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A somewhat obscure discoverer of plasmodesmata: Eduard Tangl (1848–1905)

IN MORTON'S TREATISE *History of Botanical Science* there is short information on Tangl: "a somewhat obscure professor of botany in Czernowitz",[1] a paraphrase of which is the title of our presentation.

Published papers on Tangl are not numerous. The earliest one, which we have found, is in Wurzbach's *Biographisches Lexikon des Kaiserthums Oesterreich* [...] [2] The next one is Tangl's short biography by Haberlandt.[3] Some data are included also in papers by Norst [4] and Skrzyński.[5]

Archival sources concerning Tangl are preserved mainly in: Archiwum Główne Akt Dawnych [The Central Archives of Historical Records, Warsaw], Deutsche Akademie der Naturforscher Leopoldina-Archiv, L'vovskiy oblgosarkhiv [State Archives in Lviv] and Chernivskiy oblgosarkhiv [State Archives in Chernivtsi]. We have published short biographies of Tangl based on the sources mentioned above.[6] Our presentation delivered during the conference was only another version of these published biographies.

Eduard Tangl was born on 20 March 1848 in Lemberg / Lwów (then: the capital of Galicia, which was the then name of the southern part of Poland under Austrian rule; now: Lviv, Ukraine). The Tangl family had come from Wolfsberg, Kärnten, in Austria. Andreas Tangl, Eduard's father, was a physician at the provincial prison in Lemberg. He had a predilection for natural sciences and was an excellent connoisseur of the Galician flora. Eduard's mother was Anna née Frank. Eduard Tangl had two main areas of interest in his youth: botany and music. Initially the latter predominated. He composed music. His *Requiem* was even rendered in one of Lemberg's churches. After his *matura* (i.e., secondary school-leaving examination) he studied botany at Lemberg University (1865–1869). When he obtained his own microscope, he turned his interest to plant anatomy. Eduard Tangl's tutor was professor Gustaw Adolf Weiss (1837–1894), an anatomist and plant physiologist. In 1870, Eduard Tangl gained a doctorate of philosophy in botany at Lemberg University. A year later, in 1871, he habilitated (in German and Austro-Hungarian universities one had to qualify after the doctorate before obtaining the Dozent post) at the Faculty of Philosophy, Lemberg University, on the basis of his treatise *Beitrag zur Kenntniss der Perforationen an Pflanzengefässen.*[7] Until the end of the academic year 1875/1876 he worked at Lemberg University as a *Privatdozent* of plant anatomy. At the same time, in 1874–1876, he

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[1] A. G. Morton (1981), *History of Botanical Science. An account of the development of botany from ancient times to the present day* (London – New York – Toronto – Sydney – San Francisco: Academic Press), pp. XI + 474.

[2] C. v. Wurzbach (ed.) (1881), *Biographisches Lexikon des Kaiserthums Oesterreich* [...] (Wien), vol. 43, p. 55.

[3] G. Haberlandt (1905), "Eduard Tangl", *Berichte der Deutschen Botanischen Gesellschaft* 23, p. (16)–(20).

[4] A. Norst (1900), *Alma mater Francisco-Josephina. Festschrift zu deren 25-jährigem Bestande* (Czernowitz), pp. 134.

[5] S. Skrzyński (1894), *Część II. Historya Uniwersytetu Lwowskiego 1869–1894*, [in:] L. Finkel, S. Skrzyński: *Historya Uniwersytetu Lwowskiego* (Lwów), pp. 351 + 442.

[6] P. Köhler (2004), "Leksykon Botaników Polskich. Dictionary of Polish botanists. Edward Tangl", *Wiadomości Botaniczne* 48(3/4), p. 108–112; P. Köhler, D. J. Carr (2006), "Eduard Tangl (1848–1905) — discoverer of plasmodesmata", *Huntia* 12 (2), p. 169–172.

[7] E. Tangl (1871), "Beitrag zur Kenntniss der Perforationen an Pflanzengefässen", *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften* (Wien), Abt. 1 63, p. 537–548.

was employed at the School of Farming (Szkoła Gospodarstwa Wiejskiego) in Dublany near Lemberg as a professor of agricultural chemistry and botany. In those years Eduard Tangl took active part in the Polish scientific movement. Although he was not one of the founders of the Polish "Copernicus" Society of Naturalists, established in 1875, Tangl contributed to the initial process of organising the society.

K.k. Franz-Josefs-Universität in Czernowitz, Bukowina (now: Chernivtsi, Ukraine) was established in 1875 by a decree of Francis Joseph I, emperor of the Austria-Hungary. Eduard Tangl was nominated as an extraordinary professor of botany on 23 July 1876, and ordinary professor of botany and pharmacognosy on 14 July 1881. The post gave him the long awaited financial stability. He took up his duties at Czernowitz University in the autumn of 1876. His duties included lecturing on all branches of botany and pharmacognosy of the day. He also had to establish a botanical garden and a botanical institute. The following year, in the spring of 1877, work on establishing both the garden and institute was launched. Eduard Tangl was the first director of the Czernowitz University Botanical Garden and the Botanical Institute, managing both between 1877–1905. Beside his work at the university he took on other duties: from 1877 on he was a member of the Examination Commission for College Teachers (K.k. Prüfungs-Commission für Candidaten des Gymnasial-Lehramts) in Czernowitz.

Eduard Tangl published at least 14 works: the first one in 1871, and the last in 1886. Most of them were devoted to the anatomy and cytology of plants. During the Lemberg / Lwów period of his life he published 6 papers, and during his stay in Czernowitz — 8. In 1879, when he was only 31, Tangl made a discovery, thanks to which he entered the annals of history of botany. He observed intercellular strands of cytoplasm connecting cells in cotyledons of *Strychnos nux-vomica*,[8] and then in endosperm of seeds.[9] This observation was his greatest discovery. In the 1880s he became a member of three learned societies: Deutsche Botanische Gesellschaft in Berlin, Kaiserlich Leopoldinisch-Carolinische Deutsche Akademie der Naturforscher in Halle, and K.k. Zoologisch-botanische Gesellschaft in Vienna. After 1885 he became inactive and his weakness kept him from further research. His efforts connected with establishing the Botanical Garden and the Botanical Institute of Czernowitz University had ruined his health. Despite his condition he continued lecturing. As a lecturer he gained the esteem and affection of his students, who appreciated his efforts and the clarity of his lectures. After 1885 he devoted himself almost entirely to music. Eduard Tangl died on 9 July 1905 in Czernowitz. His activities were a major contribution to botany in Bukowina.[10]

The first published paper of Eduard Tangl was his habilitation treatise on perfotations of cell walls.[11] Tangl led his research on perforations also during the next years. In 1880 Tangl published a series of observations on the cytoplasmic connections between cells of the endosperm of certain seeds.[12] Initially, it was an accidental observation during a research of the influence of organic pigments on cellulose cell walls. Tangl's own drawings, made no doubt using the improved drawing apparatus that he had described in a publication dated 1873, have been widely reproduced. Tangl come back to the problem of plasmodesmata yet in his two further papers, published in 1884 and 1885. In the first one he focused mainly on the existence of the plasmodesmata in lateral and transversal walls of *Allium*

[8] E. Tangl (1880), "Ueber offene Communicationen zwischen den Zellen des Endosperms einiger Samen", *Jahrbücher für Wissenschaftliche Botanik* 12, p. 170–190.

[9] E. Tangl (1884), "Zur Lehre von der Continuität des Protoplasmas im Pflanzengewebe", *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften* (Wien), Abt. 1 90, p. 10–38; E. Tangl (1885), "Studien über das Endosperm einiger Gramineen", *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften* (Wien), Abt. 1 92, p. 72–109, tabl. I–IV.

[10] G. Haberlandt (1905), "Eduard Tangl", *Berichte der Deutschen Botanischen Gesellschaft* 23, p. (16)–(20); P. Köhler (2004), "Leksykon Botaników Polskich. Dictionary of Polish botanists. Edward Tangl", *Wiadomości Botaniczne* 48(3/4), p. 108–112; P. Köhler, D. J. Carr (2006), "Eduard Tangl (1848–1905) — discoverer of plasmodesmata", *Huntia* 12(2), p. 169–172.

[11] E. Tangl (1871), "Beitrag zur Kenntniss der Perforationen an Pflanzengefässen", *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften* (Wien), Abt. 1 63, p. 537–548.

[12] E. Tangl (1880), "Ueber offene Communicationen zwischen den Zellen des Endosperms einiger Samen", *Jahrbücher für Wissenschaftliche Botanik* 12, p. 170–190.

cepa (onion) peel epidermis cells.[13] In the latter paper he stressed the importance of plasmodesmata for conducting matter in plants: enzymes and products of their activities.[14] The strands of cytoplasm observed in these experiments were interpreted by him as plasmical connections between protoplasts. He concluded it from the fact that the examined cells were on the way of intensive transport of nourishing substances.

The result of Tangl's observations led to a change in our concept of the plant entity. Those observations should earn a place for himself in the pantheon of distinguished plant scientists. Botany students learn about these connections, which have been found in all classes of plants and plant tissues, under the name given to them, "plasmodesmata", by Strasburger in 1901.[15] The full elucidation of the nature of the intercellular connections had to await the advent of electron microscopy and its attendant techniques. It is now apparent that the existence of plasmodesmata makes for the cell to cell continuity that unites the cellular matrix of plant tissues, such as the continuity from cell to cell of the plasma membrane and the endoplasmic reticulum.

The work of Tangl opened up new fields of investigation, new concepts and terminology, e.g., that of transmembrane fluxes, the symplast [16] and its counterpart, the apoplast, symplasmic domains,[17] and variable plasmodesmatal gating; and new techniques such as that of microinjection and the use of fluorescent and radioactive tracers. These enable botanists to follow the movement of substances of molecules of different sizes (important is the Stokes radius) from cell to cell. Recent work has centred on the progress, cell to cell, of viral infection, aided by the movement of proteins [18] and the symplastic transmission of small RNA's (c. 25 nucleotides) as "gene silencers." Special attention is being given to the sieve element-companion-cell complex which has been shown to transmit proteins of 27kD in size. An important future goal will be to elucidate the plasmodesmal functions in and near apical meristems.

Tangl himself adumbrated some aspects of these developments when he wrote that "*the connecting ducts unite them* (the cells) *to an entity of higher order*". There was an immediate surge of interest and a spate of publications on the topic following Tangl's publication. The reason Tangl's paper aroused such immediate and intense interest was that his observations provided a solution to the quandary created for biologists by Mathias Jacob Schleiden (1804–1881) and Theodor Schwann (1810–1882) in their *Zellenlehre* ("cell theory") of 1838–1839.[19] Schleiden stated:

> "every plant is an aggregate of completely individualised entities, independent and separate, which are the cells themselves".

Wilhelm Hofmeister (1824–1877) and Julius von Sachs (1832–1897) had concluded that the cell theory failed to account for growth correlations, tropisms and the transport of substances, involving the whole plant. Studies already existed to show that newly divided cells were, at least initially, interconnected by cytoplasmic threads.[20] Tangl's discovery was seized on, therefore, with considerable

[13] E. Tangl (1884), "Zur Lehre von der Continuität des Protoplasmas im Pflanzengewebe", *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften* (Wien), Abt. 1 90, p. 10–38.

[14] E. Tangl (1885), "Studien über das Endosperm einiger Gramineen", *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften* (Wien), Abt. 1 92, p. 72–109, tabl. I–IV.

[15] E. Strasburger (1901), "Über Plasmaverbindungen pflanzlicher Zellen", *Jahrbücher für Wissenschaftliche Botanik* 36, p. 493–610.

[16] E. Münch (1930), *Die Stoffbewegung in der Pflanzen* (Jena: Fischer).

[17] K. J. Oparka, A. G. Roberts (2001), "Plasmodesmata. A not so open-and-shut case", *Plant Physiology* 125 (1), p. 123–126.

[18] A. G. Roberts, K. J. Oparka (2003), "Plasmodesmata and the control of symplastic transport", *Plant, Cell & Environment* 26(1), p. 103–124.

[19] M. J. Schleiden (1838), "Beiträge zur Phytogenesis", *Archiv für Anatomie und Physiologie*; T. Schwann, 1839. *Mikroskopische Untersuchungen über die Übereinstimmung in der Structur und dem Wachsthum der Thiere und Pflanzen* (Berlin).

[20] W. Hofmeister (1867), *Die Lehre von der Pflanzenzelle* (Leipzig); J. Sachs (1865), *Handbuch der Experimental-Physiologie der Pflanzen* (Leipzig).

enthusiasm. Wilhelm Pfeffer (1845–1920) especially took up the new concept stating that

> "the continuity of the living substance is so essential (for correlative harmony in the whole plant) that it would be necessary to propose it if it were not already discovered".

The pertinent observation later by Anton de Bary (1831–1888) that "*die Pflanze macht Zellen, nicht Zellen die Pflanze*" puts the matter succinctly.[21] The new concept of the plant as an organismal entity was launched and began to explain some hitherto puzzling observations, e.g., that the chloroplasts of the plasmically isolated stomatal guard cells do not receive the presumably symplastically transmitted signal to senescence and thus retain their green colour and their starch at leaf fall.[22] This epitomises the new vision enabled by Tangl's discovery that cells are not isolated entities, rather, they form an integrated system of plant function.

Tangl published his only taxonomic paper in 1883. He described in it a new genus and new species of blue-green algae, which he named *Plaxonema oscillans*. The taxon was distinguished on the basis of blue plate-like chromatophors in cytoplasm of some cells.[23] The genus *Plaxonema* Tangl 1883 of blue-green algae belongs, according to the eminent Polish phycologist Karol Starmach (1900–1988), to the genus *Oscillatoria*.[24] Tangl also analysed the phenomena of nucleus and cell division. His two papers of 1882 on this subject did not bring any new important data.[25]

Thanks to the discovery of plasmodesmata Tangl should earn a place for himself in the pantheon of distinguished plant scientists. We want to emphasise that his discovery completely changed the scientific view on plants. Previously the plant was only "an aggregate of separate cells". Tangl's works made the plant an organismal entity. Tangl's discovery could be compared, of course in adequate proportions, to Copernicus' discovery. Both discoveries changed our basic views: the first one — on microcosmos, the latter — on cosmos.

[21] D. J. Carr (1976), "Historical perspectives on plasmodesmata", in: B.E.S. Gunning, A.W. Robards (eds.), *Intercellular Communication in Plants: Studies on Plasmodesmata* (Heidelberg and New York: Springer Verlag), p. 291–295.

[22] D. J. Carr (1976), "Plasmodesmata in growth and development", in: B. E. S. Gunning, A. W. Robards (eds.), *Intercellular Communication in Plants: Studies on Plasmodesmata* (Heidelberg and New York: Springer Verlag), p. 243–290.

[23] E. Tangl (1883), "Zur Morphologie der Cyanophyceen", *Denkschriften der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften* (Wien), Abt. 2 48, p. 1–14, tabl. I–III.

[24] K. Starmach (1966), "*Cyanophyta – sinice. Glaucophyta* – glaukofity", *Flora słodkowodna Polski*, vol. 2, p. 310.

[25] E. Tangl (1882), "Die Kern- und Zelltheilungen bei der Bildung des Pollens von *Hemerocallis fulva* L.", *Denkschriften der kaiserlichen Akademie der Wissenschaften. Mathematisch-naturwissenschaftliche Classe* (Wien), Abt. 2 45, p. 65–86, tabl. I–IV; E. Tangl (1882), "Über die Theilung der Kerne in Spirogyra-Zellen", *Sitzungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften* (Wien), Abt. 1 85, p. 268–291.