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VERSITA

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PURKYNĚ'S CONTRIBUTIONS TO NEUROSCIENCE AND BIOLOGY: PART I

Miloš Judaš*,
Goran Sedmak

University of Zagreb School of Medicine, Croatian Institute for Brain Research, Zagreb

Abstract

Jan Evangelista Purkyně (or Purkinje, as he was spelled in his German publications prior to 1850) was one of giants in the XIXth century science. His contributions are numerous, and his research interests were wide-ranging. This study is divided into two parts. In the Part I, we provide a general overview of Purkyně's life and work, focusing on his pioneering role in the rise of experimental physiology and microscopical anatomy. In the Part II, we will: (a) focus on his contributions to neuroanatomy, neurohistology and cell theory; (b) provide the first complete English translation of his relevant publications, and (c) provide a critical historical review of the importance of his contributions in comparison to his main contemporary competitors: Christian Gottfried Ehrenberg, Gabriel Gustav Valentin, Theodor Schwann, Robert Remak and Adolf Hannover.

Keywords

• History of neuroscience • Neuron structure • Cell theory • Cerebellar cortex

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Introduction

Jan Evangelista Purkyně (or Purkinje) (1787-1869) was one of the most prominent scientists in the broad fields of biology and medicine in the first half of the XIXth century (Figure 1). His research interests were wide-ranging and his contributions were numerous. Purkyně made significant contributions to physiology and physiological psychology, human anatomy, histology, embryology, and microtechnics. His investigations also concerned pharmacology, zoology, anatomy of plants, and physics, but he made significant contributions to language studies and literature as well. Perhaps the best evidence of his productivity and achievements is the number of eponyms that still bear his name: there are Purkinje cells in the cerebellum, Purkinje's fibres (anastomosing muscle fibres in subendothelial cardiac tissue), Purkinje's corpuscles (the lacunae of bone), Purkinje's granular layer (branched spaces in the tooth enamel), three pairs of Purkinje's images seen in the pupil, and Purkinje's figures (dark lines produced by the retinal vessels under certain conditions of illumination) as well as the Purkinje's shift in the visual perception. Finally, the germinal vesicle (*vesicula germinativa*) was for a long time called Purkinje's vesicle, and neuronal axon was described as Purkinje's axis cylinder (*Achsenzylinder*) throughout the XIXth century.

Recently published monographs on the history of neuroscience (Clarke & O'Malley 1996; Finger 1991, 2000; Marshall & Magoun 1994; Mayer 1971, Shepherd 1991) regularly pay tribute to Purkyně, but this is usually limited to brief and general notes concerning his life and key contributions, accompanied by his portrait and reproduction of his drawing of cerebellar (Purkinje) cells. Thus, it seems that Henry Harris in his detailed and balanced study of the history of cell theory justly pointed out that Purkyně is (Harris 2000, p. 82): „an example of a scientist whose reputation far from adequately honours his work, and for reasons that are quite other than scientific... one needs to explain why a man of this magnitude, both in his personal work and in the work of his students, should have been largely overlooked in conventional historical accounts of the cell doctrine, or, if not quite overlooked, then dismissed with a couple of lines and an occasional eponym."

The purpose of this study is to summarize numerous important discoveries of Purkyně and his students (including the bibliography of their key publications), with focus on neurohistology and cell theory (as a precursor of neuron theory). Furthermore, we provide the first complete English translation of Purkyně's seminal contributions to neurohistology and cell theory presented at the 1837 Prague

Figure 1. Jan Evangelista Purkyně (1787-1869). From: F. J. Nowahowski (1862) Życie i prace nankowe Jacia Purkyněgo. Warszawa.

* *E-mail: mjudas@hiim.hr*

meeting of German Naturalists and Physicians and several other publications. Finally, we try to provide a balanced historical view on his contributions to neuroscience by analyzing the relevant publications of his contemporaries and major competitors: Christian Gottfried Ehrenberg, Gabriel Gustav Valentin, Theodor Schwann, Johannes Müller, Robert Remak, and Adolf Hannover.

The Life of Purkyně

The general information on Purkyně's life and work is available in a number of obituary notices and brief (dictionary-type) reviews (Eiselt 1859; Gicklhorn 1937/1938; Harms 1933; Heidenhain 1887, 1888; Lemberg 1937; Pagel & Haberling 1932; Schrötter von Kristelli 1870; Volf 1938; von Wurzbach 1872), but only few of them are written in English (Bartelmez 1953, 1970; Burton-Opitz 1899). Some articles provide brief (or more extended) exposition of Purkyně's specific contributions – e.g., to the physiology of the visual, the vestibular and the oculomotor systems (Grüsser 1984), ophthalmology (Von Tschermak-Seyssenegg 1941), psychology (Brožek & Hoscoves 1987; Von Tschermak-Seyssenegg 1937), cell theory (Frankenberger 1961; Kruta 1971b; Orel & Matalová 1989; Studnička 1927/28, 1931/32, 1936a; Harris 2000), histology and embryology (Vacek 1987), neurophysiology (Kruta 1964b,c), or brief excerpts on his discovery of cerebellar Purkinje cells (Clarke and O'Malley 1996; Kruta 1969a; Viets & Garrison 1940). Again, most of these contributions are written in languages other than English. Extensive articles and monographs are published almost exclusively in German or Czech (Brožek & Hoscoves 1987; Czech Association of Physicians 1948; Eiselt 1859; Englová & Tomiček 2009; Jedlička 1920; Kirsche 1989; Kotek & Nikliček 1987; Kruta 1962, 1964a, 1969b, 1971a; Martinek 1869; Psotnicková 1955; Purkyne Society 1937; Purš 1988; Rádl 1901; Rozsivalová 1956; Societas Medicorum Bohemorum 1868; Teich 1962; Thomsen 1919; Trávničková 1986), with only two recent monographs in English (John 1959; Wade *et al.* 2001).

For composing this brief biography of Purkyně, we consulted four main sources written in English (Hykeš 1936; John 1959; Studnička 1936b; Wade *et al.* 2001), but were often forced to rely on a century-old German sources due to their accuracy and detail (Oelsner 1870; Schrötter von Kristelli 1870; Studnička 1927/1928, 1931/1932, 1936a; Thomsen 1919).

According to Hykeš (Hykeš 1936), the Purkyně family in the Northwestern part of Bohemia can be traced back to 1520. It was one of the most numerous families in the county town Litoměřice (Leitmeritz) on the river Labe (Elbe), as well as in the smaller town of Budyně on Ohře, where it members were farmers, tradesmen, artisans, officials, school teachers and members of town councils. Jan's grandfather, Kašpar Purkyně, moved from Budyně to Libochovice (Libochowitz, just north of Prague) and became a rich and distinguished citizen, but unfortunately died early. His only son Josef was the manager (*Wirthschaftsbeamter*) of Prince (*Fürst*) Dietrichstein's estate. Josef at the age of 40 married the 28 year old Rosalia Šafránková and they had three sons: Jan (the oldest one), Emanuel (who died very early), and Josef. Jan Evangelista Purkyně was born on December 17th, 1787 in the castle in Libochovice. He attended the elementary school in his birth place, but soon after that he was sent to another Dietrichstein estate, Mikulov (Nikolsburg) in South Moravia (Mähren), where he attended the gymnasium from 1797 to 1803. That school was managed by the monks of the Piarist Order (*Fratres piarum scholarum*, Piaristen), and Jan also served as a chorister (*Chorsänger*) in the Piarist monastery. He subsequently joined the Piarist order and as a novice taught in the Piaristic schools in Moravia (Stará Voda, Strážnice/Strassnic; in 1805) and Bohemia (Litomyšl/Leitomischl; in 1806). However, Jan longed for a higher grade of education and eagerly read philosophical works of Fichte, Schelling, Novalis, as well as Goethe. Although the German *Naturphilosophie* movement thus contributed to his early education and stimulated his thinking, Purkyně became and firmly remained an experimental and exact scientist, as clearly testified by the following quote from his letter to Altenstein (Hykeš 1936, p. 465): „While in the last century physiology was just a commentary on anatomy, in the beginning of this century under the influence of *Naturphilosophie* it rose almost to its heavenly independence, now it has to descend from these heights to its terrestrial and material level, and it ought to be truly living and organic."

Therefore, Purkyně left Litomyšl and went to Prague to study philosophy (1808-1810). He made his living as a tutor in some aristocratic families in Prague, and later (1810-1812) in the Czech country in the house of Baron Franz Hildprandt at Blatná where he served as *Hofmeister*. In 1813, he returned to Prague, quit studying philosophy and began to study medicine which he completed by obtaining M.D. degree in December 1818. Between 1816 and 1818, he was engaged as a *Spitalpraktikant* at a surgical clinic of the General Hospital (*Prager allgemeinen Krankenhause*), where he was noted by Professor J. N. Rust who was quite influential (he occupied a very high position of *Generalarzt* and *Geheimrat* in the Prussian ministry of health and education). Rust offered him a position of professor at the military ophthalmological institute in Berlin (*militärisches Augenheilinstitut*), but Purkyně was unable to accept that generous offer because he did not yet obtain his M.D. degree. Nevertheless, upon Rust's recommendation Purkyně in 1819 became a prosector for anatomy and physiology at the University of Prague, where he served until 1822.

Purkyně finished his thesis entitled „Contributions to the knowledge of vision from the subjective point of view" (*Beiträge zur Kenntnis des Sehens in subjektiver Hinsicht* – Purkyně 1819) and dedicated it to Goethe because he was greatly impressed with Goethe's theory of colors. Goethe, who was at that time deeply and affectionately engaged in his studies on the physiology of vision and theory of colors, became very interested in both the thesis and the young scientist – and this was important for Purkyně's future career (Schrötter von Kristelli 1870; Himmelbaur 1918; Kahn 1932; Krause 1935, 1936). Goethe invited Purkyně to visit him in Weimar, and over years left many favourable remarks on Purkyně in his diaries, such as (Schrötter von Kristelli 1870, p. 102): *„Ich wende mich zu den Naturforschung,*

und da hab' ich vor allem zu sagen, dass Purkinje's Werk über das subjective Sehen mich besonders anregte. Ich zog es aus und schrieb Noten dazu, und liess, in Absicht Gebrauch davon in meinen Heften zu machen, die beigefügte Tafel copiren etc." (I turned to researches on nature and have to say that I was especially stimulated by Purkinje's work on subjective vision. I took the manuscript and put down my notes, read it in order to put it to use in my notebooks, to copy its plates, etc.").

Therefore, Goethe warmly recommended Purkyně to his great friend Alexander von Humboldt, as well as to the famous professor of anatomy at the University of Berlin, Karl Asmund Rudolphi. Thus, with the joint support of Rust, Goethe, Humboldt and Rudolphi, young Purkyně obtained his first chair as professor of physiology and pathology at the Royal Prussian University in Breslau (Wroclaw) – King Friedrich Wilhelm signed the decree nominating him professor on January 25, 1823. The University of Breslau was founded in 1811, one year after the opening of the University of Berlin. As a consequence, Purkyně gave up his previous Austrian citizenship and became a Prussian subject; by the Easter of 1823 he was already in Breslau. He also became well acquainted with members of the Berlin intellectual and political elite and in 1827 married Rudolphi's daughter Julie (who died in 1835). They had two daughters who died very early and two sons: Emanuel (1831-1832) who was professor of botany at the Institute of forestry in Bělá, and Karel (1834-1868) who was a distinguished painter.

Purkyně spent in Breslau his most productive years, until in 1850 he moved to Prague. We will describe his scientific achievements in the following section, but for the present we may focus on his other activities. At Breslau, Purkyně was very active in different societies where he often lectured on his discoveries and new ideas – e.g., Society for National Culture (*Gesellschaft für die vaterländische Kultur*) and the Philomatic Society (*Philomatische Gesellschaft*). He was especially very active in Slav cultural life – he was in constant communication with a great many Polish and Lusitian students at the University as well as many Russians and Poles who on their way to central and western Europe stopped at Breslau. He was frequently intervening at Prussian authorities on behalf of various Slav cultural societies and student associations. Purkyně was instrumental in successful nomination of the Czech poet F. L. Čelakovský as professor of Slav literature at the University of Breslau. He also translated into Czech language the poetry of Schiller, Goethe and Torquato Tasso.

While Purkyně was materially very well off at Breslau (Hykeš 1936), nevertheless he tried to obtain the chair at the University of Prague. Indeed, in 1849, the staff of the Prague School of Medicine offered him the chair of physiology and already at Easter 1850 Purkyně left Breslau and moved to Prague. It was also at that time (1850) that he changed the spelling of his family name from Purkinje (as was written in his documents by a German administrator at his birth) to original Czech Purkyně. Thus, the interchangeable use of both is permissible especially because all his publications prior to 1850 were authored by „Purkinje" and that is how he is referred to in articles of his contemporaries.

Once in Prague, he was received enthusiastically by both the university staff and the Czech population. He again become the Austrian citizen and the Austrian government was willing to meet all his requirements and established for him an institute of physiology which was larger and considerably better equipped than that in Breslau (the laboratories were ready for use already in October 1851).

However, these relations with university gradually deteriorated, and Hykeš (Hykeš 1936) reports that in 1867 another professor of physiology (Wintschgau) was appointed for whom anoter new physiological institute was equipped. Moreover, when Purkyně died on the 28th of July 1869 (Hykeš 1936, p. 470): „the staff of the university did not even take part in the funeral ceremonies, in spite of the fact that he had been there as professor for 18 years. But there were big crowds of Czech people representing all classes of Czech society, because they saw in Purkyně not only one of the greatest scientists of their own blood, but also an undaunted fighter for their national cause."

Indeed, although Purkyně always remained man of the world (he was speaking, reading and writing fluently in Czech, German, Latin and Polish), he never forgot his roots and homeland and invested huge efforts and ardent enthusiasm to raise his Czech people culturally and nationally to the level of other cultural nations. In Prague, Purkyně became much more involved in the Czech national revival and began to write popular and scientific works in the Czech language. Harris wrily notes that (Harris 2000, p. 84): „This was no doubt appreciated by the Czechs, but meant, for practical purposes, that these works could not be read by anyone else." In this respect, Purkyně was quite similar to another giant of neuroscience, Santiago Ramón y Cajal, who devotedly strived to put his Spanish people on the world's scientific and cultural map and also published all his discoveries in Spanish and only later supervised their translations in German or French.

During his period in Prague, Purkyně asked that lectures might be conducted in Czech at the University (they were delivered in German until that time, although the majority of students were Czechs). In fact, he was the first who started to deliver his lectures in Czech. He also organized a Society of Czech Physicians (Spolek českých lékařů), initiated the edition of a Czech Medical Journal (Časopis českých lékařů). He also edited a natural history magazine called „Živa" and at the National Museum at Prague he established a scientific council where all Czech scientific activities were concentrated. Purkyně was also the initiator and co-founder of different cultural and artists societies, such as the Society of Arts (Umělecká beseda), the society of National theatre (Národní divadlo). He was a member of the well known gymnastic organisation „Sokol". Finally, he was the deputy of the Bohemian Diet. Purkyně also invested a lot of personal money to create the library which, after his death, consisted of more than 5,000 volumes.

Purkyně was member of almost all national scientific and cultural academies and societies: Silesian Society for National Culture (*Schlessische Gesellschaft für vaterländische Cultur*; 1824), Society for Pomeranian History and Archeology (*Gesellschaft für Pommersche Geschichte und Alterthumskunde*, 1830), honorary member of the Royal Bohemian

Museum in Prag (1834), Royal Bohemian Society of Sciences in Prag (*Königlichen Böhmischen Gesellschaft der Wissenschaften in Prag*, 1840), Association for Physiological Medicine in Breslau (*Verein für physiologische Heilkunde zu Breslau*, 1848), honorary member of Union of Researchers of Nature (*Naturforschende Verein*) Lotos in Prag (1848) and Brno (Brünn, 1962), honorary doctor of philosophy at the University of Prague (1848), honorary member of *Akademischen Lesevereines* in Prag (1859), and president and member of the Association of Bohemian Physicians (*Verein böhmischer Aerzte in Prag*, 1862). Governmental authorities in both Prussia and Austria awarded him with several prestigious ordains: *Ritter des königl. preussischen rothen Adlerordens 4. Classe* (1842), Honorary Commander od Infantry Corps of Prague Citizens (*Ehrenhauptmann des Prager k.k. bürgerlichen Infanteriecorps*, 1861), *Ritter des k. Leopold-Ordens and Ritter des k. preuss. rothen Adlerordens 3. Classe* (1868). Finally, he was knighted (*in den Ritterstand erhoben*) by the Austrian emperor Franz Joseph on July 15, 1869. However, that was delivered posthumously, as Purkyně died in Prague on Juni 28th, 1869.

His national fame is perhaps best illustrated by the fact that in1861-1862 he was elected as a Honorary Citizen of the following cities: Blovic, Beneschau, Zlonic, Velvarn, Libochowic, Uha, Duhan, Klobuk, Slatina, Křesin, Popels, Prělic, Radovesic, Brozan, Libušin, Svinař, Budin, Pocátek, Vraná, Písek and Straconic.

However, his efforts were not restricted narrowly to his own Czech people, but included other fellow Slavs as well. For example, he published numerous scientific and popular articles in Polish and maintained continuous relation with Russians. He became member of the Society of Physicians in Warsaw (*Societas medicorum Varsoviensium*) in 1838, member of the Literary Society of Krakow (*Societas literaria Cracoviensis*) in 1840, honorary member of the Royal University of Charkow in 1847, honorary president of the Polish Literary Society in Breslau in 1850, member of the Society of Friends of Sciences (*Gesellschaft von Freunden der Wissenschaften*) in Posen in 1860, member of the Society of Russian Physicians (*Gesellschaft russischer Aerzte*) in St. Petersburg in 1866, and honorary member of the Society of Polish Physicians in Paris in 1869.

In preparing this manuscript, we were positively surprised by finding out that even in our homeland, Croatia, Purkyně was fully recognized and praised a century ago: in 1867, he became honorary member of the Yugoslav Academy of Sciences and Arts in Zagreb (referred in German literature as the *„südslavische Akademie in Agram"*). A year after his death, Bogoslav Šulek published a volume describing life and work of Purkyně in the edition of Zagreb Academy (Šulek 1870), and another monograph on Purkyně was published in Zagreb in 1918 (Mikuličić 1918).

Purkyně's steadily growing international recognition and fame is reflected in his membership in the leading academies and societies of his time. In Berlin, he became corresponding member of the Royal Academy of Sciences (*Königlichen Akademie der Wissenschaften in Berlin*) in 1832, and member of Prussian Medical Association (*Verein für Heilkunde in Preussen zu Berlin*) in 1837). In Vienna, he was member of Imperial and Royal Society of Physicians (*K. u. K. Gesellschaft der Aerzte in Wien*) in 1839, corresponding (1848) and full member (1860) of the Imperial Academy of Sciences (*Kaiserliche Akademie der Wissenschaften in Wien*), and honorary doctor of medicine at Vienna University (1865). In Paris, he was elected as member of all major academies (*Académie royale de Médecine* in 1839, *Académie nationale de Médecine* in 1848, *Académie impériale de Médecine* in 1856, and *Académie des Sciences* in 1861). In London, he became honorary member of the Microscopical Society (1841), and member of the Royal Society (1850) and the Linnean Society (1851). He was also member of Leopoldine Academy (*Caesarea Academia Leopoldino-Carolina naturae Curiosorum*, 1829), Erlangen Physico-Medical Society (*Societas physico-medica Erlangensis*, 1830), Swedish Medical Society in Stockholm (*Societas medicorum suecica*, 1834), Royal Medical Academy of Belgium in Brussels (*Académie royale de Médecine de Belgique*, 1842), Royal Medical Society in Kopenhagen (*Societas regia medica Hafniensis*, 1844), Natural Sciences Union of Hamburg (*Naturwissenschaftliche Verein*, 1852), Natural Sciences Society of Cherbourg (*Société des sciences naturelles de Cherbourg*, 1853), Dresden Society for Natural and Medical Sciences (*Gesellschaft für Natur- und Heilkunde zu Dresden*, 1855), Budapest Society of Physicians (1865), and Hungarian Natural Science Union (*Ungarische naturwissenschaftliche Verein*, 1867).

However, for reasons not fully understood, his fortune changed after his death. Although his name lives to this day (because it seems unavoidable to remember eponyms, such as cerebellar Purkinje cells), the memory concerning his real contributions and ideas steadily deteriorated during the last third of the XIXth century. As noted by Harris (2000), serious efforts to restore his pioneering role in the field of microscopic anatomy and the cell theory were made only in the twentieth century – by Czechs and under official Czech patronage. The first to publish detailed studies on Purkyně were František Karel Studnička (then at the University of Brno/Brünn) in 1930s (Studnička 1927/1928, 1931/1932, 1936a,b) and Oldrich Vilém Hykeš (Hykeš 1935, 1936). After the Second World War these efforts were continued by Vladimir Kruta and many other Czech scientists and historians (Brožek & Hoscoves 1987; Czech Association of Physicians 1948; Englová & Tomiček 2009; Kotek & Nikliček 1987; Kruta 1962, 1964a, 1969b, 1971a; Psotnicková 1955; Purkyne Society 1937; Purš 1988; Rozsivalová 1956; Teich 1962).

In his History of physiology, Rothschuh (Rotschuh 1956) stated that, although there are several extensive German monographs on Purkyně (Ebstein 1931; Schrötter von Kristelli 1870; Von Tschermak-Seyssenegg 1937, 1941; Winterstein 1937), there is still no comprehensive Purkyně biography written in German and based on the solid and balanced review of all his publications and other historical sources. The lack of such biography written in English remains even more conspicious.

One of Purkyně's student, Theophile Eiselt, published an insightful account on why many of his contributions went almost unnoticed or were rediscovered and praised 50 or 100 years after their original publication. It seems that a combination of external circumstances and the fact that Purkyně did not really care for his own visibility and publicity often had a decisive

role. As noted by Eiselt, the fact that he was not officially listed as a coauthor on published dissertations of his students certainly did not serve his own promotion – but it served quite well for the growing reputation and fame of the University of Breslau. In fact, these dissertations were instrumental for the final successful establishment of the Institute in Breslau. Eiselt offered the following interesting comments (translated from Eiselt 1859, p. 19):

„The future destiny of novel insights and discoveries does not depend solely on their intrinsic value but also on the way they were introduced to the world. The current academic practice regards as very important that the author makes his work available to the public opinion as soon as possible. Until now, the best way to attain visibility was to get one's work published by the French Academy of Sciences which was the most authoritative in Europe due to its inner disposition, the fame of its members, the richness of its financial funds, and the thriving organism of its Journals and Memoirs. One can only hope that, as Frenchmen remain distinctly unhappy to learn languages of other cultured nations, competitive publishing enterprises would be established by other academies, ready to recognize scientific achievements of other nations and present them to the critical eye of competent judges. It may easily be that some of our younger academies (such as those in Berlin, St. Petersburg or Vienna) will soon be able to accept the challenge. However, in the light of the forementioned, Purkyně did not always made the best choices. His works were published in German, Polish or Chech, or in Latin – as dissertations which are either hardly available or completely unavailable at the book market."; and „To pursue a single discovery before it is completely exhausted – a path to glory for so many researchers – Purkyně simply did not care for such a thing. He was constantly driven from one discovery to another, and left the completion of details to the public. His publications are full of stimulating data and insights opening the path for further research. In addition, this noble mind possessed two uncommon features: he showed a deep respect for young investigators and he was determined not to speak about himself (*de nobis ipsis silemus*). While both features were quite corresponding to his noble character, they equally contributed to the lack of the full recognition of Purkyně's achievements."

And the following remark of Eiselt painfully clearly illustrates that that was a problem already in Purkyně's time (translated from Eiselt 1859, p. 20): „Purkyně's name has long ago crossed the ocean on the wings of his publications; would it not be reckonned as an instance of barbarian manners if his contributions remain better known to foreign nations than to us, his compatriots? We proudly look at the shining of his Glory!"

The Purkyně Institute in Breslau and the rise of experimental physiology

The physiology as a separate discipline came into existence around the middle of XIXth century. Before that, the physiology was everywhere tightly connected with general, comparative or pathological anatomy or certain clinical activities (Rothschuh 1956).

Upon his arrival at the University of Breslau, Purkyně immediately started to realize his plans for reform and advanced of the current teaching and research practices in physiology. Thus, in 1824 he introduced experiments and laboratory work in the teaching of physiology (Heidenhain 1887, 1888; Hykeš 1936). In 1831, he submitted to the Ministry of Education a project, asking for the establishment of an independent institute of physiology with necessary rooms, equipment and staff and describing his conception of the method of teaching of physiology. As it was already rejected by the faculty of Breslau university, the application failed (Ebstein 1930/1931; Hürthle 1909; Hykeš 1936; Schrötter von Kristelli 1870; Witte 1941/42). However, he was given a new compound achromatic microscope (see below). Purkyně applied again in 1836, and this time the establishment of a new physiological department was approved – he got an entire (but small) building which was opened on October 8, 1839. This was the first physiological institute of its kind - separate from the department of anatomy, as was the usual practice elsewhere. Therefore, Purkyně is generally regarded as the founder of the first institute of physiology in Germany (Shepherd 1991; Harris 2000). The newly acquired building was in fact not quite adequate – as wittnessed by Heidenhain (Heidenhain 1887, 1888) it was so small that in Heidenhain's time it was no longer the institute but instead used as a detention place for students penalized for breaches of academic rules and discipline (*Karzer für bestrafte Studenten*)!

However, it should be noted that, although Purkyně's new instute was historically by far the most important and productive, it was not in fact the first of its kind on the German soil. As documented by Ernst Theodor Nauck (Nauck 1950), the priority goes to Carl August Sigmund Schultze (1795-1877) who established the first physiological experimental laboratory (*Experimentalanstalt*) in 1821 in Freiburg im Breisgau (Schreiber 1829). Schultze was also delivering the first experimental physiological course in 1822, while Purkyně in Breslau started in 1824. This was also pointed out by Rothschuh (Rothschuh 1956) and according to one early historical report (Kilian 1828) the teaching of experimental physiology back in 1828 was practiced by only 7 docents at 6 German universities.

Nevertheless, the conception which Purkyně formed of physiology was much more comprehensive than that of Schultze (Eiselt 1859; Studnička 1936b) and can be recognized from notes of his university lectures preserved in manuscripts as well as from his own account (translated from Eiselt 1859, p. 16-17): „In 1828 I introduced a new system of lecturing which consisted of the following fields of knowledge: 1. Anthropology, as the introductory science for a general physiology; 2. Descriptive anatomy; 3. Histology; 4. Embryology (histogenesis and organogenesis); 5. the phaenomenology of living beings, which described the phaenomena of life in purely empirical terms, without further explanations; 6. Physiological mechanics; 7. Physiological chemistry; 8. Physiological dynamics; 9. Physiological psychology; 10. General physiology (philosophy of nature); 11. Experimental physiology; 12. Applied physiology (as in pathology or public health)". Whereas items listed under 6, 7 and 8

represented obligatory courses, the remaining was offered in a way of extraordinary (elective) lectures.

The signs of an early growth of experimental physiology and its transformation in an independent research and teaching discipline should not be followed just at the level of institutes and chairs. Other important indication stems from the history of physiological societies and journals. Historical development of physiological societies in Germany has been traced by Rothschuh (Rothschuh 1956). In 1822, Lorenz Oken in Leipzig founded the Society of German Naturalists and Physicians (*Gesellschaft Deutscher Naturforscher und Aerzte*). As proposed by Alexander von Humboldt, this Society was in 1828 divided into 7 Sections and one section encompassed anatomy, physiology and zoology. The first independent session of the Physiological Section occured in 1877 at the 50. anniversary meeting in Munich, but in the subsequent years joint sections with anatomists and zoologists were again common. During the 75. anniversary meeting in Kassel in 1903, it was decided to establish German Physiological Society (*Deutsche Physiologische Gesellschaft*) and its first independent meeting occurred in 1904 in Breslau – but concurrently with the meeting of the Society of German Naturalists and Physicians. However, the next meeting of 1905 in Marburg was completely independent. It should be noted that another physiological society (*Berliner Physiologische Gesellschaft*) was founded already in 1875 in Berlin (Trendelenburg 1936).

The history of journals is even more revealing. Johann Christian Reil of Halle founded the world's first physiological journal (*Archiv für Physiologie*) on July 1, 1795. This journal was jointly edited by Reil and Autenrieth from 1801 to 1813 (when Reil died). It was continued by Johann Friedrich Meckel, first as the *Deutsches Archiv für Physiologie* (1815) and then (since 1826) as Meckel's *Archiv für Anatomie und Physiologie*. In 1834, Johannes Müller became the editor-in-chief and the journal changed its name into Müller's *Archiv für Anatomie, Physiologie und wissenschaftliche Medizin*. After Müller's death in 1858, the joint editorship was transferred to his outstanding successors, Emil Du Bois-Reymond and Karl Bogislaus Reichert. The symbolic split of anatomy and physiology as separate disciplines was marked by 1877 division of this journal in two Divisions: *Archiv für Anatomie und Physiologie, anatomische Abtheilung* (edited by Reichert) and *Archiv für Anatomie und Physiologie, physiologische Abtheilung* (edited by Du Bois-Reymond).

For comparison, the first French physiological journal was founded in 1821 by François Magendie (*Journal de physiologie expérimentale et pathologique*), the first British *Journal of Physiology* was founded by Michael Foster in 1896, and the *American Journal of Physiology* came into existence in 1898.

The Purkyně Institute in Breslau as „the cradle of histology"

The achromatic microscope was introduced in the mid-1820s (Liddell 1960; Shepherd 1991) and during the 1830s, and especially the late 1830s, improvements in optical instruments as well as improvements in the skill of those who used them, did produce a rapid and marked change in the quality of microscopic observations (Harris 2000). As testified by a prominent pioneer and Purkinje's contemporary, Christian Gottfried Ehrenberg (Ehrenberg 1836/1837, p. 295):

„The compound microscope shows, according to the history, to all careful observers, the same fact unfolding itself in one and the same mode, and furnishes the knowledge of substantial facts, which may be entirely or partly employed as the foundation of further researches. Of erroneous representations of the objects seen, though these may also be ascribed to the prevailing notions of the time, the observer, and not the microscope, must always bear the manifest blame; and if persons otherwise meritorious have been thereby misled, the cause, as the history distinctly proves, equally lies not in the microscope, but in this, that before its employment in research so minute and intricate organica structure, they did not prepare generally, and labour urgently to render themselves confident in the use of instruments; that they built superstructures on a base whose foundations were not fixed with sufficient stability; or that they wished to recognize the structure of the delicate living brain in the boiled or indurated or dried organ. The most important assistance in acquiring more intimate knowledge of the phenomena of organic life is the compound microscope in the hand of the cautious practised observer; and though we frequently continue to recommend and prefer the simple lens before the compound one, in much stronger magnifying powers, on account of the transparency, this is because the advantage of the latter is still not sufficiently generally known, and not rightly appreciated."

These new microscopists included Christian Gottfried Ehrenberg (1795-1876), Purkyně and his student and collaborator Gabriel Gustav Valentin (1813-1883). In 1832, Purkinje acquired an excellent and expensive new achromatic compound microscope produced by the Simon Plössl in Vienna (the cost was 220 gulden = 110 dollars; John 1959), and in 1836 he obtained another excellent microscope made by Pistor and Schiek of Berlin. He and his students feverishly embarked on microscopical studies („like the pack of hungry wolves" – Eiselt 1859; Bartelmez 1970) and numerous important contributions soon followed that provided a comprehensive new look at the cellular composition of the body (Shepherd 1991). It should be noted that they did not simply pursue the microscopic description of tissues but (in the spirit of Albrecht von Haller's *anatomia animata*, enlivened anatomy) produced a physiologically inspired histological studies. Thus, Rothschuh (Rothschuh 1969) rightly remarked that Purkyně's work marks the transition between „histomorphology" and „histophysiology". Moreover, Purkyně introduced a series of important technical improvements in the microscopy technique. He devised procedures for making thin sections of animal tissues that were far superior to those previously availabe. He used prior decalcification for the study of bones and teeth. He also used artificial digestion of tissues and different methods of fixing, staining and mounting the preparations, to enhance microscopic resolution. He imployed the recently introduced Daguerreotypes, and with his assistant Oschatz constructed probably the first microtome and devised one of the first

micromanipulators. Therefore, the Institute in Breslau has been early recognized as „the craddle of histology" (Schrötter von Kristelli 1870, p. 101: „*Das Breslauer Institut war die Wiege der Histologie*").

Main contributions to physiology and medicine

A summary of his main contributions was in fact published by Purkyně himself. Namely, during his stay in Prague (after 1850), Purkyně focused his major efforts and energy in the establishment of the new physiological institute and to popularization of natural science. Thus, in collaboration with professor Krejčí, from 1853 to 1864 he edited a popular natural science journal „*Živa*" (which was at first published monthly, then quarterly). There he published a series of articles mostly intended for a wider public. In several issues of Živa (No. 2-3 in 1857; No. 1-4 in 1858) Purkyně published comments on his own publications entitled „Report on my older and recent literary works, especially those concerning natural sciences" (Purkyně 1857, 1858). Similar reports were subsequently published over the next decade (Eiselt 1859; Societas medicorum Bohemorum 1868; Schrötter von Kristelli 1870; see also Studnička 1936b).

As already mentioned, his initial contributions were in the field of physiology of vision. By observations on the subjective field of vision of his own eyes, Purkyně (Purkinje 1819, 1823a,b; 1825a) confirmed and described a number of hitherto unknown phenomena which take place in rapid changes from light to darkness, by pressure on the eyeball, when using the galvanic current etc. (for review, see Studnička 1936b). In 1825 Purkyně prepared a commissioned article to cellebrate the 50. anniversary of graduation of Johann Friedrich Blumenbach of Göttingen, the nestor of German comparative anatomy and anthropology. In this study (Purkinje 1825b; Purkinje 1830a), Purkyně, using only a hand lens, described the germinal vesicle (Keimbläschen, *vesicula germinativa*), which was subsequently on the suggestion of Karl Ernst von Baer and Coste named *vesicula Purkinjii*. This discovery, together with previous studies on the physiology of vision, firmly put Purkyně on the international stage and secured his fame and reputation.

He also published important contribution to the study of vertigo (Purkinje 1820), and his discovery of special fibres which serve for the emptying of pollen in the anthers of plants (Purkinje 1830b) secured him the prestigious Monthyon Prize of the Paris Academy of Sciences (based on recommendation of the botanist Mirbel). Togheter with Valentin, Purkyně discovered an uninterrupted vibratory movement of cilia in the genital system and in the respiratory organs of mammals, birds and amphibians (Purkinje and Valentin 1834, 1835a,b) which he later also described in the ventricles of the brain (Purkinje 1836).

In 1827, the publishing house Cotta of Stuttgart and Tübingen began (in collaboration with Professor Gans) to publish Yearbooks for scientific Critique (*Jahrbücher für wissenschaftliche Kritik*. Red. Prof. von Henning), and between 1827 and 1845 Purkyně contributed a number of recensions on then influential biological and medical books of Johannes Müller, Georg Müller, Burdach, Laurencet de Lyon, Von Baer, Dzondi, Bennatti, Velpeau, Van Deen, Girgensohn, and Schwann – but also in the literary realm of *belles lettres* (books of Schafarik, Bowring, Oleska, Kopitar, and Schafařik & Palacký).

When professors of the Berlin School of Medicine in 1828 began to edit and publish a monumental Encyclopaedic Dictionary of Medical Sciences (*Encyclopädisches Wörterbuch der medicinischen Wissenschaften* – more than 30 volumes), Purkyně contributed a series of articles for the first seven volumes (1829-1832). These were the articles entitled: *Achromatopsia, Akustik, Affekt, Ahnung, Anthropologie, Artikulirte Töne, Association, Augentäuschungen, Bauchreden, Begattung, Begierde, Beissen, Bewusstsein, Brühen, Brüten, Brunst, Calor animalis, Chylificatio, Chylus, Chymificatio, Chymus, Circulatio sanguinis, Contractilitas, Cranioscopia, Dens, Diastole, Digestio, Ei, Empfängniss, Erzeugung*.

In addition, he published three important articles for the Rudolph Wagner's Dictionary of Physiology (Handwörterbuch der Physiologie, 1842): The microscope (*Das Mikroskop*), On the senses in general (*Sinne im Allgemeinen*), and On the wakefulness, sleep, dreaming and related states (*Ueber Wachen, Schlaf, Traum und verwandte Zustände*).

Finally, a number of Purkyně's seminal discoveries were published in dissertations of his students Heinrich C. Krauss (Krauss 1824), Alphons Wendt (Wendt 1833), Carolus Deutsch (Deutsch 1834), Marcus Fränkl (Fraenkel 1835), Isacus Raschkow (Raschkow 1835), Mauritio Meckauer (Meckauer 1836), Ferdinand Räuschel (Räuschel 1836), Antonio Hanuschke (Hanuschke 1837), Bogislav Palicki (Palicki 1839), Otto Lüning (Luening 1839), Joseph Ferdinand Rosenthal (Rosenthal 1839), Georg Wilhelm Kasper (Kasper 1840) and David August Rosenthal (Rosenthal 1845). Most of these dissertations, together with Purkyně's seminal contributions to neuroanatomy, neurohistology and cell theory (Purkinje 1834, 1836, 1838, 1845) will be commented and translated in the Part II of this study.

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