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Article Addendum

Vacuolar ion channels in the liverwort *Conocephalum conicum*

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Key words: vacuole, SV channel, anion channel, *Conocephalum conicum*, *Embryophyta*

As a liverwort *Conocephalum conicum* belongs to the oldest terrestrial plants[1] and is phylogenetically located between green algae and higher plants. Recent patch-clamp recordings on Conocephalum vacuoles[2,3] demonstrate ion channels very similar to higher plants and clearly different from vacuolar ion channels described in green algae. Here we summarize the features of a vacuolar cation channel and a vacuolar anion channel that both are common in terrestrial plants but are not detected in green algae, and we speculate about the molecular identity of these channels in the liverwort Conocephalum.

SV Channel

The by far best characterized vacuolar cation channel is the so-called SV channel. It conducts monovalent as well as divalent cations, seems to be ubiquitous in terrestrial plants (*Embryophyta*), and is expressed in most plant tissues.[4,5] Electrophysiologically there is no significant difference between SV channels recorded from the liverwort *Conocephalum conicum* [2,3] and SV channels in higher plant vacuoles.[4,5] The characteristic slow activation, the voltage-dependence, and the activation by (unphysiological) high Ca^{2+} concentrations are conserved among all terrestrial plants. [4,5,6] Electrophysiological recordings on vacuoles from green algae give no indication for the existence of an SV-type channel. In Arabidopsis, SV channel activity was recently identified to be carried by AtTPC1—a two-pore domain Ca^{2+} channel (At4g03560).[7] In line with ubiquitous SV channel activity among terrestrial plants, homologs of *AtTPC1* can be found in many *Embryophyta*,[4] including the moss *Physcomitrella patens*. Most likely a *TPC1* gene will be discovered in liverworts. In green algae no homolog of *AtTPC1* is found in the sequenced genomes of *Chlamydomonas reinhardtii*, *Ostreococcus lucimarinus*, *Ostreococcus tauri* or *Volvox carteri* (AtTPC1 blasted at http://genome.jgi-psf.org/euk_home.html). The SV channel / TPC1 seems to be a unifying characteristic of terrestrial plants.

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Vacuolar Malate Channel

The best characterized vacuolar anion channel in higher plants is the vacuolar malate channel (VMAL).[8-10] It activates with a multiphasic kinetics consisting of a rapid and at least one slow phase, displays a pronounced rectification allowing anions to enter but not to leave the vacuole, and is hardly affected by cytosolic Ca^{2+} or ATP. We recently characterized a vacuolar anion channel in the liverwort Conocephalum[3] that shows all these characteristics of higher plant malate channels. However, the liverwort anion channel displays an about four-fold higher conductance for Cl^- and NO_3^- compared to mal^{2-}, while most higher plant vacuolar malate channels display higher current densities with mal^{2-}.[11] On the other hand, vacuolar malate channels in Arabidopsis give rise to comparable current amplitudes with mal^{2-} and Cl^-,[12] indicating that there might be some variation in the permeability ratio for mal^{2-} versus Cl^-. The vacuolar chloride channel (VCL) described in *Vicia faba* guard cell vacuoles with its instantaneous activation and its Ca^{2+} dependent activation[13] is clearly different from the vacuolar anion channel in Conocephalum. A vacuolar ClC-type chloride transporter in Arabidopsis functions as a NO_3^-/H^+ antiporter,[14] and these ClC-type anion/H^+ antiporters produce only sub-picosiemens apparent single channel conductance,[15] in contrast to the vacuolar anion channel in Conocephalum that has a single channel conductance of 32 pS in 100 mM Cl^-.[3] We therefore think that the vacuolar anion channel in the liverwort Conocephalum most likely belongs to the family of vacuolar malate channels (VMAL). In contrast to terrestrial plants, anion channels in vacuoles of giant *Characean* algae conduct Cl^- from the vacuole lumen to the cytosol, are activated by an increase in $[Ca^{2+}]_{cyt}$, and display different activation kinetics.[16,17]

Only recently an Arabidopsis vacuolar malate channel has been identified as AtALMT9 (At3g18440), a member of the aluminum-activated malate transporter family[18] (ArAE, Aromatic Acid Exporter family according to www.tcdb.org/[19]). In this context it is interesting to know that anion channels in vacuoles of Conocephalum are activated by high cytosolic Mg^{2+} (Ba^{2+}, Sr^{2+}) at low Ca^{2+} concentration;[3] we are currently testing the activation by Al^{3+}. Homologs of *AtALMT9* are found in higher plants as well as in the moss *Physcomitrella patens*. In green algae no *ALMT* homolog is found in the sequenced genomes of *Chlamydomonas reinhardtii*, *Ostreococcus*

lucimarinus, *Ostreococcus tauri* or *Volvox carteri* (AtALMT1 and AtALMT9 blasted at http://genome.jgi-psf.org/euk_home.html). Comparable to the SV channel/TPC1, the vacuolar malate channel/ALMT9 seems to be a unifying characteristic of terrestrial plants (*Embryophyta*).

Vacuolar ion channels in the liverwort *Conocephalum conicum* —as characterized so far[2,3]—show an amazing similarity to vacuolar ion channels in higher plants. The further study of ion channels in the liverwort Conocephalum will help to determine the basic ion channel repertoire of terrestrial plants. These studies are likely to give insight into the fundamental evolutionary changes in ion transport that happened when plants 'moved' from water to land.

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Note Added in Proof

Pineros et al. (Plant J 2008; 53:352–67) recently reported that ZmALMT1 from Maize (*Z. mays*) conducts NO_3^-, SO_4^{2-} and Cl^-, while organic acids like malate or citrate are unlikely to permeate. With this new finding, the selectivity of the vacuolar anion channel from Conocephalum is well within the range of selectiv

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