022).

3.2 Mechanisms of speciation within the family

Speciation within the Cucurbitaceae family has been influenced by several factors, including whole genome duplications (WGD), which have contributed to increased genetic diversity and morphological innovations (Guo et al., 2020). The internal transcribed spacer regions (ITS1 and ITS2) have provided insights into the phylogenetic relationships among species, suggesting a polyphyletic origin for New World species and highlighting the role of introgression and polyploidization in speciation (Jobst et al., 1998). Additionally, inter-genus variation analysis using ISSR markers has revealed significant diversification among members of the same genus, indicating the complexity of speciation processes within the family (Payel et al., 2015).

3.3 Key evolutionary adaptations

Evolutionary adaptations in fruit and flower morphology, as well as disease resistance, have been key to the success of Cucurbitaceae species. The wax gourd genome, representing the most ancestral karyotype among cucurbits, has provided insights into the genetic basis of diversity (Figure 3), particularly in fruit size (Xie et al., 2019). Comparative genomics analyses have identified candidate genes potentially selected during domestication that contribute to large fruit size (Xie et al., 2019). The family's characteristic tendrils and pepo fruits are examples of morphological innovations that have arisen following early genome duplication events, coinciding with diversification and morphological changes under paleo-climate upheavals (Guo et al., 2020). The genetic architecture of fruit size and shape variation has been comparatively studied across cucurbits, revealing widespread structure and function conservation of fruit size/shape gene homologs (Pan et al., 2019). These adaptations have not only facilitated the survival and spread of cucurbits but have also been crucial for their domestication and agricultural importance (Bisognin, 2002).

This genomic study of the wax gourd and related cucurbit species offers valuable insights into the evolutionary dynamics that have shaped the Cucurbitaceae family. By reconstructing the ancestral cucurbit karyotype and mapping the evolutionary trajectories of modern cucurbit genomes, the research by Xie et al. (2019) enhances our understanding of plant genome evolution. The identification of specific whole-genome duplications and common tetraploidization events provides a clearer picture of the genetic mechanisms behind the diversification and adaptation of cucurbit species. Such studies are crucial for informing breeding programs and conservation efforts, as they highlight genetic linkages and evolutionary pressures that could influence future crop resilience and productivity.

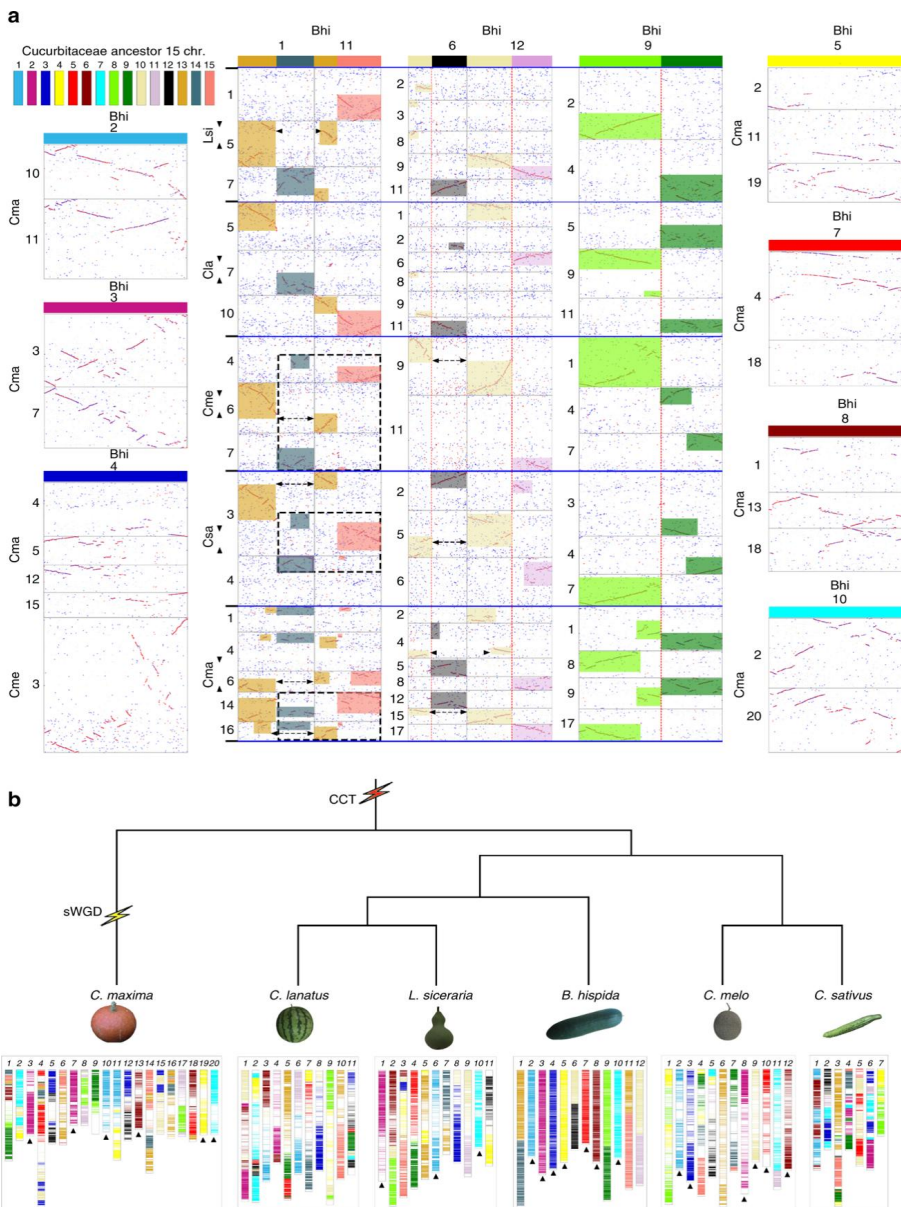


Figure 3 Genome evolution and ancestral karyotype reconstruction in Cucurbitaceae (Adopted from Xie et al., 2019)

Image caption: This figure illustrates the conserved genome karyotype of the wax gourd alongside the identification of the 15 ancestral chromosomes across six sequenced cucurbit species. Panel (a) displays the 12 wax gourd chromosomes, color-coded to indicate the origins of the ancestral chromosomes (Bhi: *Benincasa hispida*; Cma: *Cucurbita maxima*; Cme: *Cucumis melo*; Lsi: *Lagenaria siceraria*; Cla: *Citrullus lanatus*; Csa: *Cucumis sativus*). Panel (b) outlines the evolutionary scenario of the Cucurbitaceae genomes, tracing back to the ancestral Cucurbitaceae karyotype, with significant evolutionary events such as specific whole-genome duplications (sWGD) and cucurbit-common tetraploidization (CCT) marked (Adapted from Xie et al., 2019)

4 Genetic Advances in Cucurbitaceae

4.1 Mapping and characterization of key genetic traits

Recent studies have made significant strides in mapping and characterizing the genetic traits that define the Cucurbitaceae family. A comprehensive phylogenetic analysis incorporating 127 newly sequenced transcriptomes and genomes has revealed multiple whole genome duplications (WGD) that have played a pivotal role in the diversification of the family (Guo et al., 2020). These duplications have been linked to key morphological and molecular innovations, such as the development of tendrils and pepo fruits, which are characteristic of the family. The identification of the cucurbit-specific tendril identity gene TEN, which originated from a paleo-polyploidization event, underscores the importance of genetic mapping in understanding the evolutionary history of Cucurbitaceae (Figure 4) (Guo et al., 2020).

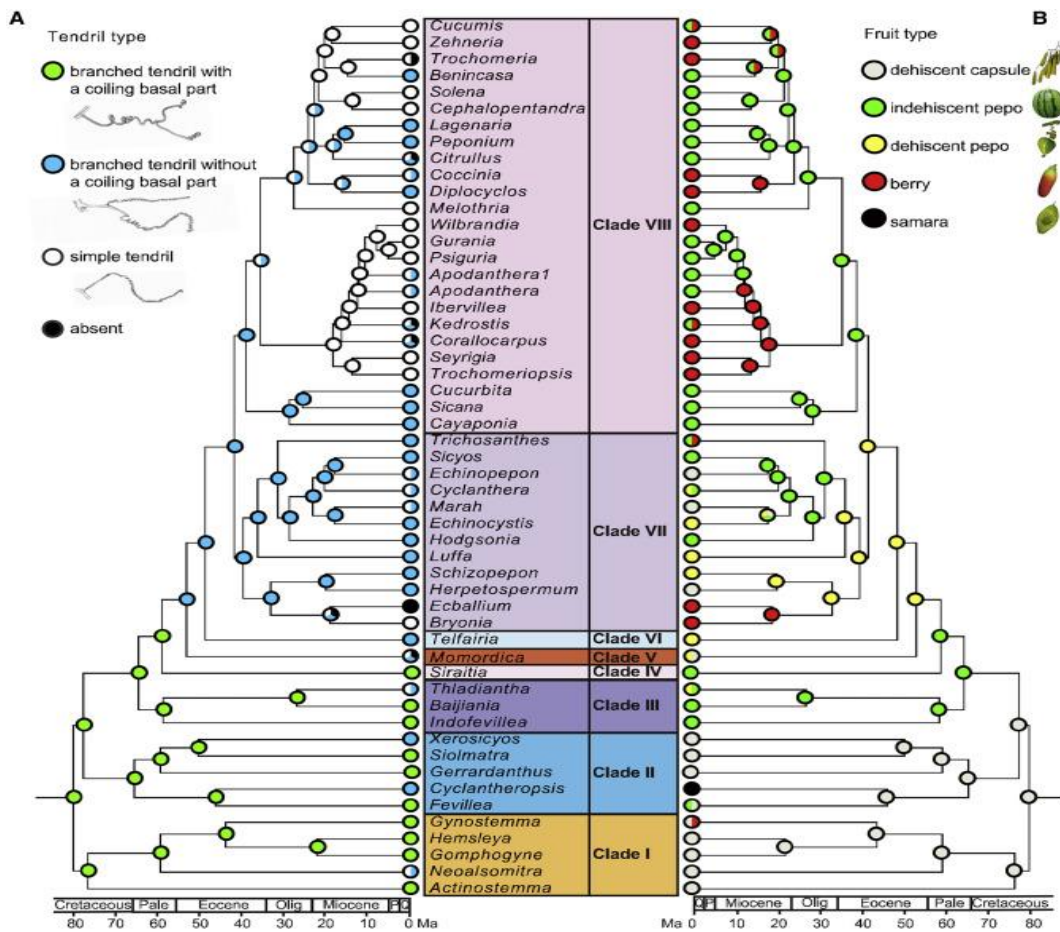


Figure 4 Evolutionary histories of tendrils and fruit type in Cucurbitaceae (Adopted from Guo et al., 2020)

Image caption: Panel A presents a chronogram at the genus level, mapping the ancestral character states of fruit types and tendrils under the maximum parsimony criterion, with ages corresponding to the timeline at the bottom. Generic names are listed, separated by different background colors indicating major clades identified in the study. Panel B showcases representative fruit types, including *Neoalsomitra integrifoliola* (dehiscent capsule), *Citrullus lanatus* (indehiscent pepo), *Schizopepon bryoniifolius* (dehiscent pepo), *Coccinia grandis* (berry), and *Cyclantheropsis parviflora* (samara), illustrating the diversity of fruit morphologies within the family (Adapted from Guo et al., 2020)

This study by Guo et al. (2020) offers significant insights into the morphological evolution within the Cucurbitaceae family, particularly focusing on the diversification of fruit types and tendrils. By employing a detailed phylogenetic framework, the research illustrates how specific traits have evolved in response to ecological and evolutionary pressures. Understanding these patterns is crucial for comprehending the adaptive strategies of Cucurbitaceae, which can have direct implications for agriculture, especially in the context of breeding and conservation. The analysis not only helps in piecing together the evolutionary history of these plant traits but also aids in predicting how they might change in response to future environmental conditions. This kind of evolutionary insight is invaluable for developing strategies to preserve the genetic diversity and adaptability of cucurbit crops.

4.2 Contributions of genomic studies to understanding genetic diversity

Genomic studies have been instrumental in unraveling the genetic diversity within the Cucurbitaceae family. By utilizing inter simple sequence repeat (ISSR) markers, researchers have been able to analyze the genetic relationships among selected species of cucurbits, revealing significant diversification even among members of the same genus (Payel et al., 2015). This level of genetic diversity is crucial for the speciation and acclimatization of plants within their environments. The phylogram generated from these studies has provided insights into the close genetic relationships between species such as *C. maderaspatanus* and *C. melo*, while highlighting the genetic distance of *C. sativus* from these species (Payel et al., 2015).

4.3 Impact of genetic engineering and biotechnological approaches

While the provided data does not explicitly detail the impact of genetic engineering and biotechnological approaches on Cucurbitaceae, the mapping and characterization of genetic traits, as well as the understanding of genetic diversity, lay the groundwork for future biotechnological interventions. The knowledge gained from these genomic studies can be applied to genetic engineering efforts aimed at improving crop traits, resistance to diseases, and adaptation to environmental stresses. The extensive genetic information available for Cucurbitaceae can facilitate targeted breeding programs and the development of genetically modified crops that meet the demands of a growing population and changing climate conditions.

5 Breeding Achievements in Cucurbitaceae

5.1 Historical perspective on breeding techniques and their evolution

The Cucurbitaceae family, encompassing a wide variety of economically and nutritionally important crops, has undergone significant breeding advancements over time. Historically, the improvement of these crops relied heavily on classical breeding and selection methods, which facilitated the rapid development of staple crops within the family, such as pumpkins, squashes, cucumbers, watermelons, and melons (Shafiin et al., 2020). These traditional techniques were the cornerstone of breeding programs aimed at enhancing the yield, quality, and nutritional value of cucurbit crops. However, the narrow genetic bases and low variation rates inherent to cucurbit crops presented challenges, leading to a breeding bottleneck that necessitated the adoption of more innovative approaches (Figure 5) (Feng et al., 2023).

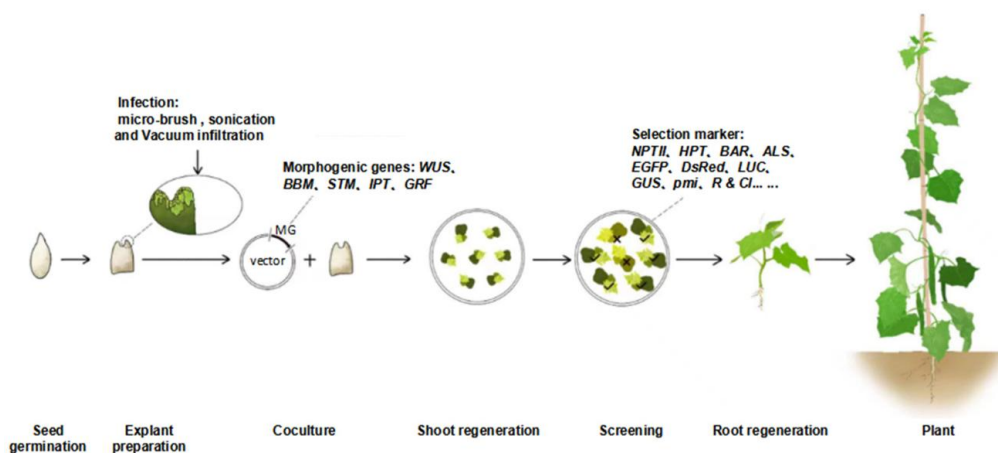


Figure 5 Agrobacterium-mediated transformation in Cucurbit crops (Adopted from Feng et al., 2023)

Image caption: This diagram illustrates the major technique currently adopted for genetic transformation in cucurbit crops using cotyledons as explants. It highlights the critical factors influencing transformation efficiency, including the choice of Agrobacterium strain, infection method, regeneration efficiency of the plant, screening methods, and the application of exogenous phytohormones. Recent advancements in the transformation process are also depicted, showing improvements through genotype screening, diverse screening markers, and the use of morphogenic genes, leading to enhanced efficiency in genetic transformation (Adapted from Feng et al., 2023)

The exploration of Agrobacterium-mediated genetic transformation techniques in cucurbit crops is a crucial advancement for cucurbit genomics and biotechnology. The detailed discussion on optimizing transformation processes based on several key factors provides valuable insights for researchers looking to improve genetic transformation efficiencies in these crops (Feng et al., 2023). The integration of new genetic tools and methodologies, such as the use of morphogenic genes and diverse screening markers, enhances the potential for developing cucurbit varieties with desired traits more efficiently. This research by Feng et al. (2023) is pivotal for addressing challenges related to disease resistance, fruit quality, and yield improvements in cucurbit crops, potentially leading to more sustainable agricultural practices and better crop varieties suited to diverse environmental conditions.

5.2 Major breakthroughs in breeding for resistance to biotic and abiotic stresses

The advent of molecular techniques has revolutionized cucurbit breeding, particularly in the context of resistance to biotic and abiotic stresses. The development of genetic transformation and gene editing technologies, such as CRISPR/Cas9-mediated gene knockout and base editing, has been a game-changer, allowing for precise modifications that confer resistance to various stresses (Feng et al., 2023). These breakthroughs have not only enhanced the resilience of cucurbit crops but have also accelerated the breeding process, bypassing some of the limitations of conventional breeding methods.

5.3 Development of cultivars with improved yield, quality, and nutritional value

In the quest to combat micronutrient malnutrition, particularly in developing countries, breeding strategies for cucurbit crops have increasingly focused on biofortification and the enhancement of nutrient content and quality (Shafiin et al., 2020). The genomic information of cucurbit species has been instrumental in this regard, enabling breeders to identify and manipulate genes associated with nutritional content, thereby developing elite varieties with improved traits (Shafiin et al., 2020; Ma et al., 2022). The genome sequences of 18 different cucurbit species have been deciphered, shedding light on evolutionary relationships and functional genes that are key to agronomic traits such as fruit quality (Ma et al., 2022). This genomic knowledge, combined with nonconventional breeding approaches, has significantly contributed to the development of cucurbit cultivars with superior yield, quality, and nutritional value, offering promising solutions to global nutritional challenges (Shafiin et al., 2020; Ma et al., 2022).

6 Case Studies

This section of the review focuses on key studies concerning major Cucurbitaceae species-cucumber, melon, and squash-highlighting the significant insights gained from genetic and genomic research and discussing their practical applications in modern agriculture.

6.1 Detailed review of key studies focusing on major Cucurbitaceae species

6.1.1 Cucumber (*Cucumis sativus*)

The landmark study in the genetic research of cucumber that involved sequencing its genome is detailed in the paper titled “A chromosome-scale genome assembly of cucumber (*Cucumis sativus* L.)” (Li et al., 2019). This study presents a high-quality and complete cucumber genome assembly using single-molecule real-time (SMRT) long reads, which provided a more accurate and comprehensive reference genome than previous versions. The assembly revealed novel features of the cucumber genome, including a higher guanine-cytosine or adenine-thymine content in newly assembled regions and the identification of novel genes and full-length long terminal retrotransposons (Li et al., 2019).

Another significant contribution to cucumber genome sequencing is described in the paper “The genome of the cucumber, *Cucumis sativus* L.” (Huang et al., 2009). This research reported the draft genome sequence of cucumber, which was assembled using a combination of Sanger and next-generation Illumina sequencing technologies. The study provided insights into the cucumber’s chromosome evolution, sex expression, disease resistance, and other traits (Huang et al., 2009).

These two papers (Huang et al., 2009; Li et al., 2019) are pivotal in the field of cucumber genetics, providing essential resources for further genetic research and breeding programs.

6.1.2 Melon (*Cucumis melo*)

Genomic studies in melon (*Cucumis melo*) have significantly advanced our understanding of the genetic determinants of fruit quality traits such as sweetness, aroma, and texture. These traits are essential for consumer preference and market value, and their genetic bases are being unraveled through various quantitative trait loci (QTL) mapping approaches.

Multiple studies have identified QTLs associated with fruit quality traits in melon, including sugar and carotenoid content, fruit and seed morphology, and color traits, using high-density genetic maps and recombinant inbred line (RIL) populations (Ramamurthy et al., 2015; Pereira et al., 2018; Galpaz et al., 2018; Zhang et al., 2020; Amanullah et al., 2020).

Specific genes within QTL intervals have been pinpointed as candidates for traits like fruit aroma and flesh color, with some studies validating the metabolic activity of these genes (Galpaz et al., 2018).

The genetic architecture of fruit quality traits appears to be complex, with many traits being controlled by polygenes and influenced by environmental factors (Zhang et al., 2020; Dantas et al., 2022).

Clustering of QTLs on certain chromosomes has been observed, and some QTLs exhibit pleiotropic effects, affecting multiple traits (Zhang et al., 2020; Amanullah et al., 2020).

The genetic diversity between wild and cultivated melon varieties, as well as between different botanical groups, provides a rich resource for breeding programs aimed at improving fruit quality and other agronomic traits (Ramamurthy et al., 2015; Maragal et al., 2019).

Earliness and ripening behavior, which are important for fruit quality, have been studied through QTL mapping, revealing associations with ethylene emission, fruit firmness, and maturity (Oren et al., 2022).

Genotypic and agro-environmental factors, including grafting, water and thermal stress, and targeted nutrition, have been shown to influence fruit quality traits in melon and watermelon (Kyriacou et al., 2018).

The synthesis of genomic research in melon has revealed a complex genetic landscape underpinning fruit quality traits. QTL mapping has been instrumental in identifying key genomic regions and candidate genes associated with sweetness, aroma, and texture. These findings are crucial for the development of marker-assisted selection strategies in melon breeding programs. The genetic diversity present in melon varieties, along with the understanding of genotypic and environmental interactions, offers valuable insights for enhancing fruit quality and other desirable traits.

6.1.3 Squash (*Cucurbita* spp.)

The domestication of squash has been a subject of scientific inquiry, focusing on the evolutionary changes and genetic diversity within the *Cucurbita* genus. Research has explored the morphological, physiological, and genetic alterations that have occurred through the domestication process, revealing the complexity of this transformation.

Domestication of *Cucurbita maxima* involved gene flow between domestic and wild variants, leading to diverse hybrid forms and not a linear evolutionary pathway, with implications for fruit size and seed dormancy patterns (Martinez et al., 2017).

Gene expression diversity is generally lower in domesticated species compared to their wild counterparts, affecting a significant portion of the genome and potentially contributing to phenotypic and physiological changes observed in domesticated plants (Liu et al., 2019).

Genetic diversity in wild squash *Cucurbita argyrosperma* subsp. *sororia* is structured latitudinally along the Mexican Pacific coast, with southern populations exhibiting greater diversity, which has implications for conservation and crop improvement (Balvino-Olvera et al., 2017).

The collective research indicates that squash domestication is a dynamic and complex process characterized by extensive hybridization and gene flow, resulting in a wide array of genetic diversity. The decrease in gene expression diversity during domestication may have played a role in the development of domesticated traits. Furthermore, the structured genetic diversity in wild squash populations highlights the importance of regional variation in conservation and agricultural practices.

6.1.4 Zucchini (*Cucurbita* spp.)

The zucchini genome, representing the *Cucurbita* genus, has been sequenced, revealing a whole-genome duplication event associated with the origin of the genus. This duplication is present in all *Cucurbita* species analyzed but not in the more distant *Cucumis* and *Citrullus* genera, suggesting a divergence that occurred approximately 30±4 million years ago (Figure 6) (Montero-Pau et al., 2017).

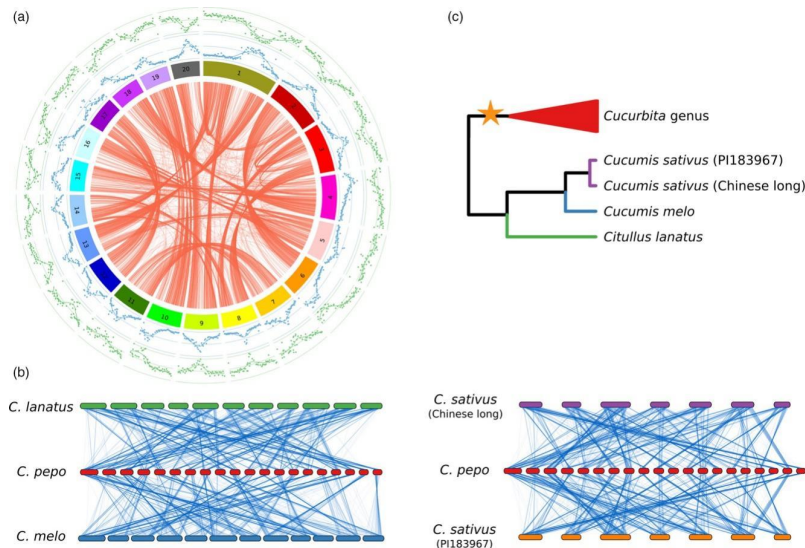


Figure 6 Genome organization and synteny in *Cucurbita pepo* (Adopted from Montero-Pau et al., 2017)

Image caption: (a) This Circos plot illustrates the distribution of paralogous gene pairs within the *Cucurbita pepo* genome (indicated by red lines), with outer plots quantifying the proportions of repetitive (blue) and gene-encoding (green) DNA in 200-Kb windows. (b) Demonstrates genomic synteny between *Cucurbita pepo* and other cucurbit species including *Cucumis melo*, *Cucumis sativus*, and *Citrullus lanatus*, with lines connecting single-copy orthologs to indicate shared genomic regions. (c) Provides a summary diagram depicting the species phylogeny and highlighting a significant whole genome duplication (WGD) event that has influenced evolutionary paths (Adapted from Montero-Pau et al., 2017)

This study by Montero-Pau et al. (2017) is pivotal in advancing our understanding of the genomic architecture and evolutionary history of cucurbit species, specifically *Cucurbita pepo*. The detailed examination of paralogous gene pairs and synteny across species sheds light on the evolutionary processes that have shaped the cucurbit genomes, highlighting the significant role of whole genome duplications. Such duplications are often key drivers of genetic diversity and innovation within plant families, providing new genetic material for adaptation and speciation. The Circos plot visualization effectively underscores the complex interplay between different genomic segments, facilitating a deeper understanding of genome evolution dynamics. This genomic insight is crucial for breeding strategies as it helps identify potential genetic resources for enhancing desirable traits such as disease resistance, fruit quality, and yield in cucurbit crops.

6.2 Insights gained from genetic and genomic research, and their practical applications

The advances in genetic and genomic technologies have transformed our understanding of the Cucurbitaceae family, leading to several practical applications:

6.2.1 Disease resistance

Genetic studies in cucurbits have increasingly focused on identifying and utilizing disease-resistance genes to improve crop resilience and reduce chemical pesticide use. These efforts have been particularly concentrated on cucumbers and melons, where resistance to powdery mildew and various viral pathogens has been a significant breeding target.

- 1) Genetic resistance to a range of viral diseases in cucurbits, including Potyviruses, Cucumoviruses, and Begomoviruses, has been identified, with melon and cucumber showing intraspecific resistance and wild relatives contributing to resistance in other species (Martín-Hernández and Picó, 2020).

- 2) The Vat gene cluster in melon, which confers resistance to pests and pathogens, has been characterized, revealing a high potential for resistance based on SNP variations and leucine-rich-repeat domains (Chovelon et al., 2021).
- 3) A major quantitative trait locus (QTL) on chromosome 8 of *Cucurbita moschata* has been linked to resistance against Tomato leaf curl New Delhi virus, with molecular markers identified for breeding programs (Sáez et al., 2020).
- 4) Inheritance analysis and SNP marker identification have been conducted for Zucchini yellow mosaic virus resistance in *Cucurbita pepo*, with specific NBS-LRR protein-encoding genes located near resistance-associated SNPs (Capuozzo et al., 2017).
- 5) QTL mapping has identified candidate genes for powdery mildew resistance in cucumber, with a particular focus on a gene encoding a leucine-rich repeat receptor-like kinase (Zhang et al., 2020).
- 6) Transcriptome profiling of pumpkin leaves infected with powdery mildew has revealed a complex regulatory network involving hormone signal transduction and defense responses, with several genes significantly up- or down-regulated in resistant plants (Guo et al., 2018).
- 7) A QTL on chromosome 6 of cucumber has been associated with resistance to Cucumber mosaic virus, and a candidate gene with differential expression upon infection has been identified (Shi et al., 2018).
- 8) The MLO gene family, which plays a role in powdery mildew resistance, has been identified and characterized in pumpkin, with certain genes up-regulated in response to infection (Win et al., 2018).
- 9) New NBS-LRR gene analogues have been discovered in native cucurbit species in Iran, suggesting a recent common ancestor and potential resistance against bacterial blight and tomato mosaic virus (Gharaei et al., 2017).
- 10) Genomic tools are being utilized to enhance disease resistance breeding in zucchini, with a focus on identifying R-gene candidates and understanding the genetic basis of resistance mechanisms (Andolfo et al., 2021).

Research across various cucurbit species has uncovered a wealth of genetic resources for disease resistance, particularly against powdery mildew and viral pathogens. The identification of resistance genes, QTLs, and gene clusters, along with the development of molecular markers, has facilitated the breeding of resistant cultivars. These advances contribute to sustainable agriculture by reducing the need for chemical pesticides and enhancing crop resilience to disease.

6.2.2 Fruit quality improvement

Genomic research has revolutionized the field of plant breeding, enabling the development of fruit varieties with enhanced qualities. By identifying genes linked to desirable traits, breeders can create fruits with improved flavor, color, and nutritional value. In melon breeding, genomic tools have facilitated the selection of varieties with increased sweetness and longer shelf life.

- 1) Genomic selection (GS) is a promising approach for improving quantitative traits in crops, outperforming traditional marker-assisted selection by using high-density marker scores to predict breeding values, which accelerates the breeding cycle and captures more variation due to small-effect quantitative trait loci (QTL) (Varshney et al., 2017).
- 2) In table grapes, genomic selection has proven more efficient than QTL analysis for inferring the genetic contribution of marker loci to agronomic traits, suggesting its utility in speeding up selection procedures (Viana et al., 2016).
- 3) Combining genome-wide association studies (GWAS) and genomic selection (GS) increases the power and

accuracy for genetic improvement of fruit quality traits in citrus, with the use of breeding population data enhancing the detection power of GWAS and the prediction accuracy of GS (Minamikawa et al., 2017).

- 4) Molecular markers linked to fruit quality traits have been identified in tropical fruits, aiding marker-assisted breeding (MAB), and genomic approaches like GWAS, GS, and genetic modifications are overcoming long breeding cycles to develop cultivars with desirable traits (Mathiazhagan et al., 2021).
- 5) In melon, SNP-based markers have been used to identify QTLs for fruit quality traits, with the potential for these insights to be applied in marker-assisted selection (MAS) after further investigation (Amanullah et al., 2020).
- 6) Molecular breeding strategies, including the use of molecular markers and genomics-assisted breeding, have been essential in improving traits such as yield, fruit quality, and disease resistance in Cucurbitaceae crops like watermelon and melon (Park et al., 2015).
- 7) Genome-wide SSR markers developed from the melon genome have facilitated genetic diversity studies and comparative mapping, providing a valuable resource for genetic linkage map construction and marker-assisted selection (MAS) in melon and related species (Zhu et al., 2016).

In conclusion, genomic selection and marker-assisted breeding have significantly advanced the development of fruit varieties with superior qualities. The integration of high-density genotyping, molecular markers, and genomic tools has enabled breeders to select for complex traits more efficiently, leading to the creation of melon varieties with enhanced sweetness, shelf life, and overall fruit quality. The use of these genomic approaches is a testament to the power of modern breeding techniques in addressing the demands for high-quality fruit production.

6.2.3 Stress tolerance

The genetic basis of abiotic stress responses in Cucurbitaceae species is a critical area of research for developing resilient cultivars. Abiotic stresses such as drought, heat, and salinity can significantly impact plant growth and yield. Understanding the genetic mechanisms behind these responses allows for the breeding of crops better suited to withstand these challenges.

- 1) The BES1 gene family, involved in brassinosteroid signaling, plays a crucial role in abiotic stress responses in Cucurbitaceae, with differential expression under various stress conditions suggesting their importance in stress adaptation (Xu et al., 2023).
- 2) Two-component system (TCS) genes in cucumber and watermelon are implicated in abiotic stress responses, with specific TCS genes showing differential expression under stress and hormone treatments, indicating their role in stress signaling pathways (He et al., 2016).
- 3) GASA gene family members in Cucurbitaceae species, particularly in cucumber, are differentially regulated under abiotic stresses and hormones, suggesting their involvement in growth and stress response mechanisms (Zhang et al., 2022).
- 4) Superoxide dismutase (SOD) genes in Cucurbitaceae species are responsive to multiple abiotic stresses, indicating their potential role in oxidative stress defense and their importance for genetic improvement of stress tolerance (Rehman et al., 2022).
- 5) Genetic diversity in *Cucurbita moschata*, as revealed by SNP analysis, is crucial for breeding programs aimed at developing stress-tolerant rootstock varieties (Lee et al., 2020).
- 6) MLO family genes in *Cucumis melo* show differential expression under various abiotic stresses, highlighting their potential role in developing stress-resistant cultivars (Howlander et al., 2017).
- 7) *VQ* genes in *Cucurbita pepo* are differentially expressed under abiotic and biotic stresses, suggesting their significance in plant stress responses (Xu et al., 2022).

- 8) Dehydrin genes in Cucurbitaceae species are associated with abiotic stress-response elements, indicating their role in stress tolerance and their potential for molecular breeding (Lee et al., 2017).
- 9) AP2/EREBP gene family members, particularly the DREB subfamily, are associated with abiotic stress responses in Cucurbitaceae species, suggesting their utility in breeding for stress resilience⁹.
- 10) HSP20 family genes in *Cucurbita moschata* are differentially expressed under heat stress, with certain genes identified as candidates for breeding heat-tolerant crops (Hu et al., 2021).

Research across multiple studies has identified several gene families in Cucurbitaceae species that are involved in abiotic stress responses. These include BES1, TCS, GASA, SOD, MLO, VQ, Dehydrin, AP2/EREBP, and HSP20. The differential expression of these genes under various stress conditions highlights their potential roles in conferring stress tolerance. The insights gained from these studies are instrumental in guiding breeding programs aimed at developing cultivars with enhanced resilience to abiotic stresses, thereby ensuring crop productivity and food security in the face of environmental challenges.

6.2.4 Conservation

Genetic and genomic research within the Cucurbitaceae family has provided significant insights into the conservation and enhancement of genetic diversity, which is crucial for the future of breeding programs.

- 1) Genome sequencing of various Cucurbitaceae species has facilitated the understanding of gene identification, genome evolution, and molecular breeding, aiding in the conservation of genetic diversity (Ma et al., 2022).
- 2) Comparative genomic analyses have revealed conserved genetic architecture for fruit size and shape across cucurbits, which can be leveraged for tailored conservation strategies (Pan et al., 2019).
- 3) Chloroplast genome sequences have been used to understand phylogenetic relationships within the Cucurbitaceae, providing insights into selective pressures and aiding in the identification of molecular markers for conservation (Zhang et al., 2018).
- 4) Genetic resources of major cucurbit crops have been documented, highlighting the importance of ex situ germplasm banks and genomic efforts in preserving genetic diversity and informing conservation policies (Grumet et al., 2021).
- 5) Studies on the genetic diversity and structure of wild cucurbit populations, such as *Cucurbita argyrosperma* subsp. *sororia*, have identified regions with high genetic diversity, which are crucial for conservation efforts (Balvino-Olvera et al., 2017).
- 6) Genetic relationship analyses using ISSR markers have demonstrated significant diversification among cucurbit cultivars, which is essential for understanding genetic conservation needs (Payel et al., 2015).
- 7) The karyotype stability and unbiased fractionation in the paleo-allotetraploid *Cucurbita* genomes suggest long-term genomic stability, which is important for conservation and breeding (Sun et al., 2017).
- 8) RAPD markers have been used to assess genetic diversity and taxonomic relationships within the Cucurbitaceae family, providing a basis for conservation decisions (Anbari et al., 2015).
- 9) Morphological and molecular approaches have revealed high genetic diversity in Portuguese landraces of *Cucurbita* spp., underscoring the value of these genetic resources for conservation (Martins et al., 2015).
- 10) SSR markers have shown high transferability across different species/genera within the Cucurbitaceae family, indicating a considerable level of genetic diversity and relationships that can inform conservation strategies (Adeyemo et al., 2019).

In conclusion, the integration of genomic and genetic data has been instrumental in identifying genetically diverse populations and understanding their evolutionary history within the Cucurbitaceae family. This knowledge is vital for developing conservation strategies that preserve the genetic resources necessary for future breeding efforts. The use of genome sequences, molecular markers, and comparative analyses has provided a foundation for informed conservation and enhancement of cucurbit genetic diversity.

7 Current Challenges and Future Directions

The Cucurbitaceae family, with its rich diversity and evolutionary history, presents a unique opportunity to understand plant evolution and adaptation. Despite significant progress in phylogenetic studies, as evidenced by the sequencing of ribosomal RNA spacer regions and various regions of the plastid and mitochondrial genome, challenges remain in fully elucidating the family's evolutionary dynamics (Renner and Schaefer, 2016). The current phylogenetic structure, while clear, is based on available genetic data, which may not fully represent the ecological, physiological, and morphological evolution of the family (Renner and Schaefer, 2016). This gap highlights the need for comprehensive studies that integrate genomics with ecological and physiological data.

The evolution of specific species within the Cucurbitaceae, such as *Benincasa hispida*, and the phylogenetic relationships of gene families like the phenylalanine ammonia-lyase (PAL) across species, have been explored (Chen et al., 2021). However, the observed gene loss during evolution and the impact of regional factors on species divergence call for a deeper investigation into the mechanisms driving these evolutionary processes (Chen et al., 2021). The conservation of the PAL gene family throughout Cucurbitaceae evolution suggests functional importance, warranting further functional genomics studies to understand the roles of such conserved genes in plant development and stress responses.

Moreover, the *Cucurbita* genus, having undergone a whole-genome duplication event, presents a case study for the evolutionary dynamics of protein-coding and long noncoding RNA (lincRNA) genes (Barrera-Redondo et al., 2019). The higher birth-death rate of protein-coding genes and the neofunctionalization of lincRNAs in *Cucurbita* species compared to other Cucurbitaceae members indicate a rapid evolutionary pace post-duplication (Barrera-Redondo et al., 2019). This rapid evolution and the significant role of lincRNAs in gene regulation underscore the importance of studying noncoding elements in plant genomes.

Future research directions should focus on the following areas:

- 1) **Integrative Genomic and Ecological Studies:** Bridging the gap between genomic data and ecological insights will be crucial for understanding the adaptive evolution of Cucurbitaceae species. This includes studying wild species in their natural habitats, many of which are threatened, to conserve genetic diversity and understand evolutionary pressures (Renner and Schaefer, 2016).
- 2) **Functional Genomics of Conserved Gene Families:** Investigating the functional roles of conserved gene families, such as PAL, will provide insights into their contribution to plant survival and adaptation. This may involve gene expression profiling under various environmental conditions and functional validation through genetic manipulation (Chen et al., 2021).
- 3) **Evolutionary Dynamics Post-Genome Duplication:** Further research is needed to elucidate the evolutionary consequences of whole-genome duplication in *Cucurbita*. This includes studying the rates of gene turnover, the process of neofunctionalization, and the impact on plant phenotypes and adaptation (Barrera-Redondo et al., 2019).
- 4) **Noncoding RNA Research:** Given the significant turnover and neofunctionalization of lincRNAs in *Cucurbita*, there is a need to explore the regulatory networks involving lincRNAs. This research will enhance our understanding of the complexity of gene regulation in plants and the evolutionary significance of noncoding RNAs (Barrera-Redondo et al., 2019).

In conclusion, while the Cucurbitaceae family has served as a model for evolutionary studies, the integration of genomic data with ecological and functional studies will pave the way for a more comprehensive understanding of plant evolution. Addressing these challenges and exploring these future directions will not only advance our knowledge of Cucurbitaceae but also contribute to the broader field of plant science.

8 Concluding Remarks

The systematic review of the Cucurbitaceae family, a lineage with a rich evolutionary history and significant agricultural value, has revealed several key insights into its origin, evolution, and genetic progress. The Cucurbitaceae family, comprising about 1000 species, has undergone complex evolutionary processes, including whole-genome duplications, gene family expansions, and contractions, as well as neofunctionalization of genes (Renner and Schaefer, 2016; Chen et al., 2021).

The whole-genome duplication event that occurred approximately 30 million years ago within the Cucurbita genus has been a pivotal moment in the evolutionary trajectory of these species. This event has led to a faster rate of evolution in protein-coding and long noncoding RNA genes in Cucurbita species compared to other members of the Cucurbitaceae family (Barrera-Redondo et al., 2019). Specifically, Cucurbita argyrosperma has shown a higher turnover rate of protein-coding genes and a significant neofunctionalization of long intergenic noncoding RNA (lincRNA) genes, which suggests a dynamic evolutionary process that has contributed to the diversity and adaptability of the genus (Barrera-Redondo et al., 2019).

The phylogenetic relationships within the Cucurbitaceae family have been clarified through extensive sequencing efforts, providing an updated phylogenetic scheme that includes the placement of all genera. The family's origin in mainland Southeast Asia during the Late Cretaceous and the subsequent divergence of its major clades highlight the ancient and complex history of these species (Renner and Schaefer, 2016).

The evolution of Benincasa hispida and the phylogenetic relationships of the phenylalanine ammonia-lyase (PAL) gene family across six Cucurbitaceae species have shed light on the genetic underpinnings of important agronomic traits. The conservation of the PAL gene family throughout the evolution of the Cucurbitaceae family underscores the importance of these genes in the survival and adaptation of these species (Chen et al., 2021).

The rapid advancement of sequencing technologies has facilitated the deciphering of genome sequences from numerous Cucurbitaceae species, enabling a deeper understanding of genome evolution, gene function, and molecular breeding. The identification of functional genes associated with key agronomic traits, such as fruit quality, has opened new avenues for the molecular breeding of cucurbit crops (Ma et al., 2022).

In conclusion, the Cucurbitaceae family's journey from its ancestral origins to the modern cultivars we know today is a testament to the power of evolutionary forces in shaping the genetic diversity of plant species. The insights gained from studying the Cucurbitaceae genomes provide a valuable framework for future research and breeding efforts aimed at enhancing the agricultural productivity and resilience of these vital crops.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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