8 First Fossil Record of Transfer Cells in Angiosperms [7]

Abstract

Transfer cells are specialised plant cells, which optimise short-distance transport by an extension of the interior surface of the cell walls. Using scanning electron microscopy, we found transfer cells in the fossil seed coat of † *Ehretia clausentia* (Ehretiaceae, Boraginales) from the London Clay flora (Lower Eocene). This is the first fossil record of transfer cells in angiosperms.

Transfer cells are specialised plant cells that improve the short-distance transport of soluble substances, especially across tissue boundaries. Transport is optimised by a surface-extension of the plasma membrane on numerous cell wall ingrowths in the form of pins or nets or spongiose structures, which are easy to identify under the SEM or TEM and are even visible under high resolution LM. Transfer cells are highly polar in their organisation; the characteristic ingrowths usually develop on one face of the cell only.

Since their first general description (GUNNING & PATE 1969), transfer cells have been observed in various tissues of embryophytes, e.g., the xylem and phloem, in haustoria of parasitic plants, in seeds, and in the placental region connecting the gametophyte and the sporophyte of archegoniate plants (gametophyte-sporophyte junction: FREY *et al.* 2001). The widespread presence of transfer cells underscores the importance of these cells in numerous structural and physiological contexts. They developed several times independently in various plant groups.

Based on the occurrence of transfer cells already in basal land plants (such as mosses and ferns), they may have arisen early in plant evolution (almost in the Silurian: FREY *et al.* 2001), possibly as a structure to bridge tissue boundaries required by living in a nonaqueous environment. However, no fossil evidence of those cells had been reported for any plant group.

Transfer cells form the seed coat and are also found along the funicle in Cordiaceae, Ehretiaceae, Heliotropiaceae, and some Hydrophyllaceae *s.str.* (Figs. **8-3**, **8-5**), but not in Boraginaceae *s.str.* In the course of a larger survey on Boraginales (DIANE et al. 2002b) we also investigated *Ehretia* fossils (endocarp remnants, Figs. **8-1** and **8-2**, **8-4**) from the London Clay flora deposited in the Natural History Museum (London, UK). We clearly observed transfer cells in the fossilised seed coat of † *Ehretia clausentia* (NHM PV.34572; Ehretiaceae, Boraginales; CHANDLER 1961, 1964) from the Lower Eocene (about 50 million years old) of southern England (Figs. **8-6** and **8-7**). In

[7] Short Communication accepted as **GOTTSCHLING M** & HH HILGER (subm.): First fossil record of transfer cells in angiosperms. Amer J Bot

Own contributions: Investigation of the fossils, writing manuscript, photographs, drawing.

position and structure, they are indistinguishable from those of extant species (e.g., *Ehretia macrophylla*, Fig. **8-8**).

The preservation of such anatomical detail is very rare and only possible under particularly favourable conditions. The Paleogene London Clay flora was preserved by rapid burial in marine systems and is therefore known as a source of high quality fossils (CHANDLER 1961, 1964, COLLINSON 1983). The typical London Clay flora is mainly pyritic, while the material from Nursling (locality of the investigated fossils of † *Ehretia clausentia*) is almost entirely carbonaceous (COLLINSON 1983). The importance of the London Clay flora is underscored by the evidence presented here on the exceptional preservation of intracellular detail. In this particular case, the excellent condition is certainly partly due to the hard endocarp of † *Ehretia clausentia*, which protected the seed coat before and during fossilisation.

Precise systematic placement of fossils (especially plant fossils) is often difficult or even impossible, especially when unambiguous cellular characters are lost during fossilisation. In this case, however, presence, position, and structure of the fossil transfer cells lend additional support to the systematic position of † *Ehretia clausentia* in the *Ehretia* II subclade (GOTTSCHLING *et al.* 2002). The fossil transfer cells together with the formerly multilayered, sclerenchymatic endocarp support that † *Ehretia clausentia* is a representative of the Primarily Woody Boraginales (Heliotropiaceae, Cordiaceae, Ehretiaceae, also including parasitic Lennoaceae) that are closely allied based both on morphological (DIANE *et al.* 2002b) and on molecular data (GOTTSCHLING *et al.* 2001, GOTTSCHLING & HILGER in prep.).

The possible functions of transfer cells have been discussed recently (FREY *et al.* 2001, THOMPSON *et al.* 2001, Diane *et al.* 2002b). Nutrient transfer, herbivore deterrence, and water uptake and transfer have all been proposed. In the Primarily Woody Boraginales, the seeds are protected by a hard and multilayered endocarp (Figs. **8-3**, **8-5**). The seed coat of transfer cells may act here as a wick ensuring rapid water uptake *via* the funicle (DIANE *et al.* 2002b): the swelling seed coat and embryo then rupture the hard endocarp along preformed lines of structural weakness.