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FROM THE ARCHIVES

Obituary: Eberhard Schnepf (April 4, 1931–April 10, 2016)

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Eberhard Schnepf was born in Nürnberg, Germany, on April 4th, 1931 and spent his youth as the oldest son of a farmer in Barnstorf, a small village south of Wolfenbüttel, Lower Saxony. As he wrote in his CV, the lovely environment around the village inspired him early to become a botanist. He finished school in Wolfenbüttel in 1950 in an apparently unusually good school class of which the mates remained close friends all over his life His parents persuaded him to learn something "decent" before studying at university. Therefore, he was examined as a gardener after a two years' apprenticeship in a nursery for ornamental plants in Einbeck, Lower Saxony. After this, he spent a few months at the Max Planck Institute for Plant Breeding in Voldagsen southwest of Hannover, which later moved to Cologne. This short internship in Voldagsen (later frequently repeated during semester breaks) apparently deeply influenced his later scientific development. He became interested in phytopathology and learned how jostaberry, a tasty hybrid between black currant and gooseberry, was generated by Dr. Rudolf Bauer at the institute at that time.

In the winter of 1952 Eberhard Schnepf began to study biology, chemistry and physics at the LMU Munich. After two years there he enrolled at the University of Bonn with the intention to develop a career in phytopathology. The chair of botany in Bonn was then occupied by Walter Schumacher who was one of the leading plant physiologists of that time and known to many botanists mostly as the author, over many years, of the physiology chapter in Strasburger's Textbook of Botany. Schumacher attracted many students for Ph. D. theses of which a large number later became professors at German universities. Eberhard Schnepf finished his Ph. D. under the guidance of Schumacher in 1958 with a microscopic study of plant ectoplasmodesmata which already revealed his extraordinary high analytic capability and skills to analyse complex cell structures and their function and development.

Immediately after his thesis, Eberhard Schnepf accepted an assistantship (equivalent to a non-tenured junior faculty member) at the Botanical Institute of the University of Marburg. Here, and later in other positions, he worked on various basic cell biological topics of plant biology such as the structure and function of microtubules and the cytoskeleton, the role of the Golgi apparatus in secretion by plant glands, membrane traffic, cell wall growth in tip-growing cells, structure and development of the endoplasmic reticulum, differentiation and effects of phytohormones on caulonemata of mosses, interactions of diverse organisms in symbioses including endosymbioses and parasitism and many more. This extremely broad approach stimulated Schnepf's critical mind to analyse complex cytological issues by careful microscopical observations using a comparative approach which led him to fundamental insights.

Eberhard Schnepf (Fig. 1) is perhaps best-known for the formulation of his "compartmentation rule" in 1964. According to it, the function of a biological membrane in cells is to separate a plasmatic from a non-plasmatic phase. A substance that needs to

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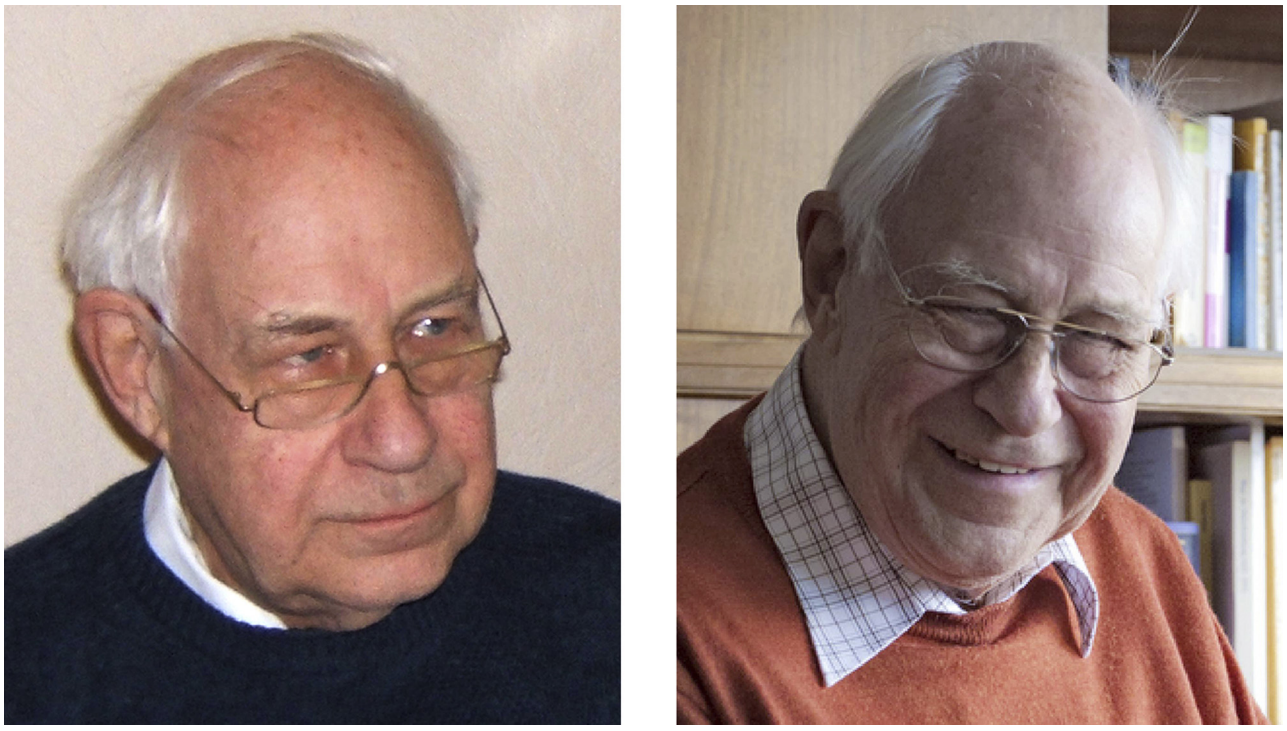

Figure 1. Two images of Eberhard Schnepf. The left (taken by H. Bothe in 2005), the right more recently (courtesy of Augustinum/Christian Topp, modified).

be transferred from one plasmatic phase to another always has to pass two membranes and a non-plasmatic phase; the reverse is true for transport from one non-plasmatic phase to another (in which case again two membranes but in this case a plasmatic phase has to be crossed). Only the plasmatic phases contain nucleic acids. Fusions or vesiculations can only occur between the same phases. Non-plasmatic phases mix frequently by vesicular flow related to metabolism and cell growth, whereas plasmatic phases mix infrequently related cell fusion and division. The compartmentation rule also explained neatly the asymmetric structure and composition of the lipid bilayer in a biological membrane as one surface is exposed to a non-plasmatic phase, the other to a plasmatic phase. The compartmentation rule was, surprisingly, only published in chapters of proceedings volumes, but was well accepted once it found its way into the well-known German textbook on cell biology by Kleinig and Sitte (1984). Although the biological significance of the theorem was initially not well understood, it later became clear that it can be traced to the evolution of fusion and vesiculation processes (exo- and endocytosis) at the plasma membrane in a proto-eukaryote cell. This would then also explain the evolution of phagocytosis and eventually the endosymbiotic origin of mitochondria and plastids. The non-plasmatic phase in a compartmentalized eukaryotic cell in this view represents the former aqueous external environment of the cell that was incorporated into the cell during evolution by endocytosis. It is unfortunate that Schnepf's compartmentation rule, a milestone in the field of classical cytology and one of the very few examples of a biological theorem did not find its way into English-language textbooks of cell biology. At the authors' institution it is currently compulsory teaching for 1st year biology undergaduates (Fig. 2).

Eberhard Schnepf was innovative when it came to using novel microscopical equipment or techniques (he was one of the first in Germany to introduce transmission electron microscopy, freeze-fracture techniques and confocal laser scanning light microscopy), but he did not move into biochemical or molecular cell biology; there was no automatic pipette, no electrophoresis apparatus or PCR machine in his laboratory. He can be regarded as the last cytologist.

In Marburg, Schnepf had close contact to two leading German botanists of that time, Hans-Adolf von Stosch (1908-1987), an internationally renowned phycologist, and Horst Drawert (1910-