Phyton-
International Journal of
Experimental Botany

Tech Science Press

http://doi.org/10.32604/phyton.2026.077185

REVIEW

Holocentric Chromosomes in Plants: Historical Overview, Developments and Challenges

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Received: 04 December 2025; Accepted: 04 February 2026; Published: 31 March 2026

ABSTRACT: Holocentric chromosomes, characterized by kinetochore activity distributed along almost their entire length, have attracted growing interest in cytogenetics and evolutionary biology, particularly because of their adaptive significance. This review provides a historical overview of research on holocentricity, from the earliest microscopic observations to recent advances made possible by modern molecular and cytogenetic techniques. We discuss the main hypotheses concerning the origin and evolution of holocentric chromosomes, emphasizing their multiple independent origins across diverse lineages, as well as the potential selective pressures underlying their maintenance and diversification. In addition, we examine the principal methods used for their identification, with particular emphasis on the immunolocalization of CENH3, a centromere-specific variant of histone H3, and discuss its applications, limitations, and recent methodological advances, including the development of universal markers. A comprehensive understanding of the structural and functional diversity of holocentric chromosomes is essential for elucidating the mechanisms of karyotype evolution across taxa and for shedding light on the processes that shaped early terrestrial life.

KEYWORDS: CENH3; centrome; cytogenetics; immunolocalization; karyotype; meiosis

1 Introduction

Cytogenetics is the branch of biology that investigates chromosomes, which are defined as DNA molecules associated with histone and non-histone proteins and organized at a high level of condensation [1]. The term *chromosome* was introduced in 1888 by Heinrich Wilhelm Gottfried Waldeyer and derives from the Greek *khrôma* (“color”) and *sôma* (“body”), reflecting what early cytologists could observe under light microscopy: intensely stained structures visible during cell division [2]. Cytotaxonomy, in turn, focuses on the classification of organisms through comparative chromosomal analyses and is closely linked to phylogenetic systematics [3]. Key cytogenetic features include chromosome number, morphology, and behavior, the latter primarily examined during meiosis [1,4]. Together, these data provide valuable insights into evolutionary relationships among species and can reinforce taxonomic delimitations based on morphological criteria [2].

Chromosomes can be morphologically characterized by the presence of a primary constriction corresponding to a centromeric unit; such chromosomes are referred to as monocentric [5]. Monocentric chromosomes are commonly classified as metacentric, submetacentric, acrocentric, or telocentric based on measurements of the arm ratio [6] or the centromeric index, which is calculated as the ratio between the length of the short arm and the total chromosome length of the haploid set [7].

On the other hand, holocentric chromosomes exhibit centromeric activity distributed along almost their entire length (Fig. 1) [8–10]. They have been reported in protists, invertebrates, and plants, with particularly high representation in the families Cyperaceae, Convolvulaceae, Droseraceae, and Juncaceae [11,12]. In addition, metapolycentric chromosomes have been identified in some species of *Pisum* L. and *Lathyrus* L. (Fabaceae). These chromosomes are characterized by elongated primary constrictions and are considered to represent an intermediate state between monocentric and holocentric chromosomal organizations [5].

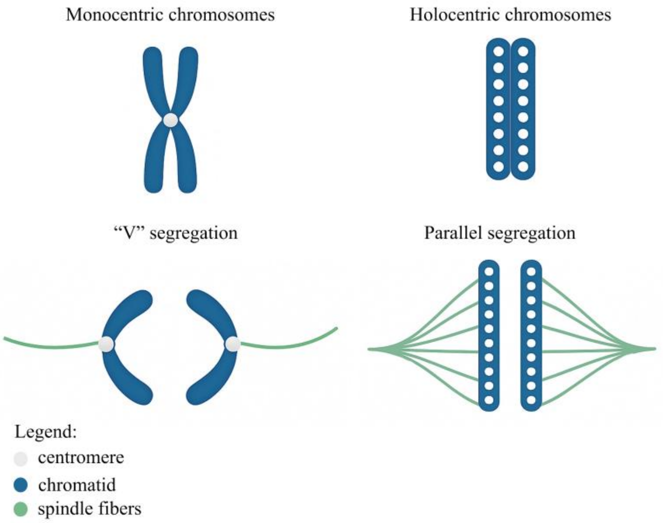

Figure 1: Main structural differences and anaphase behaviors between monocentric and holocentric chromosomes.

In general, centromeres are composed primarily of satellite DNA and/or transposable elements and are therefore highly heterochromatic, a feature that contributes to chromatid cohesion [10,13]. As a result, they are typically located in transcriptionally silent regions, although they may also harbor functionally active genes [14,15]. Accordingly, centromeric regions are characterized by pronounced sequence diversity, which may vary among chromosomes within the same individual [16–18], reflecting their rapid evolutionary dynamics [10,19].

From a structural standpoint, centromeres are characterized by the presence of a specialized variant of histone H3, known as CENH3 in plants [20,21]. This variant is essential for kinetochore assembly, a multiprotein complex responsible for microtubule attachment during cell division [22,23]. In animals, several chaperone proteins are involved in the deposition and recognition of CENH3 (CENP-A); however, the corresponding mechanisms in plants remain poorly understood [24]. Consequently, centromere activity does not depend on a specific nucleotide sequence but is instead determined by epigenetic regulation [25,26], illustrating the paradox between the high diversity of centromeric DNA sequences and the strong conservation of centromere function [27,28].

This article provides a historical overview of the main hypotheses concerning the origin and diversification of holocentric chromosomes, highlighting key advances and ongoing debates in the field. In addition, we review the principal techniques used to study these chromosomes, emphasizing their contributions to elucidating structural, functional, and evolutionary mechanisms. By doing so, we seek to establish a consolidated framework to support future investigations and to broaden the understanding of chromosomal diversity across different taxonomic groups.

2 Historical Overview, Origin and Evolution

Owing to the ability of chromosomal fragments to be stably inherited, holocentric species often exhibit natural variation in chromosome number [29–32]. The mechanisms underlying these numerical changes have been described using the terms *agmatoploidy* (chromosome fission) and *simploidy* (chromosome fusion) [33–36]. The concept of agmatoploidy was first proposed by Malheiros-Gardé and Gardé [37] to explain karyotypic variation in *Luzula* DC (Juncaceae). Based on the heritability of chromosomal fragments, the authors argued that variation in chromosome number in this genus did not result from polyploidization but rather from chromosome fission. Subsequently, the term simploidy was introduced by Luceño and Guerra [33] to describe cases in which a reduction in chromosome number is associated with an increase in chromosome size.

Chromosome fission is thought to occur at hotspots known as fragile sites, which are regions particularly prone to breakage following replication inhibition [30,38–40] and are also present in monocentric organisms [41]. For these fragments to be stabilized as independent chromosomes, the acquisition of telomeric sequences at broken or dysfunctional ends is required [42]. Telomeres prevent the formation of sticky chromosomes and, consequently, chromosome fusion [43,44]. In this context, the concepts of agmatoploidy and simploidy are indistinguishable from ascending and descending dysploidy, as all involve chromosome fissions and fusions without substantial DNA loss [44–47]. Accordingly, Guerra [48] argued that, because no distinct mechanisms have been proposed to explain these processes in holocentric chromosomes, there is no justification for adopting separate terminology.

The stable inheritance of chromosomal fragments has led to the hypothesis that holocentricity may promote higher rates of chromosome number variation [49,50]. However, a comparative study of monocentric and holocentric insects demonstrated that chromosome number evolution proceeds at statistically similar rates in both groups [51]. In Cryptangieae (Cyperaceae), for instance, a high frequency of chromosomal abnormalities has been observed during meiosis, particularly the presence of unaligned chromosomes [52]. Despite this, species in the group exhibit high pollen viability and no intraspecific variation in chromosome number (i.e., no distinct cytotypes). This pattern may be associated with the formation of pseudomonads, a process in which three of the four nuclei produced during male meiosis undergo apoptosis. This mechanism, which is recurrent in Cyperaceae but rare among other angiosperms, likely contributes to the elimination of cells carrying chromosomal anomalies [52].

In addition to structural chromosomal alterations, polyploidy and genome restructuring processes are also widespread among holocentric species [30,35,53–55]. In monocentric taxa, an increase in chromosome number is often associated with higher ploidy levels [56], although some species do not exhibit a corresponding increase in DNA content [57–59]. Under holocentric conditions, however, this relationship is rarely evident, as chromosome fissions and fusions can increase the basic chromosome number without changes in ploidy level [8].

In this context, chromosome counts should be complemented by nuclear DNA quantification to reliably assess the occurrence of polyploidy in holocentric species [8]. Additionally, the analysis of multivalent pairing during diakinesis is essential for identifying polyploids [60,61]. Finally, reconstructing the ancestral state of the basic chromosome number represents an effective strategy for mapping the mechanisms underlying changes in chromosome complements over the evolutionary history of a group, thereby allowing the distinction between polyploidy and dysploidy events [52,62–64].

Comparative phylogenetic analyses indicate that holocentricity is a homoplastic trait, having evolved independently in multiple lineages [65]. Because it occurs in relatively few groups, most authors regard holocentricity as a derived condition. Nonetheless, its evolutionary origin remains debated. Current estimates suggest that holocentricity has arisen at least 19 times among eukaryotes: six times in plants and 13 times in animals, including nematodes, velvet worms, insects, centipedes, and arachnids [65].

Holocentric chromosomes have been proposed as plesiomorphic, based on the hypothesis that intense UV radiation may have exerted strong deleterious effects during the early expansion of terrestrial life [66]. Under such conditions, organisms bearing holocentric chromosomes may have gained an adaptive advantage by tolerating chromosomal fragmentation. In contrast, the localized centromere of monocentric chromosomes represents a more specialized structure for chromosome segregation and is therefore regarded as a derived condition [67]. In this case, the confinement of centromeric activity to a single region, typically positioned away from chiasmata, may confer an adaptive advantage by concentrating kinetochore activity and promoting accurate chromosome segregation during meiosis [4,68]. By comparison, holocentric chromosomes generally exhibit a reduced number of chiasmata (usually one or two per chromosome) and the presence of three or more chiasmata may impair proper homologous chromosome separation [49,69–71]. Consequently, while monocentricity may support higher rates of gene recombination along chromosomes, holocentricity may compensate for this limitation through increased variation in chromosome number [49].

Holocentricity has been proposed to originate from an expansion of kinetochore activity mediated by transposable elements [65]. Similarly, another hypothesis suggests that centromeres evolved from telomeres, with the transposition of retroelements and the accumulation of subtelomeric repeats giving rise to the earliest centromeric regions [72,73]. In addition, Nagaki et al. [14] proposed that a 90° shift in the orientation of kinetochore assembly, extending along the chromosome axis toward the telomeric regions, may have contributed to the emergence of holocentric chromosomes.

Other hypotheses emphasize selective pressures associated with centromere structure. Malik and Henikoff [74] suggested that holocentric chromosomes may have evolved as a strategy to avoid the so-called "centromere drive", a process in which larger centromeres, or those enriched in repetitive DNA, gain a transmission advantage during meiosis [75,76]. Because centromeric activity in holocentric chromosomes is distributed along the entire chromosome length, competition among centromeres would be minimized, thereby reducing the accumulation of potentially deleterious repetitive sequences. Subsequently, Bureš and Zedek [77] proposed the concept of "holokinetic drive" to explain the evolution of holocentric chromosomes, suggesting that larger chromosomes may be preferentially transmitted during meiosis, with consequences for genome size and complexity over evolutionary time.

Holocentric chromosomes are regarded as an apomorphic feature in Droseraceae [78] and as a synapomorphy for most clades of Juncaceae and Cyperaceae [11,79]. For a long time, the principal representatives of the Cyperid clade (Thurniaceae, Juncaceae, and Cyperaceae) were thought to be exclusively holocentric [80]. However, the recent discovery that *Prionium serratum* (L.f.) Drège (Thurniaceae) possesses monocentric chromosomes indicates that holocentricity arose independently at least twice after the divergence of Juncaceae and Cyperaceae [80]. In addition, monocentric chromosomes have also been reported in species from different sections of *Juncus* L. (Juncaceae) [79]. Accordingly, Guerra et al. [79] emphasized that the assumption of holocentricity should not be generalized to other genera of Juncaceae or to groups historically considered holocentric without robust cytogenetic evidence.

Holocentric chromosomes are thought to be widespread in Cyperaceae [8]. This family exhibits the greatest variation in chromosome number among angiosperms, ranging from $2n = 4$ to $2n = 226$, largely as a result of chromosome fissions and fusions [2,30,81]. Multiple modes of chromosomal evolution occur within the family, although dysploidy predominates [82,83]. Polyploidy appears to play a more limited role and has been reported mainly in *Rhynchospora* Vahl, *Mapania* Aubl., *Fimbristylis* Vahl, and *Eleocharis* R.Br. [82]. It has further been proposed that increased species diversification rates in Cyperaceae may be associated with karyotypic changes in combination with shifts in photosynthetic pathways [82]. Nevertheless, despite the large number of species in the family, chromosome counts are available for only a small fraction, with most data concentrated in *Carex* L. [81,84].

Evolutionary transitions between monocentricity and holocentricity can occur even among species within the same genus, as exemplified by *Drosera* L. (Droseraceae), a group of carnivorous plants [78]. In the parasitic genus *Cuscuta* L. (Convolvulaceae), holocentricity is restricted to the subgenus *Cuscuta*, whereas the subgenera *Grammica* and *Monogynella* retain monocentric chromosomes [85]. The transition to holocentricity in this lineage was accompanied by pronounced changes in kinetochore organization, including gene loss and the disruption of centromeric protein localization, such as CENH3 and CENP-C [86]. In addition, degeneration of the mitotic spindle assembly checkpoint has been reported, indicating a profound reorganization of chromosome segregation mechanisms [86]. This restructuring is further reflected in epigenetic modifications, including the loss of H2A histone phosphorylation and the elimination of centromeric retrotransposons, as well as a reduction in the basic chromosome number (x = 7) relative to monocentric species (x = 15 or 16) [85].

Similarly, in animal groups such as Lepidoptera, holocentricity is associated with major evolutionary processes. In *Bombyx mori* L., for example, high rates of chromosomal rearrangements have been documented [11]. In *Erebia aethiops* Esper, chromosomal fusions have led to a reduced chromosome number, along with inversions on the Z chromosome, suggesting an important role for holocentricity in speciation through chromosomal rearrangements [87]. More broadly, the presence of holocentric chromosomes is linked to evolutionary adaptations such as increased tolerance to chromosomal breakage, which may enhance survival under stressful environmental conditions and promote rapid karyotype evolution [66]. This property likely confers a significant adaptive advantage in contexts characterized by frequent exposure to clastogenic agents. Consequently, the evolution of holocentric chromosomes involves multiple genomic mechanisms and cellular adaptations, reflecting a complex convergent process that has occurred repeatedly throughout eukaryotic evolutionary history.

3 Methods for the Study of Holocentric Chromosomes

3.1 Classical Cytogenetics

Classical (conventional) cytogenetic approaches can be used to assess V-shaped or parallel chromosome segregation, the latter being typical of holocentric chromosomes; however, such patterns are more readily observed in species with larger chromosomes. In the absence of an evident primary constriction, sister chromatids in holocentric chromosomes are oriented and segregate parallel to the metaphase plate during both mitosis and meiosis [8,88–90]. In contrast, monocentric chromosomes exhibit V-shaped segregation owing to the presence of a single, localized centromeric unit [8].

Meiosis in holocentric species also displays distinctive features and can be categorized into two main types. In the telokinetic type, homologous chromosomes form a configuration known as a “box”, which ensures their movement as a single unit during meiosis I [8,91–93]. In the holokinetic type, the reductional division occurs during meiosis II, which is why this process is also referred to as “inverted meiosis” [8,9,90,94]. These meiotic behaviors can be observed using light microscopy [52,90], but they are more accurately characterized using molecular cytogenetic techniques [9].

3.2 Chromosomal Break Induction Experiments

One of the earliest experimental approaches used to detect holocentric chromosomes involved the induction of chromosomal breaks by ionizing radiation, followed by analysis using flow cytometry.

In holocentric species, the CENH3 protein is distributed along the entire chromosome, allowing fragments generated by breakage to segregate normally during both mitosis and meiosis without forming micronuclei [11,42,94]. Micronuclei are extranuclear structures that arise from chromosomal breakage or segregation errors and typically result in the loss of genetic material [95].

Based on this principle, ionizing radiation, including X-rays and gamma rays, has been applied to various plant tissues as an experimental strategy to assess the presence of holocentricity. The key evidence considered is the occurrence of chromosomal fragmentation without substantial DNA loss, measured in picograms, which suggests that the resulting fragments remain functional [96,97].

3.3 Immunolocalization

Currently, the primary technique for identifying holocentric chromosomes is the immunolocalization of CENH3. In monocentric chromosomes, CENH3 is confined to the primary constriction, whereas in holocentric chromosomes it is distributed along nearly the entire chromosome length [98]. These contrasting patterns can be confirmed by immunolocalization using specific antibodies [71,98]. However, as with centromeric DNA sequences, CENH3 exhibits considerable variability in amino acid composition and may be species-specific, which can limit its applicability [27,99,100]. Recently, Oliveira et al. [101] introduced new universal markers for the detection of functional centromeres, which are expected to facilitate their use in non-model plant systems.

Because of the high cost associated with the development and production of species-specific CENH3 antibodies, tubulin labeling has emerged as a viable alternative [100–102]. Tubulin, the main structural component of mitotic spindle fibers, can be visualized to directly assess spindle–chromosome interactions during cell division. This approach enables the indirect inference of centromere distribution and behavior, particularly in holocentric chromosomes, where spindle fibers attach along almost the entire chromosome length.

4 Conclusions and Future Perspectives

Despite methodological and conceptual advances in recent decades, research on holocentric chromosomes continues to face significant challenges, particularly regarding the accurate identification of this condition in non-model organisms. The limited availability of specific molecular tools, interspecific variation in centromeric proteins, and the scarcity of cytogenetic data for many taxa hinder the systematic characterization of holocentricity across extant biodiversity.

Addressing these challenges requires clearly defined criteria for selecting suitable model organisms. Species with small, stable chromosome numbers are particularly valuable. Ideal models should also combine well-characterized genomes supported by robust genomic resources (e.g., high-quality genome assemblies and linkage maps) and practical traits that facilitate experimental handling. These traits include straightforward cultivation, rapid and reliable propagation, and consistent flowering. Additionally, organisms amenable to controlled experimental manipulation, such as induced chromosome fragmentation, can provide key insights into kinetochore organization, chromosome segregation, and karyotype evolution. Comparative approaches integrating plants, invertebrates, and nematodes may further elucidate the evolutionary and functional significance of holocentricity across different ecological and selective contexts.

Building on these considerations, plant lineages in which sex chromosomes could occur in a holocentric background represent a particularly promising avenue for research, as this scenario is rare and largely unexplored [103–105]. Although dioecious species exist in several holocentric plant families, there is currently no formally published cytogenetic evidence of heteromorphic sex chromosomes (i.e., differentiated

XY or ZW systems) in any of them. This lack of documented sex chromosomes makes these groups especially valuable for investigating whether and how sex-linked regions might arise and evolve in a holocentric background. The potential interaction between holocentricity and putative sex-determining regions could have profound implications for meiotic behavior, genome stability, and karyotype evolution, representing an unexplored frontier in plant cytogenetics. Beyond contributing to our understanding of holocentric chromosome organization, this review emphasizes the importance of expanding cytogenetic and genomic studies to taxonomically diverse plant groups, particularly those combining dioecy with holocentric chromosomes.

Acknowledgement: Not applicable.

Funding Statement: The authors received no specific funding for this study.

Author Contributions: The authors confirm contribution to the paper as follows: conceptualization, Ana Luisa Arantes Chaves and Marco Tulio Mendes Ferreira; methodology, Ana Luisa Arantes Chaves; validation, Ana Luisa Arantes Chaves and Marco Tulio Mendes Ferreira; formal analysis, Ana Luisa Arantes Chaves; investigation, Ana Luisa Arantes Chaves; data curation, Ana Luisa Arantes Chaves; writing—original draft preparation, Ana Luisa Arantes Chaves; writing—review and editing, Marco Tulio Mendes Ferreira; visualization, Ana Luisa Arantes Chaves. All authors reviewed and approved the final version of the manuscript.

Availability of Data and Materials: Not applicable.

Ethics Approval: Not applicable.

Conflicts of Interest: The authors declare no conflicts of interest.

Glossary

CENH3	Centromeric Histone H3 variant. Centromere-specific variant of histone H3 that replaces canonical H3 in nucleosomes at functional centromeres. It plays an essential role in specifying centromere identity and assembling the kinetochore, thereby ensuring accurate chromosome segregation during cell division. Term A name traditionally used for plants.
CENP-A	Centromere Protein A. Centromere-specific histone H3 variant that replaces canonical H3 in nucleosomes at active centromeres. It is essential for establishing centromere identity and serves as the foundation for kinetochore assembly, ensuring faithful chromosome segregation during cell division. Term name traditionally used for animals, especially vertebrates.

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