Hornwort stomata: Architecture and fate shared with 400 million year old fossil plants without leaves [1]

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Title	Hornwort stomata: Architecture and fate shared with 400 million year old fossil plants without leaves
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Abstract	As one of the earliest plant groups to evolve stomata, hornworts are key to understanding stomata origin and function. Hornwort stomata are large and scattered on sporangia that grow from their bases and release spores at their tips. We present data from development and immunocytochemistry that identify a role for hornwort stomata that is correlated with sporangial and spore maturation. We measured guard cells across the genera with stomata to assess developmental changes in size and to analyze any correlation with genome size. Stomata form at the base of the sporophyte in the green region, where they develop differential wall thickenings, form a pore and die. Guard cells collapse inwardly, increase in surface area and remain perched over a substomatal cavity and network of intercellular spaces that is initially fluid filled. Following pore formation, the sporophyte dries from the outside inwardly and continues to do so after guard cells die and collapse. Spore tetrads develop in spore mother cell walls within a mucilaginous matrix, both of which progressively dry before sporophyte dehiscence. A lack of correlation between guard cell size and DNA content, lack of arabinans in cell walls, and perpetually open pores are consistent with inactivity of hornwort stomata. Stomata are expendable in hornworts as they have been lost twice in derived taxa. Guard cells and epidermal cells of hornworts show striking similarities with the earliest plant fossils. Our findings identify an architecture and fate of stomata in hornworts that is ancient and common to plants without sporophytic leaves.
