The Plant Cell, Vol. 22: 2104, July 2010, www.plantcell.org

IN BRIEF

The Podostemad Puzzle: The Evolution of Unusual Morphology in the Podostemaceae

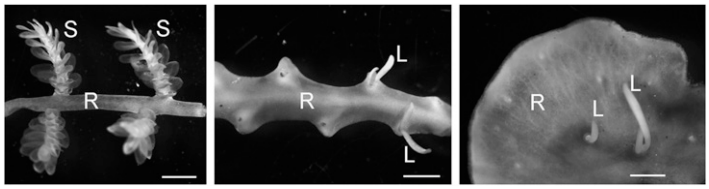
The family Podostemaceae is a family of aquatic eudicots known as river weeds that grow on rocks in rapids and waterfalls, mostly in tropical and subtropical regions. They have a unique body plan (see figure) that appears specialized for clinging to rocks in moving water. In the subfamily Podostemoideae (including *Hydrobryum* and *Cladopus*), leaves develop from an apparent shoot that lacks a recognizable shoot apical meristem (SAM), which, in turn, develops from the root. The other two subfamilies, Tristichoideae (including *Terniopsis*) and Weddellinoideae, have root derived shoots but otherwise show rather typical shoot organogenesis, with SAMs producing leaves on their flanks. In a study that sheds light on the evolution of novel morphologies, **Katayama et al. (pages 2131–2140)** investigate the mechanisms underlying shoot development in these unusual plants through a detailed analysis of the expression patterns of orthologs of genes that are key developmental regulators in typical eudicots: *SHOOT MERISTEMLESS* (*STM*) and *WUSCHEL* (*WUS*), which are involved in meristem initiation and maintenance, and *ASYMMETRIC LEAVES1/ROUGH SHEATH1/PHANTASTICA* (*ARP*), which promotes leaf identity.

Katayama et al. first isolated homologs of *STM*, *WUS*, and *ARP* from *Terniopsis minor* and the SAM-less *Hydrobryum japonicum* and *Cladopus doianus* using phylogenetic analyses to confirm orthology. Expression patterns were then examined with a combination of in situ hybridization and RT-PCR. The expression patterns of *STM* and *WUS* orthologs in *T. minor* were consistent with those of typical angiosperms, being expressed in the SAM, including an adventitious SAM formed in a cavity within the root, but not in leaf primordia. The SAM-less species were similar, but showed *STM* and *WUS* expression, suggestive of meristem identity, in the initiating leaf and bract primordia. As they developed, *WUS* expression disappeared and *STM* expression was restricted to the base of leaf and bract primordia, with complementary expression of *ARP* in the apical portion of the leaf and bract primordium. The results suggest that the leaves and bracts of the SAM-less species produce cryptic meristems near their bases, which subsequently differentiate into another leaf or bract. The leaves are thus sympodial units consisting of a meristematic shoot zone and a single, apical leaf/bract. As a result, the leaves have a mixture of leaf and shoot identity. This unusual developmental mechanism does not seem to apply to floral organs, since expression patterns of the three genes in the flower primordia and floral meristem were consistent with typical flower development in other angiosperms. Based on these and other data, the authors suggest that the spathella in podostemads may be homologous to the calyx in other angiosperms.

It is now generally accepted that compound leaves express both leaf and shoot properties and that this at least partly reflects ectopic expression of genes related to *STM* in the leaf (Uchida et al., 2010). Katayama et al. put forward a similar model for the evolution of novel shoot organogenesis in the Podostemoideae, suggesting that the SAM-less shoots, like compound leaves, combine features of leaves and shoots. They propose that these structures evolved by the transformation of the shoot apex into a single, terminal leaf-like organ. However, whereas compound leaves are thought to have evolved by the addition of shoot identity to leaves, their model suggests the opposite for podostemad leaf/stem organs. The shoot apex appears to have been converted into a single, terminal leaf by losing *STM/WUS* expression and gaining *ARP* expression. Thus, it appears that changes in the expression patterns of the developmental regulatory genes *STM*, *WUS*, and *ARP* have contributed not only to diverse leaf forms but also to the unique podostemad body plan with its apparent role in allowing for growth in fast-flowing tropical rivers.

Nancy A. Eckardt
Senior Features Editor
neckardt@aspb.org

David Baum
University of Wisconsin
Madison, WI 53706



Morphology of Podostemaceae. Left, *T. brevis* shoots (S) arising from the lateral side of subcylindrical root (R); middle, *C. doianus* leaves (L) arising from lateral side of ribbonlike root (R); right, *H. japonicum* leaves (L) arising from the dorsal side of a crustose root (R). Bars = 1 mm. (*Reprinted from Supplemental Figure 1 of Katayama et al. [2010]*.)

REFERENCES

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