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Organization and evolution of *Drosophila* telomeres

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Drosophila telomeres are elongated by occasional transposition of specialized retroelements rather than telomerase activity, and are assembled independently of the sequence of the DNA termini. *Drosophila* telomeres are capped by terminin, a complex formed by the HOAP, Moi, Ver and HipHop proteins that localize exclusively at telomeres and protect them from fusion events. Other proteins required to prevent end-to-end fusion include HP1, Eff/UbcD1, ATM, the components of the Mre11-Rad50-Nbs (MRN) complex, the Woc transcription factor, and the Peo ubiquitin E2 variant enzyme. The terminin proteins are encoded by fast-evolving genes and are not evolutionarily conserved outside the *Drosophila* species. In contrast, the non-terminin telomere capping proteins are not fast-evolving, do not localize only at telomeres and are conserved from yeasts to mammals. We propose that following telomerase loss, *Drosophila* rapidly evolved terminin to bind chromosome ends in a sequence-independent manner, and that non-terminin proteins did not evolve as rapidly as terminin because of the functional constraints imposed by their involvement in diverse cellular processes. Thus, the *Drosophila* non-terminin proteins might correspond to ancestral telomere-associated proteins with homologues in other organisms including humans. This hypothesis is supported by our recent findings that the mammalian homologues Peo interact with the mammalian telomere capping complex shelterin and are required for proper telomere replication.

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