

THE DISCOVERY OF TYLOSE FORMATION BY A VIENNESE LADY IN 1845

by

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Introduction

This fascinating detective story began a few years ago when I was working on a chapter entitled 'Dysfunction in the flow of food' for a five-volume treatise on plant pathology (Zimmermann & McDonough, 1978). Tyloses, occasionally regarded as causing interruption of water flow in the xylem, are more likely the result of cessation of water conduction (Klein, 1923). During a search for older literature on tyloses I came across the paper of Wieler (1888), and found in the same volume an article by Praël (1888). The latter contained a very peculiar paragraph. Freely translated, it reads as follows:

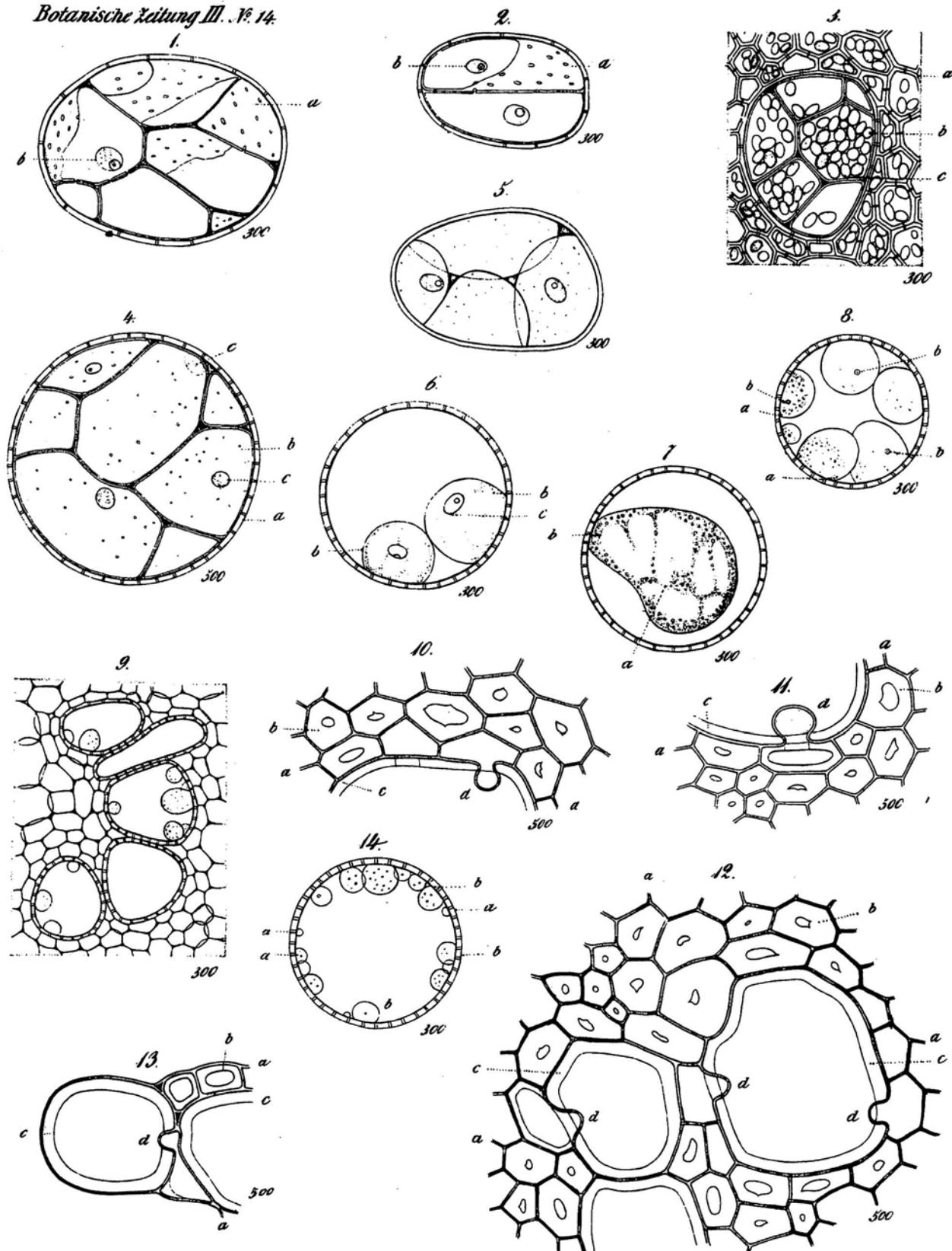
'Tyloses formation has been explained by an anonymous paper in 1845. His (correctly her) observations indicated that tyloses were outgrowths, through the pits, of neighboring wood parenchyma cells. This was generally accepted until it was questioned by Böhm who maintained that 'those peculiar structures are the result of accumulation of cytoplasm between the lamellae of the vessel wall, whose innermost layer grows into a tylosis.' However, Reess (1868) and Unger (1867) defended the earlier view successfully.'

The German grammar (here translated by 'his' and 'her') implies that the author was a lady. I immediately went to the library of the Harvard University Herbaria to look up Volume 3 of the 'Botanische Zeitung' where, indeed, I found an anonymous paper, published in two parts in two successive issues. Interestingly, the wording 'von einem Ungekannten' (by an anonymous author) implies a male author. My fascination increased as I read the text: here was such a comprehensive description of tyloses, based on such careful observations that many later papers seemed redundant. Who was the author of this? After a long search I finally came across the answer in the 'Physiological Plant Anatomy' of Haberlandt (1914) who begins his section on tyloses, 'These intrusive vesicles, the development of which was first studied and explained by Hermine von Reichenbach, are known as tyloses.' In the bibliography Haberlandt cites the paper under the name

Reichenbach, followed by the words 'published anonymously'. So, the name was found, but two questions remained, (1) who was Hermine von Reichenbach, and (2) why did she publish anonymously?

Anyone interested in the history of botany will consult Julius Sachs (1875, 1890). But Sachs, it turned out, does not mention her. So, I went to the stacks of the Harvard University Herbarium Library, settled down in the history section and went through all likely books. There was a Heinrich Gottlieb Ludwig Reichenbach (1793–1879), Professor in Dresden, who published a 'Conspicetus regni vegetabilis' in 1828 (Möbius, 1937). There was also a father and son, Gustav Reichenbach who published on phanerogams in 1820 (Jessen, 1864). I originally suspected that Hermine might be the daughter of one of these botanists. But then, finally, I discovered her real identity in Winckler (1854) who mentions 'Hermine, Baroness von Reichenbach of Vienna' who had published, also anonymously, on laticifers (Reichenbach, 1846). The story had taken a new twist: maybe her papers were published anonymously not because, as a woman, the author was not permitted to publish, but because as a baroness she might not have wanted to use her name. At this point, the sources of the Harvard University Herbarium Library were obviously exhausted and to make further progress, the search had to be continued in Vienna. Fortunately, the author has a good friend in Vienna whose help was successfully solicited.* Before we go further into this, let us have a look at Reichenbach's (1845) paper on tyloses, which has some surprises to offer.

* Dr. Peter Ruckenbauer of the Institut für Pflanzenbau und Pflanzenzüchtung, Universität für Bodenkultur. The biographical material, given at the end of this paper, has been found by Drs. Birgit and Robert Kartusch of the Botany Department of the same university. In spite of considerable efforts on their part, no picture of Hermine von Reichenbach could be found. Their help is greatly appreciated.



Summary of Reichenbach's paper, *Investigations on the cell-like structures that fill some vessels.* (The original illustrations, reproduced here, are re-arranged to fit the IAWA Bulletin page size).

In many plants cell-like structures fill the lumen of vessels more or less as soon as these have reached a certain age. This phenomenon had been described earlier by Malpighi, Leeuwenhoek, Spengel, Kieser and Mirbel. Meyen gave a historical survey of earlier reports and added his own observations. Many authors considered these vesicles to be separate entities, without contact with each other and with neighboring cells. Schleiden, Endlicher and Unger made little progress, the origin of these little 'bubbles' remained unknown. There follows a long list of plants, including several tropical and subtropical species, the vessels of which show the phenomenon. However, it has never been observed in the tracheids of conifers.

A detailed description follows, based upon the author's own observations in many species. The size of these structures varies considerably, even within one vessel. They look like real cells, in some plants they are thin-, in others thick-walled. Where they touch there are pit pairs between them, where one can clearly distinguish a primary and secondary wall. The slight unevenness of the wall thickness is exactly like von Mohl describes it for parenchyma cells. They contain variable amounts of starch, depending on the species. They also contain the substance that von Mohl calls 'Primordialschlauch' (cytoplasm) which is characterized by certain staining reactions and shows plasmolysis under the influence of certain solutions. Brownian movement can be seen clearly. In many plants the nucleus and nucleolus can be observed suspended in the cytoplasm, either freely within the cell lumen, or next to the wall. The cytoplasm shows streaming, particularly clearly in *Cucurbita*. The conclusion is inevitable: these are real cells.

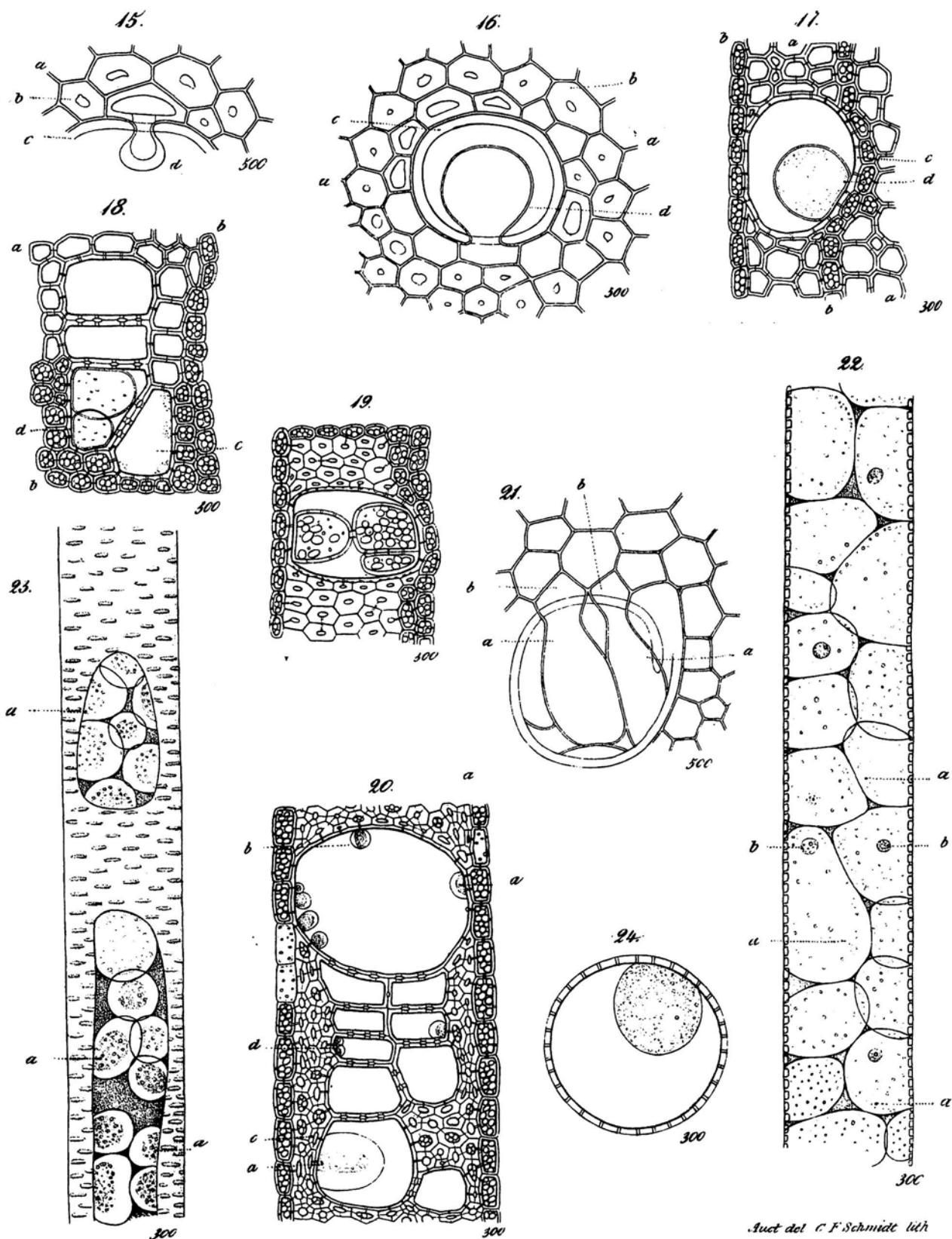
A description of a series of observations follows, beginning in the summer and continuing throughout autumn and winter. In a four-year-old

Robinia branch, for example, all of this year's vessels are open, all older vessels are completely filled. Formation of these cells in the current year's vessels begins in October and is completed in December. One-year-old twigs behave like this year's growth ring of older branches. Several other species have been investigated and found to behave similarly. Young cells are always attached to the vessel wall where axial or radial parenchyma cells are, never next to an adjacent vessel element; there is no doubt that they originate from pits. Thinner sections finally revealed that the growing cell is part of the neighboring cell. Sections of *Vitis vinifera* and *Sambucus nigra* show this particularly well, especially when treated with KOH solution. The author concludes that these vesicles are parts of the neighboring cells.

The second part of the paper begins with the suggestion of the name 'Thylen' (tyloses), deriving from the Greek word θύλλις, meaning bag, or container. A very detailed description of tyloses development then follows; the author takes pride to be working with the most modern and excellent microscope made by Plössl (Fig. 25). The range of plants inspected is remarkable, it includes not only European species, but 'exotic' ones such as *Musa* and *Strelitzia* as well. A budding tylosis is first very transparent, eventually cytoplasm can be identified (staining brownish-yellowish with iodine). Starch grains, nucleus and nucleolus appear later. A more detailed description of cytoplasmic streaming, staining and plasmolysis experiments then follows. Nuclei and cytoplasm eventually disappear with age.

During formation of a tylosis, the primary wall does not get thinner, it is therefore not merely stretched, but actually grows. When different tyloses in a vessel element finally touch each other and cannot expand any further, secondary wall formation begins and neighboring tyloses develop pit pairs. Pits never appear between tyloses and vessel walls. The tylosis and its mother cell remain a unit and do not separate. Starch is always found in quantities corresponding to starch quantities in other, nearby tissue.

Legends to Figures 1–14 of the original plate of Reichenbach's paper. — Figs. 1, 2. Transverse sections of two vessels of *Robinia pseudacacia*. a. Walls of the tyloses with pits and pit canals. b. Nuclei. — Fig. 3. Transverse section of the innermost growth ring of a four-year-old grape stem, stained with iodine. a. Wood (parenchyma) cells. b. Vessel. c. Tyloses, containing starch. — Fig. 4. Transverse section of a vessel of *Cucurbita pepo*. a. Vessel wall. b. Tyloses with cytoplasm. c. Nuclei. — Fig. 5. A tylose-filled vessel of *Strelitzia reginae*. — Figs. 6, 7. Two vessels of *Cucurbita pepo*. b. Tyloses with cytoplasmic streaming. c. Nuclei. — Fig. 8. A vessel from the same plant with young tyloses. a. Cytoplasm (plasmolized). b. Nucleoli. — Fig. 9. Transverse section from *Cucumis sativus*. — Figs. 10, 11. Transverse sections of one-year-old shoots of *Vitis vinifera*. a. Primary cell walls. b. Secondary cell walls of wood parenchyma. c. Secondary vessel wall. d. Young tyloses with their respective mother cells. — Figs. 12, 13. Transverse sections of one-year-old shoots of *Sambucus nigra*, treated with KOH. Legend as in Fig. 10. — Fig. 14. Vessel of *Cucurbita pepo*. a. Very young, translucent tyloses. b. Somewhat older tyloses with granular content (cytoplasm).



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The author concludes that tyloses develop when the vessels are air filled, they appear in the fall after cessation of water conduction. They remain in contact with their mother cells because they cannot get any water or nutrients from the vessels. A similar phenomenon, but unrelated, is that in some plants non-functional vessels are filled with gum ('körniger Schleim'), which oozes through the pits into vessels. When a gum deposit is followed along the vessel in serial sections, its origin can almost invariably be traced to a wound. Tyloses are produced by thin-walled parenchyma cells that have only primary and, at most, very little secondary wall. The mother cells are axial or radial parenchyma. Tyloses are usually found in pitted vessel members, rarely in elements with ring- or spiral-shaped secondary wall.

The paper concludes with a description of the course of vascular bundles in the *Cucurbita* stem. General comments about the origin of plant cells then follow, the logic of which is somewhat difficult for us to follow today. It is obviously not easy for us 20th century biologists to judge these general remarks fairly, without studying the knowledge and philosophies of the time. Taking the paper for what it is, namely a description of the most careful and detailed original observations, the reader is left with the greatest admiration. Most impressive perhaps is the clear recognition that tyloses formation and gum production are the result (not the cause) of the cessation of water conduction (or of injury), an observation that only much later found firmer experimental support (e.g. Klein, 1923).

A brief biography of Hermine von Reichenbach

Hermine's father, Karl Ludwig (1788–1869), came from a middle-class family of surgeons, civil servants, etc. He was a very colorful personality. Right at the outset of writing about Hermine, one runs into the danger of having her overshadowed by her father, as it probably happened during her lifetime. Karl Ludwig studied the natural sciences and married Frederike Luise Erhard, the daughter of a wealthy Stuttgart book dealer. He traveled widely during his studies and did extensive work on charcoal manufacture whereby he isolated and

described wood distillates, such as paraffin and creosote. His interests ranged very widely; he worked on steel production (e.g. the manufacture of railroad tracks), collected and studied meteorites and even tried to cultivate silk worms. The King of Württemberg made him a Baron in 1839. Later in his life he became quite interested in spiritualism and made considerable efforts to investigate and describe some of the obscure phenomena scientifically, thereby causing endless controversies.

Hermine was born on September 5, 1819, as the fourth child and second daughter of a family to which, three years later, a fifth child was added. Her mother died on May 11, 1835 when Hermine was fifteen. We have not been able to find out where she studied, but it is safe to assume that she was stimulated by her father's love for natural history. She was twenty years old when her father became a Baron, thus becoming a Baroness herself. She published her tylosis papers at the age of twenty-six, and her papers on laticifers at twenty-seven. On November 11, 1849, she married Karl Schuh. She seems to have discontinued her studies at this point, at least no further publications are known to us. Her husband died fourteen years later and she spent the rest of her life as a widow.

Two more entries in botanical journals have come to our attention. The first is a note in Bot. Z. 7: 104 (1849), where she is listed as one of eleven corresponding members admitted to the Royal Botanical Society of Regensburg during the years 1847 and 1848. In addition, seven regular members are listed. The second entry was found in Flora 61(4): 64 (1878), in 'Kurze Mittheilungen' (brief notes) prepared by M. Göppert of Breslau (now Wroclaw, Poland). The paragraph is entitled 'Honor to whom honor is due' and reveals the identity of the author of the articles on tylosis and laticifers. But Göppert knows neither if any further publications exist and if she continued her botanical studies at all. He appeals to his Viennese colleagues for further information. He praises her for having assembled a very rich herbarium collection and being very knowledgeable in systematic botany.

Legends to Figures 15–24 of the original plate of Reichenbach's paper. — Figs. 15, 16. Transverse sections from *Vitis vinifera*, treated with KOH. a. Primary cell walls. b. Secondary cell walls of wood parenchyma. c. Secondary vessel wall. d. Young tyloses with their respective mother cells. — Figs. 17, 18. Transverse sections of *Juglans regia*. a. Wood (parenchyma) cells. b. Ray parenchyma. c. Vessels. d. Tyloses. — Fig. 19. Transverse section from *Quercus robur*; tyloses containing starch. — Fig. 20. Transverse section of a one-year-old shoot of *Robinia pseudacacia* with young tyloses and (a) plasmolyzed cytoplasm. — Fig. 21. Transverse section of the stem of *Strelitzia reginae*. Vessel with spiral thickening, filled with tyloses. a. Tyloses, with their mother cells (b). — Figs. 22, 23. Two vessels of *Cucurbita pepo* in longitudinal section. a. Cytoplasm of the tyloses. b. Nuclei. Both are from a stem which had been fixed in alcohol (brandy!) for a longer period of time. — Fig. 24. Transverse section of a vessel of *Cucurbita pepo* with a tylosis and appearing nucleus.

The elusive question why she published her papers anonymously remained unanswered. The earlier suspicion that, as a baroness, she might not have wanted to use her name is almost certainly wrong, because her father published so many papers and books. A possible clue may be the one I found in a recent article about the history of the 'Allgemeine Forst- und Jagdzeitung' (published

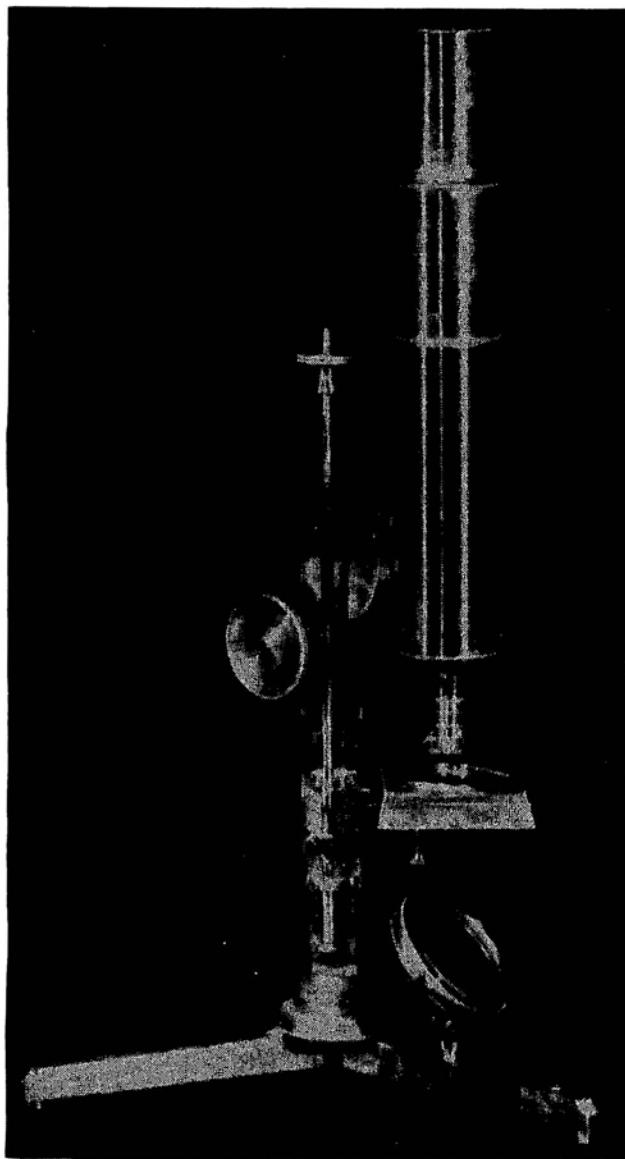


Fig. 25. A microscope by the Austrian maker Simon Plössl (1794–1868) in the collection of the Department of Plant Physiology, University of Vienna. An article describing the historical importance of Plössl has been published by Patzelt (1947).

by Sauerländer, Frankfurt am Main, Germany) which now celebrates its 150th year of existence (Hasel, 1979). It is a forestry journal, but botanists may remember that much of Theodor Hartig's work on forest botany was published there during the mid-19th century. Th. Hartig is, of course, best known for the discovery of the sieve tubes. Hasel (1979, page 2) makes the following statement about the early days (before 1850). 'As was customary at the time, authors remained often anonymous. Anonymousness was not even lifted in the case of controversy so that a quarrel had to be carried out against an unknown or suspected opponent. Only well-known authorities signed their articles.' (Free translation by this writer). This may be the very simple answer to our seemingly elusive question.

References

- Göppert, M. 1878. Kurze Mittheilungen. *Flora* 61(4): 63–64.
- Haberlandt, G. 1914. Physiological Plant Anatomy. (Translated from the 4th German edition by M. Drummond). MacMillan & Co., London.
- Hasel, K. 1979. Zum Erscheinen des 150. Jahrgangs der Allgemeinen Forst- und Jagdzeitung – ein geschichtlicher Rückblick. *Allg. Forst- u. Jagdztg.* 150: 2–9.
- Jessen, K.F.W. 1864. Botanik der Gegenwart und Vorzeit. Brockhaus, Leipzig.
- Klein, G. 1923. Zur Aetiologie der Thyllen. *Z. Botanik* 15: 418–439.
- Möbius, M. 1937. Geschichte der Botanik von den Anfängen bis zur Gegenwart. Fischer, Jena.
- Patzelt, V. 1947. Die Bedeutung des Wiener Optikers Simon Plössl für die Mikroskopie. *Mikroskopie* 2: 1–12.
- Praöl, E. 1888. Vergleichende Untersuchungen über Schutz- und Kernholz der Laubbäume. *Jb. wiss. Bot.* 19: 1–81.
- Reichenbach, H. von (Anonymous). 1845. Untersuchungen über die zellenartigen Ausfüllungen der Gefässe. *Bot. Z.* 3: 225–231, 241–253.
- (Anonymous). 1846. Die Milchsaftgefässe, ihr Ursprung und ihre Entwicklung. *Bot. Z.* 4: 833–843, 849–859, 856–872.
- Sachs, J. 1875. Geschichte der Botanik. Oldenbourg, München.
- 1890. History of Botany. (English translation by H.E.F. Garnsey, revised by I.B. Balfour). Clarendon Press, Oxford.
- Wieler, A. 1888. Ueber den Anteil des secundären Holzes der dicotyledonen Gewächse an der Saftleitung und über die Bedeutung der Anastomosen für die Wasserversorgung der transpirierenden Flächen. *Jb. wiss. Bot.* 19: 82–137.
- Winckler, E. 1854. Geschichte der Botanik. Literarische Anstalt (J. Rütten), Frankfurt.
- Zimmermann, M.H. & J. McDonough. 1978. Dysfunction in the flow of food. In: *Plant Disease. An Advanced Treatise*. Vol. 3: 117–140 (J.G. Horsfall & E.B. Cowling, eds.). Academic Press, New York.