



## **Evolution of a sterile soldier caste by heterochronic expression of seasonal polyphenism in social aphids**

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Mechanistic hypotheses for the evolution of eusociality suggest that preexisting developmental plasticity in ancestral species is a source of novel caste phenotypes. Current supports for the hypotheses using genomic data come from correlation in gene expression between a presumably ancestral reproductive morph and a presumably derived sterile morph within a single species. However, to validate that the two morphs are developmentally co-regulated, evolutionary correlation based on phylogenetically-grounded comparison provides convincing evidence. Most social aphids alternate their host plants with the seasons, by forming closed galls on their primary host and free-living colonies on their secondary host, and producing different phenotypes on each host plant. In *Colophina* aphids, they produce monomorphic and non-sterile defensive nymphs in the galls, while produce sterile soldier nymphs in the free-living colonies. The morphologies of the soldiers in the free-living colonies resemble those of monomorphic defenders in the galls, suggesting the possibility that these two defensive morphs share a common developmental program. By using phylogenetic comparative methods, we found that the morphologies and transcriptomes of the two defensive morphs in four *Colophina* species showed correlated evolution. In addition, their morphologies and transcriptomes were almost identical in *Colophina clematicola*, which is placed in a basal position within the genus. Their attacking behaviors also resemble each other, despite of their different ecological conditions. These results suggest that the sterile soldiers of *Colophina* species first evolved by a heterochronic expression of gall defenders, and later diverged from the gall defenders to have more specialized morphology.