

## Invited Review

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## Integrative Insights into the Systematic Classification and Phylogenesis of Cucurbitaceae: A Comprehensive Review of Genetic and Genomic Advances

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**Abstract** The Cucurbitaceae family, with approximately 800 species across 130 genera, is of significant economic and botanical interest. Recent systematic reviews and phylogenetic analyses have provided new insights into the classification and evolutionary relationships within this diverse group. This systematic review synthesizes findings from multiple molecular studies, including chloroplast DNA sequences, nuclear ribosomal RNA genes, and various DNA regions from three plant genomes, to present an integrative perspective on the phylogeny of Cucurbitaceae. The traditional subfamilies and tribes have been re-evaluated, revealing weak support for the traditional subfamilies Cucurbitoideae and Nhandiroboideae, and the need for a reclassification of several genera due to polyphyly or paraphyly. Morphological characters such as flower and seed traits have been correlated with molecular data, providing a more comprehensive understanding of character evolution. Additionally, the review highlights the importance of molecular tools for species identification, particularly in genera with complex morphological variation. The proposed new classification system includes significant changes, with the establishment of new tribes and the re-circumscription of genera, reflecting a more natural phylogenetic order. This review underscores the dynamic nature of Cucurbitaceae systematics and the ongoing need for integrative approaches to understand the evolutionary history of this family.

**Keywords** Cucurbitaceae; Phylogeny; Systematics; Molecular evolution; Classification; Species identification; Chloroplast DNA; Nuclear ribosomal RNA; Morphological characters

The Cucurbitaceae family, commonly known as the gourd family, encompasses a diverse array of species that are of significant economic and ecological importance. This family includes a variety of crops that are integral to agriculture and human nutrition, as well as species that play crucial roles in their native ecosystems. The systematic classification and phylogenesis of Cucurbitaceae have been subjects of extensive research due to their complex evolutionary history and the challenges posed by their wide geographical distribution.

Recent advances in genetic and genomic research have provided new insights into the phylogenetic relationships within the Cucurbitaceae family. A comprehensive phylogeny that includes 114 of the 115 genera and 25 percent of the species has revealed an Asian origin of the family in the Late Cretaceous, with subsequent dispersal events leading to the colonization of various continents (Schaefer et al., 2009). This extensive study utilized herbarium specimens from 30 different collections, highlighting the importance of museum collections in achieving broad geographical sampling for plant phylogenetics.

Furthermore, the phylogeny of the broader order Cucurbitales, which includes Cucurbitaceae, has been elucidated through the sequencing of DNA from nine loci across three genomes. This research has provided a clearer picture of the morphological and sexual system evolution within the order, suggesting that features such as stipulate leaves, inferior ovaries, and parietal placentation are ancestral, while dioecy may have evolved early in the lineage that includes Cucurbitaceae (Zhang et al., 2006).

The purpose of this systematic review is to integrate these recent genetic and genomic advances with existing knowledge to refine our understanding of the systematic classification and phylogenesis of the Cucurbitaceae family. By doing so, we aim to provide a more comprehensive framework that can inform future research in plant science, conservation efforts, and agricultural practices involving this vital group of plants.

## 1 Systematic Classification of Cucurbitaceae

### 1.1 Historical perspective on the classification of Cucurbitaceae

The Cucurbitaceae family, with approximately 800 species across 130 genera, has been traditionally divided into subfamilies such as Cucurbitoideae and Nhandiroboideae, with further classification into tribes and subtribes. Historically, the classification within Cucurbitaceae has been based on morphological and floral characteristics, which have been used to delineate genera and species. However, this approach has often led to polyphyletic or paraphyletic groupings due to convergent evolution and the plasticity of certain morphological traits (Kocyan et al., 2007; Rahman, 2013).

### 1.2 Current systematic framework and taxonomic updates

Recent systematic studies have proposed a new classification for the Cucurbitaceae family, based on comprehensive molecular data from multiple DNA regions across the three plant genomes. This has resulted in a more natural classification system that comprises 95 genera in 15 tribes, with the introduction of five new tribes: Actinostemmataeae, Indofevilleae, Thladiantheae, Momordiceae, and Siraitieae. This reclassification necessitated 44 new combinations and two new names within the family, reflecting a significant update to the systematic framework of Cucurbitaceae (Schaefer and Renner, 2011).

### 1.3 Role of molecular markers and phylogenetic studies in reshaping classification

Molecular markers, such as chloroplast DNA sequences, nuclear ribosomal RNA genes, and low-copy nuclear genes, have played a pivotal role in reshaping the classification of Cucurbitaceae. Phylogenetic analyses using these markers have provided insights into the relationships among species and genera, often challenging traditional classifications based on morphology alone. For instance, the internal transcribed spacer (ITS) regions have revealed genus-specific variations in length and have suggested a polyphyletic origin for New World species within the family (Jobst et al., 1998). Additionally, molecular systematics has clarified species boundaries within genera, such as *Psiguria*, and has provided DNA barcodes for species identification (Steele et al., 2010). Phylogenetic informativeness analyses have also been employed to interpret phylogenomic datasets, leading to a better understanding of diversification processes within the family (Bellot et al., 2020).

Moreover, molecular phylogenetics has unraveled relationships within the *Cucumis* genus, indicating multiple introductions from Africa to Asia and highlighting the complex biogeographical history of these species (Ghebretinsae et al., 2007). Seed coat diversity studies have further supported the findings of molecular phylogenetic research, providing additional evidence for the systematic classification of tribes and genera within Cucurbitaceae (Heneidak and Khalik, 2015). The comprehensive phylogeny of the Cucurbitales order, based on DNA sequences from nine loci across three genomes, has implications for the evolution of morphological traits and sexual systems, offering a broader context for the classification of Cucurbitaceae (Zhang et al., 2006; Jaklitsch et al., 2017).

In conclusion, the integration of molecular markers and phylogenetic studies has been instrumental in developing a more robust and natural classification system for the Cucurbitaceae family, highlighting the dynamic nature of plant taxonomy in the era of molecular systematics.

## 2 Phylogenesis of Cucurbitaceae

### 2.1 Overview of phylogenetic methods used in Cucurbitaceae studies

Phylogenetic studies within the Cucurbitaceae family have employed a variety of methods to elucidate the evolutionary relationships among its species. Genome skimming and target sequence capture have been commonly used, despite their limitations such as representation bias and sometimes insufficient resolution of relationships even with hundreds of loci (Bellot et al., 2020). Phylogenetic informativeness and tree confidence analyses have also been applied to interpret phylogenomic datasets, which can help clarify tribe-level relationships within the family (Bellot et al., 2020). Chloroplast DNA sequences from multiple genes and spacers have been used to infer phylogenies, providing insights into the systematic classification of the family (Kocyan et al., 2007). Additionally, the *rbcL* gene and protein sequences have been utilized to address systematic questions,

employing methods such as UPGMA and Maximum Parsimony to infer evolutionary distances (Reddy, 2009). Comparative analyses of complete chloroplast genomes have also shed light on selective pressures and phylogenetic relationships, identifying genes under selection and supporting the phylogenetic positions of certain lineages (Zhang et al., 2018).

## 2.2 Synthesis of major phylogenetic findings

### 2.2.1 Evolutionary relationships within Cucurbitaceae

The Cucurbitaceae family, with its small genome size, has been the subject of extensive phylogenomic studies. These studies have revealed a fast divergence among the plastid loci of Cucurbitaceae tribes (Bellot et al., 2020). The traditional subfamilies, Cucurbitoideae and Nhandiroboideae, have been weakly supported by molecular data, and while most of the tribes are recovered, subtribes are almost non-existent (Kocyan et al., 2007). Certain genera such as *Trichosanthes* and *Luffa* have been found to be paraphyletic, indicating a complex evolutionary history within the family (Reddy, 2009).

### 2.2.2 Identification of major clades and their evolutionary significance

Major clades within the Cucurbitaceae have been identified, with some genera forming a large clade with ancestral ties to Asia, and the New World tribe Sicyeae (Kocyan et al., 2007). The identification of poly- and paraphyletic genera suggests the need for a reevaluation of the systematic classification within the family (Reddy, 2009). Phylogenetic analysis has also supported the relatively original lineage of genera such as *Gomphogyne*, *Hemsleya*, and *Gynostemma* (Zhang et al., 2018).

## 2.3 Discussion on divergence times and evolutionary events

Divergence times within the Cucurbitaceae family have been associated with significant evolutionary events such as radiation and adaptation. The lack of phylogenetic signal among plastid loci suggests rapid divergence events (Bellot et al., 2020). The correlation of flower characters with the chloroplast phylogeny indicates that certain morphological features have a strong evolutionary basis (Kocyan et al., 2007). Whole genome duplications (WGDs) have been identified as pivotal events that coincide with bursts of diversification and morphological innovations, particularly during the Early Eocene climate optimum (Guo et al., 2020). These WGDs have been linked to the origin of key traits such as tendrils and pepo fruits, which are characteristic of the Cucurbitaceae family (Guo et al., 2020). The study of phylotranscriptomics has revealed that these genomic changes facilitated the adaptive evolution of the family, allowing for the exploitation of new ecological niches and contributing to the success of Cucurbitaceae as climbers (Figure 1) (Guo et al., 2020).

This phylogenetic study by Guo et al. (2020) is a crucial contribution to the botanical and evolutionary biology fields, offering insights into the relationships and divergence among species in the Cucurbitaceae family. The use of multiple gene sets enhances the reliability of the phylogenetic inferences, allowing for a more nuanced understanding of how different genes contribute to the evolutionary history of these plants. Such detailed phylogenetic trees are essential for resolving taxonomic ambiguities and can guide further research on the co-evolution of traits and adaptation strategies within the family. This analysis is particularly valuable for breeders and biologists interested in crop improvement, conservation, and the study of plant evolution, providing a genetic.

## 3 Genetic Advances

### 3.1 Overview of genetic tools and technologies used in Cucurbitaceae research

The Cucurbitaceae family, encompassing a wide range of economically significant crops, has seen substantial advancements in genetic research facilitated by the advent of next-generation sequencing technologies and bioinformatics tools. These technologies have enabled the sequencing of genomes across various Cucurbitaceae species, leading to significant progress in understanding gene identification, genome evolution, and molecular breeding (Ma et al., 2022). The development of highly polymorphic simple sequence repeat (SSR) markers from whole genome shotgun sequencing has been instrumental in constructing high-density genetic linkage maps, which are crucial for genome sequencing and molecular breeding in cucurbits (Ren et al., 2009). Additionally, the integration of omics technologies in breeding programs has allowed for a deeper understanding of the genotype-phenotype relationship, particularly for complex traits (Pawelkiewicz et al., 2016).

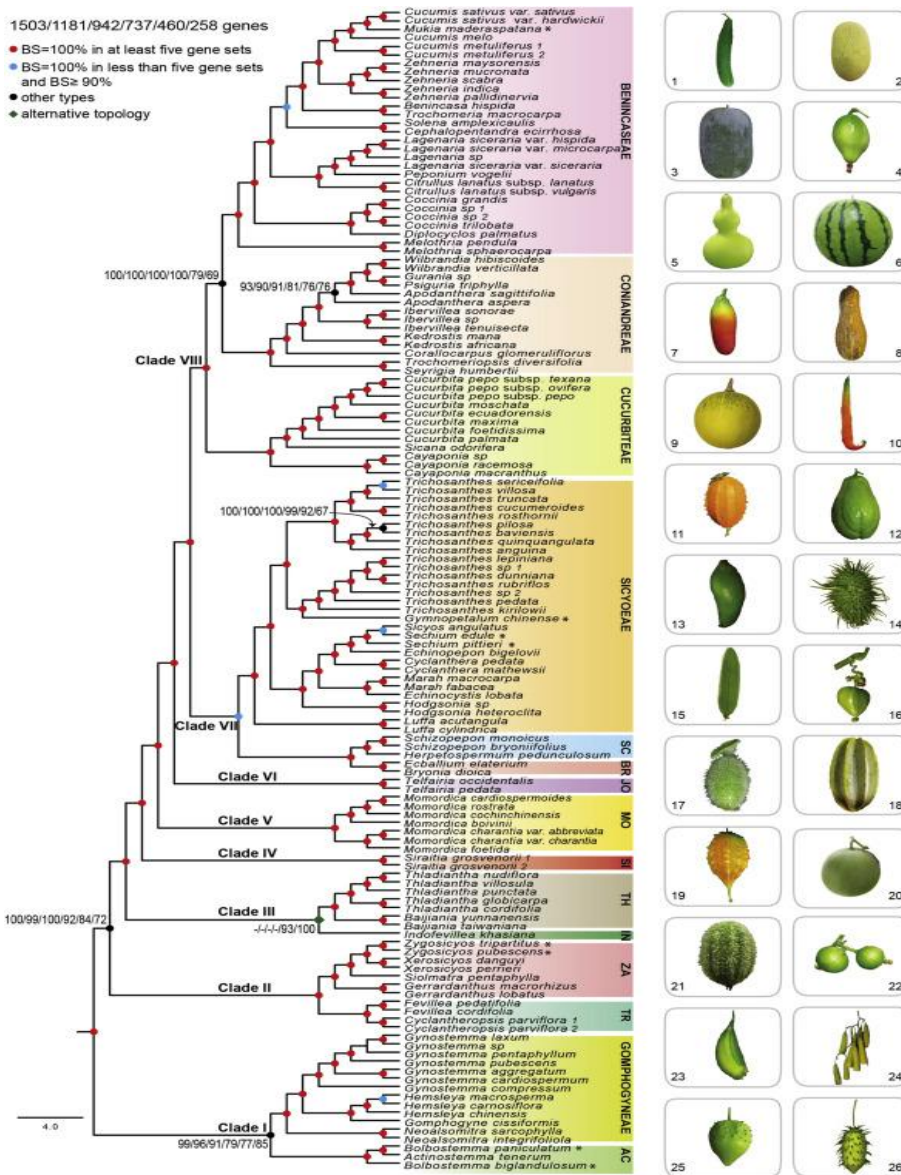


Figure 1 Phylogenetic relationships of Cucurbitaceae estimated by Astral using six gene sets (Photo credit: Guo et al., 2020)  
 Note: The eight major clades (I–VIII) are noted above the branches; Names of 10 tribes are abbreviated: SC, Schizopeponeae; BR, Bryonieae; JO, Joliffieae; MO, Momordiceae; SI, Siraitieae; TH, Thladiantheae; IN, Indofevilleae; ZA, Zanoniceae; TR, Triceratieae; AC, Actinostemmatae; Fruit photographs are not to scale and are provided by Jing Guo, Hong Ma, Weibin Xu, Jingjian Li, Jing Liu, and Chun-Yu Zou; 1 *Cucumis sativus*; 2 *Cucumis melo*; 3 *Benincasa hispida*; 4 *Solena amplexicaulis*; 5 *Lagenaria siceraria*; 6 *Citrullus lanatus*; 7 *Coccinia grandis*; 8 *Cucurbita moschata*; 9 *Cucurbita foetidissima*; 10 *Trichosanthes anguina*; 11 *Gymnopetalum chinensis*; 12 *Sechium edule*; 13 *Cyclanthera pedata*; 14 *Marah macrocarpa*; 15 *Luffa cylindrica*; 16 *Schinopepon bryoniifolius*; 17 *Ecballium elaterium*; 18 *Telfairia pedate*; 19 *Momordica charantia* var. *abbreviata*; 20 *Siraitia grovesenorii*; 21 *Thladiantha globicarpa*; 22 *Gynostemma pentaphyllum*; 23 *Hemsleya chinensis*; 24 *Neosalsomitra integrifoliola*; 25 *Actinostemma tenerum*; 26 *Bolbostemma biglandulosum* (Adopted from Guo et al., 2020)

Image caption: This phylogenetic tree illustrates the relationships among various Cucurbitaceae species as estimated by the Astral method using data from six gene sets; Bootstrap support values for major nodes are shown with solid circles or diamonds, indicating the consistency of relationships across all trees: solid circles in three colors represent maximum support (100%) in at least five trees (red), maximum support in fewer than five trees and >90% support in all six trees (blue), and lower levels of support (black); Green diamonds denote nodes with alternative topological outcomes in this study. Species names are displayed adjacent to the branches, with tribal affiliations noted on the far right, highlighted by colored backgrounds; Key clades (I–VIII) are labeled above the branches, with tribe abbreviations provided below; Fruit images associated with selected species enhance visual understanding of the diversity within the family (Adapted from Guo et al., 2020)



### 3.2 Key genetic discoveries

#### 3.2.1 Genetic markers associated with important traits

Genetic linkage maps have been constructed with phenotypic traits and quantitative trait loci (QTLs), leading to the development of DNA markers for marker-assisted selection in Cucurbitaceae breeding. The discovery of a large number of DNA markers, such as SSRs and single nucleotide polymorphisms (SNPs), has been propelled by massive sequencing efforts. These markers are highly polymorphic, codominant, and transferable, providing a foundation for high-density genetic linkage maps and gene identification (Fukino and Kawazu, 2016).

#### 3.2.2 Gene families of particular interest and their evolutionary roles

The genome-wide characterization of SSRs in *Cucurbita* genomes has revealed a high density of SSRs, which are useful for genetic mapping, genetic diversity analysis, and genome-wide association studies. Comparative genomics using these SSR markers has demonstrated high collinearity between *Cucurbita* species and other Cucurbitaceae, indicating the evolutionary roles of these gene families (Zhu et al., 2020).

### 3.3 Role of genetic diversity and its implications for conservation and breeding

The assessment of genetic diversity using molecular markers is valuable for genotype identification and selection in crop improvement programs. Studies using isozyme, RAPD, and ISSR markers have shown high variations among Cucurbitaceae species, which is crucial for understanding interspecific diversity and for the coherent management of germplasm collections (Sikdar et al., 2010). Furthermore, the evaluation of genetic diversity within a collection of *Cucurbita maxima* accessions using *Cucurbita*-conserved SSR markers has provided insights into the fundamental divisions above the level of horticultural groups, which is expected to be of great value for further germplasm characterization and taxonomical identifications within the genus *Cucurbita* (Kaźmińska et al., 2017). The differentiation of Cucurbitaceae members at the intra and inter-genus levels through seed protein profiling also contributes to the understanding of evolutionary relationships among crop species, which is essential for breeding programs (Dudwadkar et al., 2015).

## 4 Genomic Advances

### 4.1 Summarization of completed genome sequencing projects within Cucurbitaceae

Genomic studies within the Cucurbitaceae family have provided significant insights into the size and complexity of genomes across various species. Comparative analyses of chloroplast genomes from ten representative species revealed genome sizes ranging from 155 293 bp to 158 844 bp, with coding and inverted repeat (IR) regions being highly conserved (Zhang et al., 2018). The *rbcL* gene and protein sequences have been utilized to elucidate systematic positions among selected members of the family, indicating monophyletic and paraphyletic relationships within genera (Reddy, 2009). Additionally, the complete chloroplast genome sequences have been instrumental in phylogenetic studies, identifying potential molecular markers and enriching the genomic resources of the family (Schaefer and Renner, 2011; Zhang et al., 2018).

### 4.2 Impact of genomics on understanding species relationships and trait evolution

Genomic advances have significantly impacted our understanding of species relationships and trait evolution within the Cucurbitaceae. Phylogenetic analyses based on chloroplast DNA sequences have provided a framework for character evolution and classification, correlating well with flower characters such as the number of free styles and filament fusion (Kocyan et al., 2007). Moreover, phylogenetic informativeness analyses have clarified tribe-level relationships and supported two independent evolutions of fringed petals in the family (Bellot et al., 2020). The molecular evolution of the ITS regions has also shed light on the phylogenetic relationships among different members of the family, suggesting a polyphyletic origin of New World species (Jobst et al., 1998).

### 4.3 Discussion on comparative genomics research and its revelation of genome evolution and function

Comparative genomics studies have revealed selective pressures and phylogenetic relationships within Cucurbitaceae. For instance, three protein-coding genes (*accD*, *clpP*, and *matK*) were found to be under selection, which are involved in crucial functions such as chloroplast protein synthesis and plant development (Zhang et al., 2018). The phylogeny of the Cucurbitales, based on DNA sequences from three genomes, has implications for

morphological and sexual system evolution, suggesting that dioecy may have evolved early in the order's history and was subsequently lost in some lineages (Zhang et al., 2006). Seed coat diversity studies have also provided insights into taxonomy and species identification, supporting the monophyly of certain tribes and indicating polyphyly within others (Heneidak and Khalik, 2015). These comparative genomics studies have been pivotal in understanding genome evolution and functionality, offering a more comprehensive view of the genetic underpinnings of the Cucurbitaceae family.

## **5 Integration of Genetic and Genomic Insights**

### **5.1 Altered understanding of systematic classification and phylogenesis**

The advent of genetic and genomic research has significantly reshaped our understanding of the systematic classification and phylogenesis within the Cucurbitaceae family. Chloroplast DNA sequences have been instrumental in inferring phylogenies, revealing weak support for traditional subfamilies and uncovering poly- or paraphyletic genera, thus challenging previous morphological classifications (Kocyan et al., 2007). Similarly, phylogenetic informativeness analyses have clarified tribe-level relationships and supported independent evolutions of certain morphological traits, suggesting that genome skimming and PCR can overcome biases associated with target sequence capture (Figure 2) (Bellot et al., 2020). Comprehensive analyses using DNA regions from multiple plant genomes have led to a more natural classification of the family, proposing new tribes and genera based on molecular data (Schaefer and Renner, 2011). These insights demonstrate that genetic and genomic data provide a more robust framework for understanding the evolutionary history of Cucurbitaceae. This analysis of Cucurbitaceae plastomes is crucial for understanding the evolutionary biology and genetic diversity within this plant family. By dissecting the structural variations and gene content across different species' plastomes, the study by Bellot et al., 2020 offers significant insights into the phylogenetic relationships and adaptive evolution of the Cucurbitaceae. The detailed comparisons of IR, SSC, and LSC regions help elucidate how these plastome structures have diverged among species, potentially in response to environmental pressures or other evolutionary forces. This genomic information can be instrumental for further phylogenetic studies, as well as for improving breeding strategies through better understanding of genetic resources. This research effectively bridges detailed genetic mapping with practical implications for biodiversity conservation and agricultural applications, especially in improving crop resilience and efficiency.

### **5.2 Case studies of integrative approaches**

Case studies have highlighted the power of integrative genetic and genomic approaches in resolving complex taxonomic and evolutionary puzzles within Cucurbitaceae. Comparative analyses of chloroplast genomes have identified selective pressures and phylogenetic relationships, pinpointing protein-coding genes under selection and suggesting RNA editing events (Zhang et al., 2018). Cladistic analyses using *rbcL* nucleotide and amino acid sequences have elucidated systematic positions and supported supra-generic groupings, offering a framework for further systematic studies (Reddy, 2009). Moreover, the study of internal transcribed spacers in nuclear ribosomal RNA genes has provided insights into intraspecific variability and the polyphyletic origins of New World species (Jobst et al., 1998; Zhang et al., 2006). These case studies exemplify the utility of combining different genetic and genomic data sources to address evolutionary questions.

### **5.3 Future perspectives in genomics and genetics research**

The future of genomics and genetics research in Cucurbitaceae holds great promise for further unraveling the complexities of this diverse family. The potential for seed coat diversity to inform taxonomy and species identification has been demonstrated, suggesting that integrating micromorphological data with molecular analyses can enhance systematic studies (Heneidak and Khalik, 2015). Phylotranscriptomics has revealed multiple whole genome duplications and key morphological and molecular innovations, such as the origin of the tendril identity gene *TEN*, which may have facilitated the adaptive evolution of Cucurbitaceae (Guo et al., 2020). As new technologies and methodologies emerge, they will undoubtedly contribute to a deeper understanding of the genetic underpinnings of diversity and adaptation in this economically and ecologically important family.

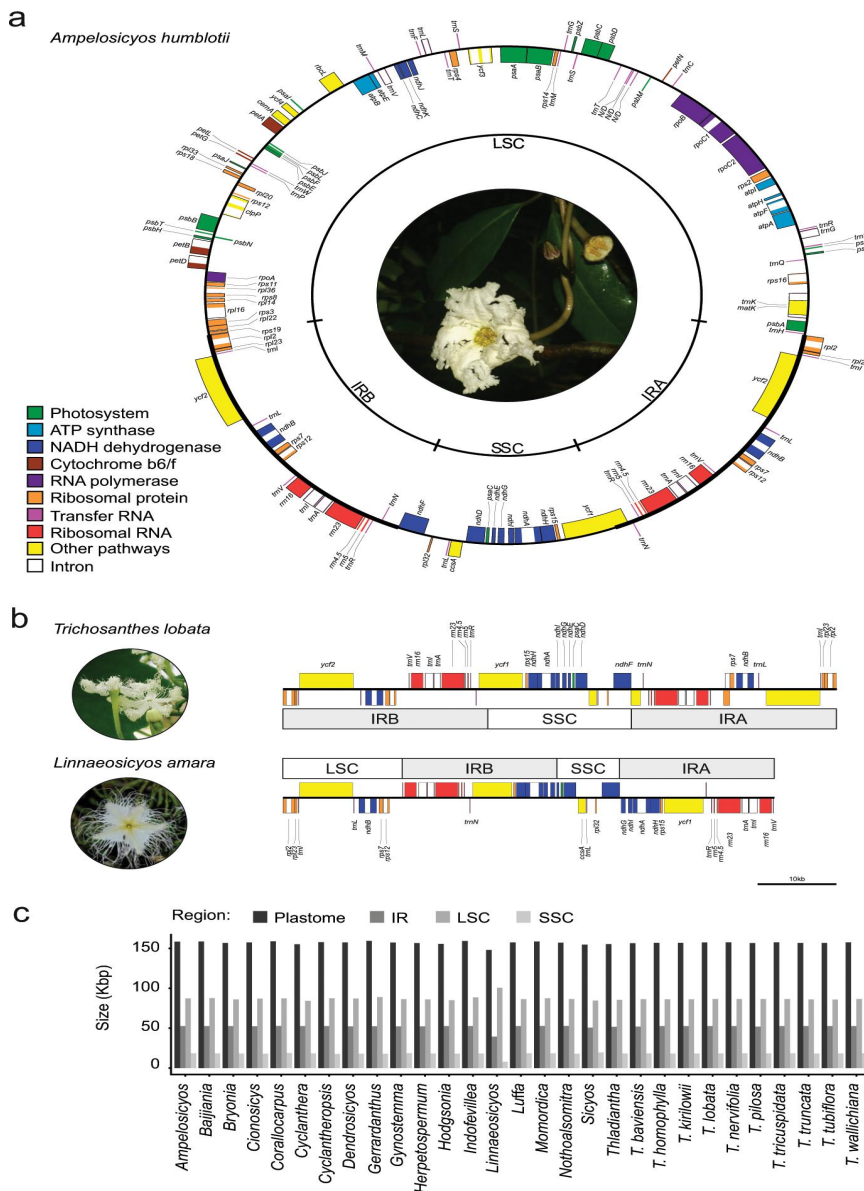


Figure 2 Structure and gene content of *Cucurbitaceae* plastomes (Photo credit: Bellot et al., 2020)

Image caption: (a) Plastid genome of *Ampeloscycos humblotii* (Picture: HS); (b) Comparison of the location and gene content of the inverted repeat and small single copy regions of *Trichosanthes lobata* and *Linnaeosicyos amara* (Pictures: HS and TM); The large single copy region of *T. lobata* and most of that of *L. amara* were truncated to improve visualisation; (c) Size comparison of the different plastid genome regions across Cucurbitaceae; the sizes of both copies of the inverted repeat were summed (Adopted from Bellot et al., 2020)

## 6 Challenges and Opportunities

### 6.1 Current limitations in genetic and genomic research of Cucurbitaceae

Despite the advancements in phylogenomic studies, there are still significant limitations in the genetic and genomic research of Cucurbitaceae. One of the main challenges is the representation bias inherent in genome skimming or target sequence capture methods, which can lead to unresolved relationships even when analyzing hundreds of loci (Bellot et al., 2020). Additionally, the lack of phylogenetic signal among plastid loci, as revealed by node support analyses, suggests a rapid divergence of Cucurbitaceae tribes, complicating the resolution of phylogenetic relationships (Bellot et al., 2020). Furthermore, the polyphyly and paraphyly observed in certain genera, such as *Cucumis* and *Trichosanthes*, indicate the need for a more comprehensive and systematic approach to clarify the classification within the family (Kocyan et al., 2007; Reddy, 2009).

## 6.2 Emerging technologies and their potential impact on future research

Emerging technologies, such as high-throughput sequencing and advanced bioinformatics tools, hold the potential to overcome current limitations in Cucurbitaceae research. The application of these technologies could lead to a more accurate and detailed understanding of the phylogenetic relationships within the family. For instance, the use of phylogenetic informativeness and tree confidence analyses has already shown promise in interpreting phylogenomic datasets and clarifying tribe-level relationships (Bellot et al., 2020). As these technologies become more accessible and cost-efficient, they are likely to play a pivotal role in future research, enabling the study of a broader range of species and genetic markers.

## 6.3 Implications of genetic and genomic findings for breeding and conservation strategies

The genetic and genomic findings in Cucurbitaceae have significant implications for breeding and conservation strategies. Understanding the phylogenetic relationships and character evolution within the family can inform the selection of traits for crop improvement and the identification of species with desirable genetic characteristics (Kocyan et al., 2007). Moreover, the clarification of taxonomic relationships based on seed coat diversity and other morphological traits can aid in species identification and conservation efforts (Heneidak and Khalik, 2015). As the genetic and genomic research progresses, it will be crucial to integrate these findings into practical applications that enhance the sustainability and diversity of Cucurbitaceae species.

## 7 Concluding Remarks

The systematic classification and phylogenesis of the Cucurbitaceae family, which encompasses around 800 species in 130 genera, have been significantly advanced by recent molecular phylogenetic studies. The integration of chloroplast DNA sequences, nuclear genes, and morphological data has provided a more comprehensive understanding of the evolutionary relationships within this economically important family.

### 7.1 Summary of key insights

Key insights from the reviewed literature include the weak support for traditional subfamilies such as Cucurbitoideae and Nhandiroboideae, and the recovery of most of the eleven tribes, although subtribes are almost non-existent. The discovery of a large clade consisting of ancestrally Asian genera and the New World tribe Sicyeae suggests a complex biogeographical history. Additionally, the polyphyly and paraphyly of several genera, such as *Cucumis* and *Trichosanthes*, indicate the need for a reevaluation of the current taxonomic classifications.

The use of phylogenetic informativeness and tree confidence analyses has clarified tribe-level relationships and supported two independent evolutions of fringed petals within the family. A more natural classification of the family has been proposed, with 95 genera in 15 tribes, based on molecular and morphological data. Seed coat diversity has also been shown to have taxonomic and phylogenetic implications, supporting the monophyly of certain tribes and indicating polyphyly within others.

The implications of these findings for the systematic classification and phylogenesis of Cucurbitaceae are profound. They suggest that morphological characters such as flower and fruit traits, as well as karyotype, exhibit evolutionary flexibility and may not always reflect phylogenetic relationships accurately. This underscores the importance of integrating multiple data types, including molecular, morphological, and cytological data, for a more robust systematic framework.

### 7.2 Recommendations for future research directions

- 1) **Enhanced Genomic Coverage:** Despite substantial progress, the genomic representation of the Cucurbitaceae family is still skewed towards economically significant species. Future efforts should focus on expanding genomic resources to include underrepresented and wild relatives. This would provide a more comprehensive genomic baseline, facilitating studies on genetic diversity, evolution, and the potential for breeding programs.
- 2) **Functional Genomics and Transcriptomics:** There is a pressing need to link genomic data with functional outcomes. Integrating transcriptomic, proteomic, and metabolomic data with existing genomic information will help elucidate gene function, regulatory networks, and biochemical pathways involved in critical traits and stress responses.



- 3) **Ecological Genomics:** Investigating the interaction between Cucurbitaceae species and their environments through the lens of ecological genomics can yield insights into how these plants adapt to biotic and abiotic stresses. Such studies are crucial for understanding the impact of climate change on plant distributions and for developing resilient Cucurbitaceae cultivars.
- 4) **Evolutionary Developmental Biology (Evo-Devo):** Exploring the developmental basis of morphological traits in Cucurbitaceae through an evolutionary framework will aid in understanding how developmental processes have been shaped by natural selection and how they contribute to the ecological success of the family.
- 5) **Enhanced Collaboration and Data Sharing:** Given the rapid pace of technological advancement in genomics, fostering an international collaborative network and promoting open data sharing policies would accelerate the pace of discovery and application in Cucurbitaceae research.

In conclusion, while the advancements in genetics and genomics have dramatically advanced our understanding of the Cucurbitaceae family, continued exploration and integration of these insights into a coherent framework for plant research and breeding are essential for harnessing the full potential of these findings. The future of Cucurbitaceae research holds great promise for revealing even deeper insights into plant biology and for the development of sustainable agricultural practices.

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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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