



# Interplay between Polycomb-group associated histone modifiers and accessory proteins in plant evolution

Ahamed Khan, Biswajit Ghosh and Daniel Schubert

Epigenetic regulators are multiprotein complexes that modify chromatin architecture to control gene expression in response to developmental and environmental cues. These complexes function in a highly coordinated manner, often collaborating with various accessory proteins to precisely regulate the dynamic nature of chromatin states. However, our understanding of how these core histone-modifying regulators co-evolved with accessory proteins during plant evolution remains limited. Therefore, in this review, we summarize the evolution of major histone modification regulators, with a focus on Polycomb group complexes and their associated accessory proteins. We discuss how accessory proteins have evolved to modulate the activity of conserved core components, supporting key innovations during plant evolution. Lastly, we highlight the role of accessory proteins in mediating crosstalk between histone-modifying complexes, emerging as key evolutionary factors that shape the epigenetic landscape and influence plant development and environmental adaptation.

## Addresses

Institute of Biology, Freie Universität Berlin, 14195 Berlin, Germany

Corresponding author: Schubert, Daniel ([dan.schubert@fu-berlin.de](mailto:dan.schubert@fu-berlin.de))

Current Opinion in Plant Biology 2025, 88:102783

This review comes from a themed issue on **Epigenetics and gene regulation\_2025**

Edited by **Sara Farrona** and **Ralf Müller-Xing**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online xxx

<https://doi.org/10.1016/j.pbi.2025.102783>

1369-5266/© 2025 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

## Introduction

Over the past few decades, numerous studies have identified diverse histone-modifying complexes and elucidated their roles in shaping chromatin architecture and regulating gene expression in plants [1]. Among these, the core catalytic subunits responsible for key histone modifications such as methylation, acetylation, ubiquitination, and phosphorylation are largely conserved across eukaryotes [1–4], with the notable exception of

*Saccharomyces cerevisiae*, which lacks canonical Polycomb group (PcG) components [5]. In plants, PcG function as key epigenetic regulators that shape chromatin structure to ensure proper development, maintain cellular identity and phase transitions, and coordinate stress responses [6–8]. Throughout plant evolution, these complexes have incorporated diverse accessory proteins in a lineage-specific manner, enabling fine-tuning of their molecular functions to effectively respond to evolving cellular and environmental challenges [9–14]. The emergence of accessory proteins closely coincided with major evolutionary innovations in plants, such as the transition from unicellularity to multicellularity, shifts in life cycle from gametophyte to sporophyte dominance, adaptation from aquatic to terrestrial habitats, development of vascular tissues, and the origin of seed formation [12,15–17]. These innovations likely involved changes in chromatin regulation, with accessory proteins possibly modulating core subunits to diversify their functions by rewiring molecular circuits and fine-tuning their activity, potentially contributing to major evolutionary transitions. Collectively, the evolutionary integration of core histone modifiers such as writers and erasers with accessory proteins, often functioning as epigenetic readers or proteins that connect core components to other regulatory proteins, underscores the remarkable adaptability and precision of plant epigenetic regulation [10,11,14,16,18–21]. Beyond enhancing complex specificity, many accessory proteins serve as critical nodes of crosstalk between similar or distinct histone-modifying complexes, often with opposing activities [14,17,18]. Such crosstalk is essential for integrating multiple regulatory signals to coordinate dynamic chromatin states, balancing gene activation and repression in a context-dependent manner. These processes are crucial for plant evolution and adaptation as without this flexibility, chromatin would be unable to dynamically adjust gene expression in response to developmental and environmental cues [18,21,22]. Thus, accessory proteins contribute not only to the diversification of complex functions but also to the coordination of distinct chromatin-modifying activities, thereby influencing transcriptional regulation.

Therefore, a comprehensive study of core histone-modifying complexes alongside their lineage-specific

accessory proteins is essential to fully grasp the diversification of their functions during plant evolution. This integrated perspective remains largely unexplored but holds great promise for revealing how plants adapt at the molecular level to changing environments and developmental demands. This review focuses on Polycomb group (PcG) complexes and their accessory proteins, emphasizing their crosstalk and integration with other chromatin-modifying complexes during plant evolution. It also briefly highlights non-PcG complexes that contribute to the regulation of dynamic chromatin states, particularly those functioning in coordination with PcG-associated proteins.

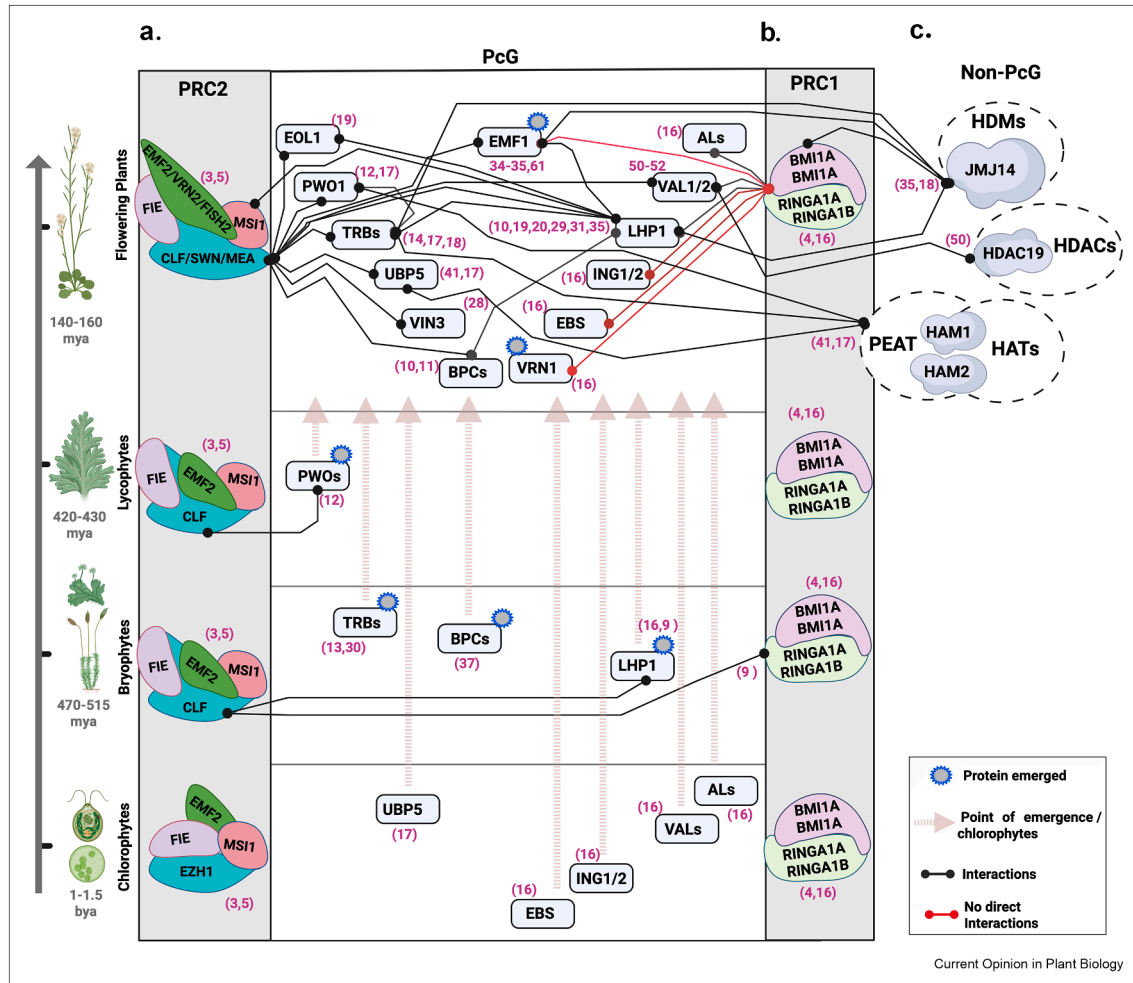
### Accessory proteins serve as key regulators of core PcG functions, contributing to the evolutionary diversification of chromatin regulation in plants

In plants, gene duplications and divergence of PcG complexes, together with the association of accessory proteins, have likely facilitated the functional diversification and specialization of PcG functions, enabling more complex regulation during development [3,23,24]. The two main PcG complexes, Polycomb Repressive Complex 1 (PRC1) and PRC2, functionally cooperate in plants, with PRC2 depositing H3K27me3 marks while PRC1 catalyzes H2A monoubiquitination, collectively compacting chromatin and preventing transcription factors from accessing DNA to reinforce gene repression [8,25]. The core components of the PRC2 complex have been extensively discussed in plants, often in comparison to their counterparts in *Drosophila melanogaster*, where PRC2 consists of Enhancer of zeste (E(z)), Extra sex combs (Esc), Suppressor of zeste 12 (Su(z)12), and Nucleosome remodeling factor (Nurf55, also known as p55) [26]. In *Arabidopsis thaliana* (Arabidopsis), core PRC2 components include the E(z) paralogs CURLY LEAF (CLF), SWINGER (SWN), and MEDEA (MEA); the Su(z)12 homologs EMBRYONIC FLOWER 2 (EMF2), VERNALIZATION 2 (VRN2), and FERTILIZATION INDEPENDENT SEED 2 (FIS2); the ESC homolog FERTILIZATION INDEPENDENT ENDOSPERM (FIE); and the p55-related MULTICOPY SUPPRESSOR OF IRA proteins MSI1-5 [8,25,27]. The core PRC2 subunits are evolutionarily conserved, indicating that PRC2 originated early in eukaryotes with a basic functional core composed of E(z), Su(z)12, ESC, and p55 homologs [5] (Figure 1a). In addition to its core subunits, the PRC2 is guided and regulated by a various accessory protein [14,19–21,28,29], as reviewed in detail by Godwin et al., 2022 [15]. Among these, certain accessory proteins have evolved and become functionally integrated into the PRC2 core complex during key evolutionary transitions. For example, the TELOMERE REPEAT-BINDING FACTORS (TRBs) originated early in plant evolution, with their emergence traceable to bryophytes [13,30] (Figure 1a and b). The PWWP-

DOMAIN INTERACTOR OF POLYCOMBS (PWOs) appears to have emerged in lycophytes, coinciding with the evolutionary transition from aquatic to terrestrial habitats and the development of vascular tissues [12] (Figure 1a and b). In contrast, UBIQUITIN-SPECIFIC PROTEASE 5 (UBP5) and VIVIPAROUS1/ABI3-LIKE 1 (VAL1) homolog are conserved throughout the green lineage, including green algae [16,17] (Figure 1a and b). Similarly, the core PRC1 components, including RING-finger proteins (RING1A/1B) and B lymphoma MO-MLV insertion region 1 homologs (BMI1A/1B/1C), are evolutionarily conserved from algae to higher plants (Figure 1b). In contrast, LIKE HETEROCHROMATIN PROTEIN 1 (LHP1), which first appears in mosses [16], binds to H3K27me3-marked chromatin deposited by PRC2 and recruits PRC1 components, promoting H2Aub1 deposition and reinforcing transcriptional repression [20,31,32]. In addition to the core subunits, accessory proteins are also essential for the proper functioning of the PRC1 complex [19,20,31]. These include EMBRYONIC FLOWER 1 (EMF1) [33–35], VERNALIZATION 1 (VRN1) [36], VAL1/2, ALFINK-LIKE 1–7 (AL1–7), INHIBITOR OF GROWTH 1/2 (ING1/2), BASIC PENTACysteine (BPC) [37] and EARLY BOLTING IN SHORT DAYS/SHORT LIFE (EBS/SHL) [16] (Figure 1b). While core subunits of PRC1 such as BMI1 and RING1 are well conserved across the green lineage [4], the emergence of accessory proteins at different points in plant evolution has been crucial for fine-tuning PRC1 function. For instance, EMF1 and VRN1 are specific to dicotyledonous species, whereas BPC-type proteins are present in bryophytes and lycophytes but absent in algal lineages, indicating an origin early in land plant evolution followed by lineage-specific diversification and losses (Figure 1a and b) [37]. In contrast, VALs, ALs, ING1/2, and EBS/SHL are conserved throughout the plant kingdom, including in algae (Figure 1a and b) [16].

Therefore, the expansion and emergence of PRC1/2-associated accessory proteins (e.g., TRBs, PWOs, EMF1, VRN1, LHP1, BPCs) (Figure 1a and b) in early land and vascular plants may have driven lineage-specific shifts in PRC2 targeting, for example, shifting from transposable elements in Archaeplastida and diatoms (e.g., *Cyanidioschyzon merolae*, *Chlamydomonas reinhardtii*, *Phaeodactylum tricorutum*), to broader gene repression in bryophytes (*Marchantia polymorpha*), and predominantly to gene bodies and promoters in flowering plants (*Arabidopsis*). This also suggests that evolving accessory proteins could have guided PRC2 to relocate H3K27me3 marks from repeat-rich heterochromatin in lower plants to gene-rich euchromatin in higher plants [38]. Similarly, the integration of PRC1 accessory proteins with its core components, BMI1 and RING1 in flowering plants was likely a key step in the neofunctionalization of PcG-mediated repression,

Figure 1



A simplified evolutionary timescale [63] illustrates the emergence and diversification of major green plant lineages, including chlorophytes, bryophytes, lycophytes, and flowering plants. **(a-b)** The figure highlights the conservation of core Polycomb group (PcG) components (indicated by a light gray background), including subunits of PRC2 (left) and PRC1 (right), across the green lineage. In addition to these core components, both conserved and lineage-specific accessory proteins are shown (annotated in boxes within the figure), forming dynamic interaction networks within the PcG complex, particularly in flowering plants, with a few similar examples observed in non-seed plants. **(c)** The interactions of non-PcG histone modifiers, including HDMs, HDACs, HATs, and PEAT complex, are also depicted, highlighting the expanding crosstalk among chromatin-modifying complexes and PcG-associated accessory proteins. ‘Interactions’ (Black lines) indicate a direct physical interaction, while ‘No direct interactions’ (Red lines) refer to genetic or indirect associations. Created with BioRender.com.

although the precise evolutionary trajectory of this functional shift remains an important area for future investigation.

### Pc-G associated proteins modulating further histone-modifying complexes in plants

In addition to PcG complexes, further histone-modifying proteins play parallel, often PcG-connected roles in regulating gene transcription in plants and depend on PcG-associated accessory proteins to achieve specificity during development and environmental

responses [18,35,39]. These include histone demethylases (HDMs), histone acetyltransferases (HATs), histone deacetylases (HDACs), and the recently identified PEAT complex (comprising PWWPs/PWOs, ENHANCER OF POLYCOMB-RELATED proteins (EPCRs), AT-rich interaction domain-containing proteins (ARIDs), and TRBs). The PEAT complex has been shown to maintain heterochromatin silencing through its interaction with histone deacetylases [40] and, together with UBP5 and HAM1/2, induces gene expression via histone H4 acetylation and H2A deubiquitination [17,41]. Though the PEAT complex functions as a histone modifier with conserved

components like UBP5, HAMs, and EPCRs. In contrast, TRBs and PWOs, which emerged early in land plants, may also contribute to diversifying its functions [12,17,30]. While the specific *cis*-targets of PEAT on chromatin are not yet fully clear, it is plausible that TRBs, which bind the *tele*-box [30], together with PWOs, help direct the complex to such *cis*-motifs from non-seed plants, although further studies are needed to confirm this. Moreover, HDMs, responsible for removing methyl groups from histone tails, are classified into two major families: the Lysine-Specific Demethylase 1 (LSD1) type, which targets H3K4me1/2 and H3K9me1/2, and the JmjC domain-containing family and removes mono-, di-, and tri-methyl marks from residues such as H3K4, H3K9, and H3K27 (Figure 1c) [42,43]. The JmjC and LSD1-type KDMs are conserved across kingdoms, with JmjC genes diversifying in different numbers across land plants [44]. In Arabidopsis, the JmjC domain-containing protein JMJ14 actively demethylates H3K4me3 and relies on accessory proteins, including the TRBs, which help recruit it for this specific demethylation [18] (Figure 1c). JMJ14 also associates with EMF1, LHP1, and AtBMI1 proteins in a repressive PcG-like complex [35] (Figure 1c). HATs and HDACs regulate gene transcription by catalyzing dynamic acetylation and deacetylation and therefore providing a key regulatory switch, controlling the transition between transcriptionally active (open) and inactive (closed) chromatin states [45]. Among these, the HATs; HAM1 and HAM2 play central roles as catalytic subunits of a Nucleosome Acetyltransferase of H4 (NuA4)-like complex, which primarily acetylates histones H4 and H2A. This function is conserved across eukaryotes [46,47]. Notably, HAM1 and HAM2 also participate in PEAT complex (Figure 1c), where they directly interact with EPCR1/2, proteins essential for their H4K5 acetylation activity [17]. This dual involvement in both the conserved NuA4 complex and the lineage-specific PEAT complex highlights HAMs' versatile roles in transcriptional regulation during plant evolution. On the other hand, plants possess two conserved HDAC families; RPD3/HDAC1-type and SIR2-type (sirtuins), as well as the plant-specific HD2 (HD-tuin) family, all of which remove acetyl marks from histones [48,49]. Although HDACs are generally considered non-PcG modifiers, recent studies have demonstrated that transcriptional repressors such as VALs recruit HDACs via their EAR domain (Figure 1c) while simultaneously interacting with PRC1 components like AtBMI1A-B and connects PRC2 component SWN and CLF to mediate chromatin silencing [48,50–52]. This highlights a functional crosstalk between PcG complexes and HDACs, facilitated by accessory proteins that integrate distinct chromatin-modifying activities into a unified repression mechanism.

### Accessory proteins mediate crosstalk within similar or contrasting histone modifier complexes

Accessory proteins are central architects of the epigenetic regulatory network, acting as molecular hubs that create physical and functional bridges between different chromatin-modifying complexes. A primary example is the crosstalk within the Polycomb silencing pathway itself. Accessory proteins like LHP1, EMF1, and VAL, which are integral to PRC1 function, also physically interact with core PRC2 subunits [8,19,53,54] (Figure 1a and b) ensuring coordinated repression. This suggests that LHP1 may act as a linker between PRC1 and PRC2 complexes during plant evolution (Figure 1a and b) [9]. Expanding this network, certain accessory proteins function as master integrators connecting distinct epigenetic pathways. For instance, TRBs are emerging as key factors linking core chromatin and histone modifiers, including CLF and SWN (PRC2), LHP1 (PRC1), JMJ14 (HDMs) and EPCRs (PEAT complex) thereby regulating both repressive and active chromatin states. Notably, TRBs and LHP1 appear in non-seed plants [13,16] (Figure 1a and b) and may associate with similar core components to diversify their functions, although this remains to be investigated. While LHP1's binding to PRC2 is well established in Arabidopsis, similar interactions occur in *Physcomitrium patens* (*Pp*), where PpLHP1 interacts with PpRING1A/B, and PpRING1A connects with PRC2 subunits such as PpCLF, suggesting conserved crosstalk between PRC1 and PRC2 complexes across plant lineages [9]. Similarly, PWO1 has been shown to interact with PRC2, and this association appears to be evolutionarily conserved, emerging in lycophytes, as suggested by the confirmed interaction between *Selaginella moellendorffii* (*Sm*) SmPWOa and SmCLF [12,21] (Figure 1a). This suggests that the interaction between PWOs and the conserved PRC2 complex in early vascular plants may contribute to functional diversification. Moreover, PWO1 does not exclusively associate with PRC2 members; it is also found in the PEAT complex, which promotes gene activation via HAMs and UBP5 in Arabidopsis [17]. Both PWO and TRB proteins mediate crosstalk between two contrasting complexes, PRC2 and PEAT, but the molecular implications of this association remain unclear. Interestingly, PWO1 binding sites are mutually exclusive with H3K27me3/PRC2 [55], making it tempting to speculate that PWO might antagonize PRC2 activity while associating with TRBs. In contrast, TRBs can promote silencing independently of PWOs, as shown previously [14,18]. Moreover, UBP5 associates the PEAT complex and PRC2, but since its target genes enriched in H2Aub fail to gain H3K27me3, this suggests that UBP5 has PRC2-independent functions [41], although the underlying mechanisms of the UBP5–PRC2 interaction in

chromatin regulation remain unclear (Figure 1). In addition, Enhancer of LHP1 (EOL1) functions as an integrative mediator between PRC2 and LHP1, physically interacting with both complexes during DNA replication to ensure the maintenance of H3K27me3-mediated gene repression at target loci (Figure 1a and b) [19]. Similarly, BPC proteins recruit PRC1 components via LHP1 and interact with PRC2–SWN to mediate gene silencing at loci containing GAGA/PRE motifs in *Arabidopsis* (Figure 1a and b) [10,11]. Interestingly, some accessory proteins engage with different chromatin regulators in a spatially and temporally restricted manner. For instance, VRN1 interacts with multiple chromatin regulatory complexes, including HDACs, chromatin remodelers from the INO80 and SWI/SNF families, and components of both PRC1 and PRC2. Many of these associations are sustained during vernalization, indicating a dynamic regulatory role influenced by developmental or environmental cues [56]. Similarly, AL proteins interact with various regulatory proteins, including chromatin modifiers. They function as PRC1 subunits mediating H2A monoubiquitination linked to H3K4me3, and associate with PWO proteins of the PEAT complex involved in H2A deubiquitination, suggesting a role in coordinating opposing chromatin modifications in a context-specific manner [57]. Therefore, unraveling how accessory proteins operate within opposing complexes in a spatiotemporal, cell type-specific, and environmentally responsive context remains a major frontier in epigenetic research.

## Conclusion and perspective

Although core histone-modifying enzymes such as HDMs, HATs, HDACs, and Polycomb group complexes are broadly conserved across eukaryotes, mounting evidence reveals that their regulatory landscapes have been significantly diversified through the lineage-specific emergence of accessory proteins. These subunits, often absent in ancestral eukaryotes, appear to have evolved in response to developmental and environmental challenges unique to plant lineages [5,38,58]. A compelling hypothesis is that these accessory proteins provided additional regulatory layers that enabled conserved core histone modifiers to be co-opted for new functions, fine-tuning chromatin states in response to emerging biological needs. Innovations and neofunctionalization may not only permit the adaptation to increasing developmental complexity and conquest of ecological niches, but also contribute to more complex genome organization and genome defense. Particularly, an important role in 3D genome organization was recently revealed for EMF1 and the PEAT component PWO [55,59], which may depend on interactions of spatially restricted proteins. In addition, the association of PcG and accessory proteins may regulate different classes of genomic elements such as transposable elements (TEs) and genes, possibly depending on the evolutionary age of the regulated genes

and its potential emergence from TEs [38,58,60]. Lastly, accessory proteins may participate in only certain steps towards the final silencing state of a genomic element, which includes nucleation, spreading of the silencing mark and restriction of spreading within a boundary region [61].

Importantly, crosstalk between different histone-modifying complexes is often facilitated by accessory proteins, which help coordinate gene regulation within the spatial context of chromatin organization. This highlights their essential role in dynamically linking multiple epigenetic pathways. Moving forward, elucidating the molecular function, composition and structure of chromatin-modifying complexes in non-model plants will be critical. Structural studies may reveal conserved functional domains even in the absence of strong sequence similarity, while genome-wide localization analyses, such as those presented in the QHistone database [62], can uncover overlapping or distinct genomic targets of core and accessory subunits. Together, these efforts will clarify how modular chromatin complexes have evolved and been repurposed to support plant developmental innovation and environmental adaptation, particularly by revealing novel regulatory modules in lineages that faced distinct evolutionary pressures.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgments

This work was supported by the Rising Star (2024–2025); Junior Fellowship Program of the Department of Biology, Chemistry, Pharmacy at Freie Universität Berlin, awarded to AK.

## Data availability

No data was used for the research described in the article.

## References

Papers of particular interest, published within the period of review, have been highlighted as:

- \* of special interest
- \*\* of outstanding interest

1. Le H, Simmons CH, Zhong X: **Functions and mechanisms of histone modifications in plants**. *Annu Rev Plant Biol* 2025, **76**: 551–578.
2. Pfluger J, Wagner D: **Histone modifications and dynamic regulation of genome accessibility in plants**. *Curr Opin Plant Biol* 2007, **10**:645–652.
3. Vijayanathan M, Trejo-Arellano MG, Mozgová I: **Polycomb repressive complex 2 in Eukaryotes—An evolutionary perspective**. *Epigenomes* 2022, **6**:3.

4. Chen D, Huang Y, Ruan Y, Shen W-H: **The evolutionary landscape of PRC1 core components in green lineage.** *Planta* 2016, **243**:825–846.

5. Sharaf A, Vijayanathan M, Oborník M, Mozgová I: **Phylogenetic profiling resolves early emergence of PRC2 and illuminates its functional core.** *Life Sci Alliance* 2022, **5**, e202101271.

The study uses phylogenetic analyses to trace the early emergence of PRC2 across eukaryotic lineages and investigates its core subunits, highlighting its early presence in evolution. Their findings reveal evolutionary adaptations of PRC2's core subunits, clarifying the possible role of PRC2 in epigenome regulation throughout evolution.

6. Mozgova I, Köhler C, Hennig L: **Keeping the gate closed: functions of the polycomb repressive complex <scp>PRC</scp> 2 in development.** *Plant J* 2015, **83**:121–132.

7. Faivre L, Kinscher N-F, Kuhlmann AB, Xu X, Kaufmann K, Schubert D: **Cold stress induces rapid gene-specific changes in the levels of H3K4me3 and H3K27me3 in Arabidopsis thaliana.** *Front Plant Sci* 2024, **15**.

8. Baile F, Gómez-Zambrano Á, Calonje M: **Roles of polycomb complexes in regulating gene expression and chromatin structure in plants.** *Plant Commun* 2022, **3**, 100267.

9. Parihar V, Arya D, Walia A, Tyagi V, Dangwal M, Verma V, Khurana R, Boora N, Kapoor S, Kapoor M: **Functional characterization of LIKE HETEROCHROMATIN PROTEIN 1 in the moss *Physcomitrella patens*: its conserved protein interactions in land plants.** *Plant J* 2019, **97**:221–239.

10. Hecker A, Brand LH, Peter S, Simoncello N, Kilian J, Harter K, Gaudin V, Wanke D: **The Arabidopsis GAGA-Binding factor BASIC PENTACYSTEINE6 recruits the POLYCOMB-REPRESSIVE COMPLEX1 component LIKE HETEROCHROMATIN PROTEIN1 to GAGA DNA motifs.** *Plant Physiol* 2015, **168**:1013–1024.

11. Mu Y, Zou M, Sun X, He B, Xu X, Liu Y, Zhang L, Chi W: **Basic pentacysteine proteins repress abscisic acid Insensitive4 expression via direct recruitment of the polycomb-repressive complex 2 in Arabidopsis root development.** *Plant Cell Physiol* 2017, <https://doi.org/10.1093/pcp/pcx006>.

12. Khan A, Haider S, Sharaf A, Kusová A, Skalák J, Jourdain C, Rennie M, Schrupfová PP, Hejálko J, Schubert D, et al.: **PWO proteins are associated with PRC2 since their emergence in vascular plants.** 2025, <https://doi.org/10.1101/2025.03.15.643013>.

This preprint provides evolutionary and functional insights into PWO proteins, demonstrating their emergence alongside vascular plant evolution and their conserved association with PRC2. The study supports the hypothesis that accessory proteins like PWOs co-evolved with developmental complexity and chromatin regulatory needs in land plants.

13. Amiard S, Feit L, Vanrobays E, Simon L, Le Goff S, Loizeau L, Wolff L, Butter F, Bourbousse C, Barneche F, et al.: **The TELOMERE REPEAT BINDING proteins TRB4 and TRB5 function as transcriptional activators of PRC2-controlled genes to regulate plant development.** *Plant Commun* 2024, **5**, 100890.

This study shows that TRB4 and TRB5, from a distinct TRB clade, regulate hundreds of genes involved in developmental responses to environmental cues. TRB4 interacts with PRC2 components, and both proteins are required for the distinctive *clf* mutant phenotypes. Overall, TRBs control plant development through PRC2-dependent and independent mechanisms.

14. Zhou Y, Wang Y, Krause K, Yang T, Dongus JA, Zhang Y, Turck F: **Telobox motifs recruit CLF/SWN-PRC2 for H3K27me3 deposition via TRB factors in Arabidopsis.** *Nat Genet* 2018, **50**:638–644.

15. Godwin J, Farrona S: **The importance of networking: plant polycomb repressive complex 2 and its interactors.** *Epigenomes* 2022, **6**:8.

This review provides an overview of accessory proteins that physically and genetically interact with the PRC2 complex, detailing its interaction networks with PRC1 components, transcriptional activators and repressors, ubiquitin–26S proteasomal machinery, DNA replication factors, histone modifiers, and long non-coding RNAs. It focuses on their roles in PRC2-dependent transcriptional regulation and how these interactions modulate PRC2 function and recruitment to

chromatin, highlighting the complexity and diversity of PRC2-associated networks in plant development.

16. Huang Y, Jiang L, Liu B-Y, Tan C-F, Chen D-H, Shen W-H, Ruan Y: **Evolution and conservation of polycomb repressive complex 1 core components and putative associated factors in the green lineage.** *BMC Genom* 2019, **20**:533.

17. Zheng S-Y, Guan B-B, Yuan D-Y, Zhao Q-Q, Ge W, Tan L-M, Chen S-S, Li L, Chen S, Xu R-M, et al.: **Dual roles of the Arabidopsis PEAT complex in histone H2A deubiquitination and H4K5 acetylation.** *Mol Plant* 2023, **16**:1847–1865.

This study identifies the Arabidopsis PEAT complex as a chromatin-modifying module with dual functionality, integrating the deubiquitinase UBP5, which removes H2A monoubiquitination genome-wide, and the histone acetyltransferases HAM1/2, which mediate H4K5 acetylation, thereby coordinating transcriptional activation and supporting proper plant development.

18. Wang M, Zhong Z, Gallego-Bartolomé J, Feng S, Shih Y-H, Liu M, Zhou J, Richey JC, Ng C, Jami-Allahmadi Y, et al.: **Arabidopsis TRB proteins function in H3K4me3 demethylation by recruiting JMJ14.** *Nat Commun* 2023, **14**:1736.

This study demonstrates that Arabidopsis TRB proteins recruit JMJ14, a histone demethylase, to target loci, leading to the removal of H3K4me3 marks and subsequent gene silencing. In *trb1/2/3* and *jmj14-1* mutants, elevated H3K4me3 levels correlate with upregulation of target genes. The research underscores how TRB proteins coordinate PRC2 and JMJ14 activities to repress gene expression via H3K27me3 deposition and H3K4me3 removal, highlighting their role in epigenetic regulation.

19. Zhou Y, Tergemina E, Cui H, Förderer A, Hartwig B, Velikkakam James G, Schneeberger K, Turck F: **Ctf4-related protein recruits LHP1-PRC2 to maintain H3K27me3 levels in dividing cells in Arabidopsis thaliana.** *Proc Natl Acad Sci* 2017, **114**:4833–4838.

20. Derkacheva M, Steinbach Y, Wildhaber T, Mozgová I, Mahrez W, Nanni P, Bischof S, Grussem W, Hennig L: **Arabidopsis MSH1 connects LHP1 to PRC2 complexes.** *EMBO J* 2013, **32**:2073–2085.

21. Hohenstatt ML, Mikulski P, Komarynets O, Klose C, Kycia I, Jeltsch A, Farrona S, Schubert D: **PWWP-DOMAIN INTERACTOR OF POLYCOMBS1 interacts with polycomb-group proteins and histones and regulates Arabidopsis flowering and development.** *Plant Cell* 2018, **30**:117–133.

22. Zhou Y, Hartwig B, James GV, Schneeberger K, Turck F: **Complementary activities of TELOMERE REPEAT BINDING Proteins and Polycomb Group complexes in transcriptional regulation of target genes.** *Plant Cell* 2016, **28**:87–101.

23. Schubert D: **Evolution of Polycomb-group function in the green lineage.** *F1000Res* 2019, **8**:268.

24. Fischer S, Weber LM, Liefke R: **Evolutionary adaptation of the Polycomb repressive complex 2.** *Epigenetics Chromatin* 2022, **15**:7.

25. Bieluszewski T, Xiao J, Yang Y, Wagner D: **PRC2 activity, recruitment, and silencing: a comparative perspective.** *Trends Plant Sci* 2021, **26**:1186–1198.

26. Nekrasov M, Wild B, Müller J: **Nucleosome binding and histone methyltransferase activity of Drosophila PRC2.** *EMBO Rep* 2005, **6**:348–353.

27. Mozgova I, Hennig L: **The Polycomb Group protein regulatory network.** *Annu Rev Plant Biol* 2015, **66**:269–296.

28. Franco-Echevarría E, Nielsen M, Schulten A, Cheema J, Morgan TE, Bienz M, Dean C: **Distinct accessory roles of Arabidopsis VEL proteins in Polycomb silencing.** *Genes Dev* 2023, **37**:801–817.

This study elucidates the distinct roles of Arabidopsis VEL proteins, VRN5 and VIN3, in PRC2-mediated gene silencing. VRN5 interacts with PRC2 components and is necessary for H3K27me2 deposition, while both VRN5 and VIN3 are required for H3K27me3. VIN3 also associates with the transcriptional repressor VAL1 to facilitate cold-induced silencing of FLC. These findings highlight the specialized accessory functions of VEL proteins in PRC2-mediated epigenetic regulation.

29. Kim D-H, Zografos BR, Sung S: **Vernalization-Mediated *VIN3* induction overcomes the LIKE-HETEROCHROMATIN PROTEIN1/POLYCOMB REPRESSION COMPLEX2-Mediated epigenetic repression.** *Plant Physiol* 2010, **154**:949–957.
30. Kusová A, Steinbachová L, Přerovská T, Drábková LZ, Paleček J, Khan A, Rigóová G, Gadiou Z, Jourdain C, Stricker T, *et al.*: **Completing the TRB family: newly characterized members show ancient evolutionary origins and distinct localization, yet similar interactions.** *Plant Mol Biol* 2023, **112**: 61–83.
- This study characterizes TRB4 and TRB5 in *A. thaliana*. Phylogenetic analyses indicate that TRB4 and TRB5 originated in non-seed plants. The Myb-like domains of both proteins bind long arrays of telomeric repeats in vitro. TRB4 and TRB5 physically interact with TERT fragments, the PEAT component PWO1, as well as PRC2 core subunits CLF, SWN, EMF2, and VRN2. These findings suggest that TRB4 and TRB5 engage with diverse regulatory complexes to control gene function.
31. Bratzel F, López-Torrejón G, Koch M, Del Pozo JC, Calonje M: **Keeping cell identity in arabidopsis requires PRC1 RING-Finger homologs that catalyze H2A monoubiquitination.** *Curr Biol* 2010, **20**:1853–1859.
32. Chen D, Molitor A, Liu C, Shen W-H: **The Arabidopsis PRC1-like ring-finger proteins are necessary for repression of embryonic traits during vegetative growth.** *Cell Res* 2010, **20**: 1332–1344.
33. Liang SC, Hartwig B, Perera P, Mora-García S, de Leau E, Thornton H, de Alves FL, Rapsilber J, Yang S, James GV, *et al.*: **Kicking against the PRCs – a domesticated transposase antagonises Silencing mediated by polycomb group proteins and is an accessory component of polycomb repressive complex 2.** *PLoS Genet* 2015, **11**, e1005660.
34. Merini W, Romero-Campero FJ, Gomez-Zambrano A, Zhou Y, Turck F, Calonje M: **The arabidopsis polycomb repressive complex 1 (PRC1) components AtBMI1A, B, and C impact gene networks throughout all stages of plant development.** *Plant Physiol* 2017, **173**:627–641.
35. Wang Y, Gu X, Yuan W, Schmitz RJ, He Y: **Photoperiodic control of the floral transition through a distinct polycomb repressive complex.** *Dev Cell* 2014, **28**:727–736.
36. Huang Y, Chen D-H, Liu B-Y, Shen W-H, Ruan Y: **Conservation and diversification of polycomb repressive complex 2 (PRC2) proteins in the green lineage.** *Brief Funct Genomics* 2017, **16**:106–119.
37. Theune ML, Bloss U, Brand LH, Ladwig F, Wanke D: **Phylogenetic analyses and GAGA-motif binding studies of BBR/BPC proteins lend to clues in GAGA-motif recognition and a regulatory role in brassinosteroid signaling.** *Front Plant Sci* 2019, **10**.
38. Hisanaga T, Romani F, Wu S, Kowar T, Wu Y, Lintermann R, Fridrich A, Cho CH, Chaumier T, Jamge B, *et al.*: **The polycomb repressive complex 2 deposits H3K27me3 and represses transposable elements in a broad range of eukaryotes.** *Curr Biol* 2023, **33**:4367–4380.e9.
- This study demonstrates that PRC2-mediated H3K27me3 deposition and transposable element (TE) repression are conserved features across diverse eukaryotic lineages, including plant groups that diverged before the emergence of seed plants. Through comparative epigenomics, it shows that TE silencing via PRC2 predates land colonization, providing critical insight into the ancestral functions of Polycomb complexes and their evolutionary role in maintaining genome stability.
39. Zhou Y, Tan B, Luo M, Li Y, Liu C, Chen C, Yu C-W, Yang S, Dong S, Ruan J, *et al.*: **HISTONE DEACETYLASE19 interacts with HSL1 and participates in the repression of seed maturation genes in arabidopsis seedlings.** *Plant Cell* 2013, **25**: 134–148.
40. Tan L, Zhang C, Hou X, Shao C, Lu Y, Zhou J, Li Y, Li L, Chen S, He X: **The <scp>PEAT</scp> protein complexes are required for histone deacetylation and heterochromatin silencing.** *EMBO J* 2018, **37**.
41. Godwin J, Govindasamy M, Nedounsejian K, March E, Halton R, Bourbousse C, Wolff L, Fort A, Krzyszton M, López Corrales J, *et al.*: **The UBP5 histone H2A deubiquitinase counteracts PRCs-mediated repression to regulate arabidopsis development.** *Nat Commun* 2024, **15**:667.
- This study demonstrates that UBP5 directly erases H2Aub to alleviate repression by both PRC1 and PRC2, redefining the regulatory landscape of Polycomb control in Arabidopsis development. Through CRISPR-Cas9 knockout and ChIP/RNA seq analyses, it shows UBP5 targets PRC2 recruiting motifs and influences H3K27me3 deposition, representing a major advance in understanding chromatin cross talk in plant epigenetics.
42. Klose RJ, Kallin EM, Zhang Y: **JmjC-domain-containing proteins and histone demethylation.** *Nat Rev Genet* 2006, **7**: 715–727.
43. Spedaletti V, Polticelli F, Capodaglio V, Schininà ME, Stano P, Federico R, Tavladoraki P: **Characterization of a lysine-specific histone demethylase from Arabidopsis thaliana.** *Biochemistry* 2008, **47**:4936–4947.
44. Ma S, Zhang Z, Long Y, Huo W, Zhang Y, Yang X, Zhang J, Li X, Du Q, Liu W, *et al.*: **Evolutionary history and functional diversification of the JmjC domain-containing histone demethylase gene family in plants.** *Plants* 2022, **11**:1041.
45. Liu X, Yang S, Yu C-W, Chen C-Y, Wu K: **Histone acetylation and plant development.** 2016:173–199.
46. Espinosa-Cores L, Bouza-Morcillo L, Barrero-Gil J, Jiménez-Suárez V, Lázaro A, Piqueras R, Jarillo JA, Piñeiro M: **Insights into the function of the NuA4 complex in plants.** *Front Plant Sci* 2020, **11**.
47. Zhou J, Su X, Zheng S, Wu C, Su Y, Jiang Z, Li L, Chen S, He X: **The arabidopsis NuA4 histone acetyltransferase complex is required for chlorophyll biosynthesis and photosynthesis.** *J Integr Plant Biol* 2022, **64**:901–914.
48. Chen X, Ding AB, Zhong X: **Functions and mechanisms of plant histone deacetylases.** *Sci China Life Sci* 2020, **63**:206–216.
49. Bourque S, Jeandroz S, Grandperret V, Lehotai N, Aimé S, Soltis DE, Miles NW, Melkonian M, Deyholos MK, Leebens-Mack JH, *et al.*: **The evolution of HD2 proteins in green plants.** *Trends Plant Sci* 2016, **21**:1008–1016.
50. Zeng X, Gao Z, Jiang C, Yang Y, Liu R, He Y: **HISTONE DEACETYLASE 9 functions with polycomb silencing to repress FLOWERING LOCUS C expression.** *Plant Physiol* 2020, **182**:555–565.
51. Yuan L, Song X, Zhang L, Yu Y, Liang Z, Lei Y, Ruan J, Tan B, Liu J, Li C: **The transcriptional repressors VAL1 and VAL2 recruit PRC2 for genome-wide Polycomb silencing in Arabidopsis.** *Nucleic Acids Res* 2021, **49**:98–113.
52. Yang C, Bratzel F, Hohmann N, Koch M, Turck F, Calonje M: **VAL- and AtBMI1-Mediated H2Aub initiate the switch from embryonic to postgerminative growth in arabidopsis.** *Curr Biol* 2013, **23**:1324–1329.
53. Feng J, Lu J: **LHP1 could act as an activator and a repressor of transcription in plants.** *Front Plant Sci* 2017, **8**.
54. Kim SY, Lee J, Eshed-Williams L, Zilberman D, Sung ZR: **EMF1 and PRC2 cooperate to repress key regulators of arabidopsis development.** *PLoS Genet* 2012, **8**, e1002512.
55. Yang T, Wang D, Luo L, Yin X, Song Z, Yang M, Zhou Y: **PWOs repress gene transcription by regulating chromatin structures in Arabidopsis.** *Nucleic Acids Res* 2024, **52**: 12918–12929.
- This study sheds further light on the PWO1-PRC2 interaction by revealing a localization of PWO1 at H3K27me3 boundary regions, influencing H3K27me3-enriched compartment domains.
56. Montez M, Zhu D, Huertas Martin J, Maristany MJ, Rutjens B, Nielsen M, Collepardo-Guevara R, Dean C: **Cold-induced nucleosome dynamics linked to silencing of Arabidopsis FLC.** 2025, <https://doi.org/10.1101/2025.02.17.638618>.
57. Su X-M, Yuan D-Y, Liu N, Zhang Z-C, Yang M, Li L, Chen S, Zhou Y, He X-J: **ALFIN-like proteins link histone H3K4me3 to H2A ubiquitination and coordinate diverse chromatin modifications in Arabidopsis.** *Mol Plant* 2025, **18**:130–150.
58. Petroll R, Papareddy RK, Krella R, Laigle A, Rivière Q, Bišova K, Mozgová I, Borg M: **The expansion and diversification of**

**epigenetic regulatory networks underpins major transitions in the evolution of land plants.** *Mol Biol Evol* 2025, **42**.

59. Shu J, Sun L, Wang D, Yin X, Yang M, Yang Z, Gao Z, He Y, Calonge M, Lai J, *et al.*: **EMF1 functions as a 3D chromatin modulator in Arabidopsis.** *Mol Cell* 2024, **84**:4729–4739.e6.  
 The PcG protein EMF1, associated with PRC1, is shown to modulate 3D chromatin organization by interacting with the cohesin protein SCC3, linking a highly conserved DNA looping regulator (SCC3) with a plant-specific protein.
60. Hure V, Piron-Prunier F, Yehouessi T, Vitte C, Kornienko AE, Adam G, Nordborg M, Délérís A: **Alternative silencing states of transposable elements in Arabidopsis associated with H3K27me3.** *Genome Biol* 2025, **26**:11.  
 This study shows that in *Arabidopsis thaliana*, transposable elements (TEs) can be silenced by H3K27me3 even in the absence of DNA methylation. Some TEs, termed "bifrons," switch between DNA methylation and H3K27me3-based silencing across different natural accessions, influenced by TE features and trans-acting factors. These

findings reveal a dynamic interplay between epigenetic mechanisms in TE regulation.

61. Liang Z, Zhu T, Yu Y, Wu C, Huang Y, Hao Y, Song X, Fu W, Yuan L, Cui Y, *et al.*: **PICKLE-mediated nucleosome condensing drives H3K27me3 spreading for the inheritance of Polycomb memory during differentiation.** *Mol Cell* 2024, **84**:3438–3454.e8.
62. Hsieh C-H, Chang Y-TS, Yen M-R, Hsieh J-WA, Chen P-Y: **Predicting protein synergistic effect in arabidopsis using epigenome profiling.** *Nat Commun* 2024, **15**:9160.  
 This paper provides and describes a new database/analysis platform, QHistone, which offers machine learning based algorithms to predict co-binding analysis of chromatin associated proteins and histone modifications, thus predicting co-regulation and co-localization of different proteins. It utilizes publicly available epigenome data thus offering a valuable resource for the community
63. Kumar S, Stecher G, Suleski M, Hedges SB: **TimeTree: a resource for timelines, timetrees, and divergence times.** *Mol Biol Evol* 2017, **34**:1812–1819.