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T H E  
**PLANT**  
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EVOLUTIONARY ORIGINS OF SEED PEPTIDES BURIED IN DAISY ALBUMIN

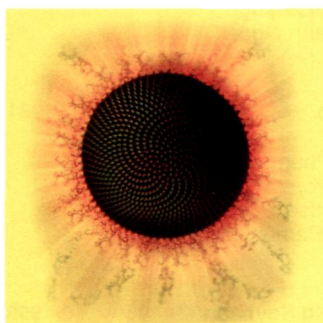
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**ON THE COVER**



Common sunflower (*Helianthus annuus*) contains the unusual gene *PawS1* (*Preproalbumin with SFTI-1*) that encodes both a precursor for seed storage albumin and the protease-inhibiting peptide SFTI-1. Elliott et al. (pages 981–995) show that this dual biosynthesis process is of ancient evolutionary origin and propose the biochemical sequence of events that allowed the peptide to arise de novo. On the cover, a stylized sunflower floret is ringed by structural models of the various peptides, solved by nuclear magnetic resonance spectroscopy. Artwork by Scot Nicholls, Domokun Design.

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- Shibata, M., Oikawa, K., Yoshimoto, K., Kondo, M., Mano, S., Yamada, K., Hayashi, M., Sakamoto, W., Ohsumi, Y., and Nishimura, M. (2013). Highly oxidized peroxisomes are selectively degraded via autophagy in *Arabidopsis*. *Plant Cell* 25: 4967–4983. 1377
- Li, S., Lauri, A., Ziemann, M., Busch, A., Bhawe, M., and Zachgo, S. (2009). Nuclear activity of ROXY1, a glutaredoxin interacting with TGA factors, is required for petal development in *Arabidopsis thaliana*. *Plant Cell* 21: 429–441. 1378

<sup>C</sup> Some figures in this article are displayed in color online but in black and white in the print edition.

<sup>W</sup> Online version contains Web-only data.

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