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Letters Response

The missing link: inter-organellar connections in mitochondria and peroxisomes?

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In their review of mitochondrial redox biology in plants, Graham Noctor *et al.* [1] discuss the role of stromules (stroma-filled plastid tubules [2,3]) in the transport of metabolites and proteins between cellular compartments. In contrast to their comment that no similar extensions have been described in mitochondria, we would like to draw attention to previous research showing that such protuberances are also common to both mitochondria and peroxisomes in plants (Figure 1) ([4–7]; and see movies by Professor Brian E.S. Gunning FRS available from <http://www.plantcellbiologyondvd.com>). Indeed, such membranous extensions have been reported to be emanating from mitochondria in chick spinal cord [8], from hydrogenosomes in trichomonad species [9] and from the apicoplasts of *Sarcocystis*, an apicomplexan parasite [10]. These membranous extensions are thus a feature common to endosymbiosis-derived organelles and peroxisomes.

Logan *et al.* reported that mitochondria, in a line expressing mitochondrial matrix-targeted GFP and homozygous for a T-DNA insertion in *DRP3A* (encoding an *Arabidopsis* dynamin homologue), were larger in size and fewer in number per cell than in wild type, suggesting

that *DRP3A* is involved in mitochondrial division [5,11]. An unexpected consequence of the disruption of *DRP3A* was the increased incidence of individual mitochondria displaying narrow protrusions, usually many micrometres in length, that we named ‘matrixules’ (following the name given to stromules). Matrixules are also observed in wild-type plants, and are similar in both appearance and behaviour to the tails formed during peroxisomal elongation as described by Cutler *et al.* [4]. Using random GFP:cDNA fusion proteins to visualize subcellular structures, Cutler and colleagues showed that peroxisomes can change from a spherical to an elongate morphology in a few seconds. This process begins with the production of a short tubular tail, which then rapidly expands to become longer than the original organelle (similar morphological changes in mitochondria have been recorded, (see Refs [5,7] and supplemental movies therein). Interestingly, *DRP3A* is involved in both mitochondrial and peroxisomal division in plants [5,12]. Mutations in this gene lead to peroxisomes with extended tails or ‘peroxules’ that, in root hairs, can reach over 50 μm in length [12]. One interpretation of these data is that matrixules and peroxules might be artefacts of defective organelle division.

However, given that (i) matrixules, peroxules and stromules are commonly found in wild-type plants, (ii) membranous protuberances are common to other endosym-

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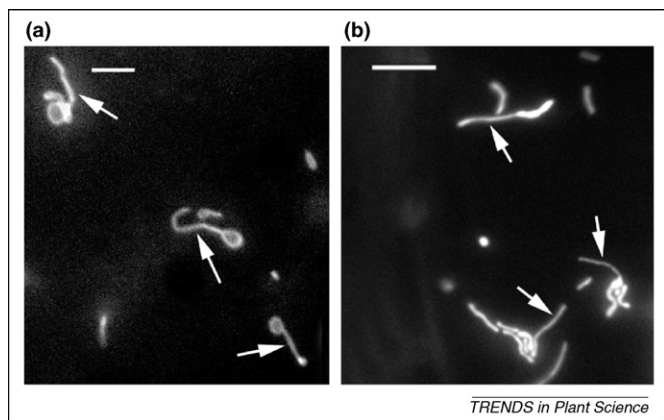


Figure 1. Epifluorescence micrographs of matrixules and peroxules in leaf epidermal cells of stable-transformed *Arabidopsis* plants (ecotype Columbia) expressing mitochondrial-target GFP [15] or PEX10-eYFP [7], the plants are otherwise wild type. (a) Peroxisomes visualized by the expression of membrane localized PEX10-eYFP. (b) Long matrixules in *DRP3A* T-DNA knockout line, mitochondria visualized by expression of mito-GFP. Arrows indicate protuberances. Scale bars = 5 µm.

biosis-derived organelles [9,10], and (iii) stromules are postulated to play a role in metabolite transport by increasing plastid surface area, a more intriguing possibility is that all these structures are involved in similar processes. For example, during photorespiration, there is a highly coordinated transfer of metabolites between chloroplasts, peroxisomes and mitochondria [13]. In sublethal mutants of *PEX10* (which is involved in peroxisome biogenesis) a loss of physical contact between chloroplasts and peroxisomes has been linked to photorespiratory defects, indicating that the shuttling of metabolites is aided by the juxtaposition of organelles [14]. Short-term increases in the surface area of all three organelles through the formation of tubules, perhaps even transient physical interactions between the respective tubules, might increase the efficiency of inter-organelle metabolite transfer. Furthermore, it is possible that these membranous protuberances have more than one function and that one of these (in mitochondria and plastids) might be analogous to the role of the filamentous pili involved in bacterial conjugation – namely the transfer of genetic material.

As Noctor *et al.* stated, much remains to be discovered regarding physical interactions between organelles [1]. We

do not think it unreasonable to imagine that knowledge of stromules, peroxules and matrixules will improve our understanding not only of basic cellular compartmentalization, but also of plant biochemistry, organelle genetics, and of the mechanisms by which plants interact with their environment.

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Shape-shifters building bridges? Stromules, matrixules and metabolite channelling in photorespiration

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mitochondrial structures that could be partly homologous to chloroplast stromules, which were mentioned in our recent review [1]. The description of such structures in mitochondria is a potentially exciting development, and we acknowledge the term ‘matrixule’ introduced by Logan

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