

# Leopold Auerbach's heritage in the field of morphology and embryology with special emphasis on gametogenesis of invertebrates

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## Abstract

*Plexus myentericus Auerbachi* and Friedreich–Auerbach disease are widely used eponyms that are associated with eminent morphologist Leopold Auerbach (1828–1897), whose life is relatively little known due to limited access to his German-written XIX century biographies and lack of English biographical papers about him in world literature. Hereby we focused on hardly known achievements of Leopold Auerbach in the field of gametogenesis and embryology of invertebrates. Auerbach did not only confirm unicellularity of amoebas, which was previously discovered. He described cleavage of fertilized eggs of *Ascaris nigrovenosa* and *Strongylus auricularis*. Moreover, his accurate descriptions on germination of *Paracentrotus lividus* inspired a recognized German zoologist Oscar Hertwig (1849–1922). Auerbach also profoundly studied an encystation of *Oxytricha pellionella* on morphological grounds. His descriptions referred to karyokinesis as well as oogenesis and spermatogenesis to discover conjugations of spermatozoa in pairs in the epididymis of a beetle, *Dytiscus marginalis*. He also distinguished two types of spermatozoa of *Paludina vivipara*: the hairlike-shaped (German: *haarförmigen*) and the worm-shaped (*wurmförmigen*) ones of these fresh water (river) snails. His studies on germination (including cell division during cleavage of nematodes) inspired the others, e.g., Oscar Hertwig, and following generations to conclude that “Auerbach deserves the credit for having provided the first scientific foundation for modern teaching on fertilization” according to professor of anatomy Gustav Born (1851–1900) at Breslau University.

**Keywords:** cell division, gametogenesis, embryology of invertebrates, Leopold Auerbach, *Academia Leopoldina*.

Review paper with elements of original biographical study.

## ☞ Introduction

Quite often great titans of medicine, who are famous for certain achievements in world medicine, turn out to contribute to something more. For example, Ambroise Paré (1510–1590), whose name is renowned for surgical hemostasis, was shown to be versatile in various fields of medicine with his valuable remarks on venous origin of subdural hemorrhage, cephalic hematoma or hydrocephalus that are findings on the ground of anatomy and pathology of nervous system of great significance for neurosurgery [1]. Similarly, Leopold Auerbach, who is mainly recognized due to his description of *plexus myentericus*, had important accomplishments in other fields of medicine. Actually, a great deal of his scientific work was focused on species of invertebrates [2, 3]. Therefore, putting aside his well-known merits for development of neurology, we took extensive care to prepare a biographical paper that would summarize his heritage in the field of parasitology and particularly cell biology, as well as embryology of invertebrates. The biography of Leopold Auerbach is a story of heroic life of Jewish medical doctor and researcher, who devoted all his life to medical science facing discrimination [2, 3]. It is worth to recall about his calm personality and still consequence with which he dealt with problems that lied ahead his academic work [2, 3].

This commemorative paper is based on original historical sources and is thematically focused on analysis of scientific heritage of Professor Leopold Auerbach from morphological point of view with some legal remarks. Being world famous for his eponymous discoveries in neurology, until 2020 Leopold Auerbach has not been commemorated by English-written biographical paper. After more than hundred years since historical publications of like German-written biographical obituaries by Ferdinand Cohn and Gustav Born, these reports are scarcely accessible for medical audience worldwide. In opposition – for example – his close friend, world-famous botanist and zoologist Ferdinand Cohn, is described in more than five biographical papers about him in *PubMed* records. In the paper, we retrieved and verified biographical data about Auerbach, who is recognized as an eponymous world-famous figure in neurology [2, 3].

His achievements in the field of biology of invertebrates are completely unknown but they reflect his perceptiveness and charm with universality of areas that Auerbach explored in that content [2–7]. The attractiveness of the topic of invertebrate pathology is truly emphasized by the whole route of scientific activity of Auerbach, who started with research on neuromuscular issues of vertebrates to get completely absorbed with germination of invertebrates

[2–7]. In his life, Auerbach belonged to such a versatile XIX century scientists whose nature should be reminded to all scientists at present who could discover a great usefulness of cooperation in the scientific team as currently hardly any individual shares all the universal features of academic titans like Auerbach.

## ☞ Materials and Methods

There has still not been written in English his comprehensive biography that would address in the first place to his studies on invertebrates. Two of his cooperators – eminent zoologist and botanist Ferdinand Julius Cohn (1828–1898) and professor of histology and comparative anatomy in Wrocław, Gustav Jacob Born (1851–1900) – prepared fine extensive obituaries in German to commemorate Leopold Auerbach in the end of XIX century and to constitute a *in situ* resources as they witnessed a great deal of biographical facts from his life [2, 3]. These two papers were followed by two important biographical reports by eminent physiologist Paul Friedrich Ferdinand von Grützner (1847–1919) and great German medical historian Julius Leopold Pagel (1851–1912) in such fundamental documents as respectively *Allgemeine Deutsche Biographie* dated on 1902 and *Biographisches Lexikon* from the year 1901 [4, 5].

The current biography of Leopold Auerbach is placed also in a broader context of the contemporary society to explain – at least in part – the determination of Leopold Auerbach in his professional efforts. In provided sources, we point that different dates can be given for various events of Leopold Auerbach's life depending on a biographer. Our work was to highlight these details and, in some cases, to choose the right one from accessed data in order to provide the most official and reliable version of Auerbach's life.

## ☞ Results

### Biographical note

Leopold Auerbach was born on April 28, 1828 in Wrocław (Breslau at the time) in Jewish merchant family [2–5]. His education started with private lessons to be continued at the age of 11 years old with admission to the Elisabeth-Gymnasium in Breslau with break for the years 1841–1842 and return school in St. Matthias Gymnasium where he passed a graduate exam of matriculation in 1844 at the age of 16. He enrolled University of Wrocław for medical studies which he continued in Berlin (*Friedrich-Wilhelms-Universität* at the time, now *Humboldt-Universität zu Berlin*) to defend Latin-written inaugural dissertation of his doctorate about critical studies on stimulation of nerves on 18 January 1849 [2–8]. He returned to soon pass the state medical examination and work as general practitioner, with special emphasis on the field of neural sufferings, as well as electrotherapy (Figure 1) [2, 3].

His fundamental academic education was greatly influenced by Breslauer Professors: mainly Jan Evangelista Purkyně (1787–1869) and Johann Heinrich Robert Göppert (1800–1884) as well as Berliner masters Johann Lukas Schönlein (1793–1864), Christian Gottfried Ehrenberg (1795–1876), Johannes Peter Müller (1801–1858), Robert Remak (1815–1865), Rudolf Ludwig Carl Virchow (1821–

1902), and then deepened in his tireless cooperation with his friends, especially Hermann Rudolph Aubert (1826–1892) and Ferdinand Cohn. In 1862, Auerbach made a first-class discovery of a ganglion plexus between longitudinal and circular layers of intestinal *tunica muscularis propria* in vertebrates, which he called the *plexus myentericus* [9, 10]. Then, he wrote his habilitation dissertation on innervations of the gizzard of the birds, which was issued on May 5, 1863, as it was formally and the most officially documented at the title page of its original publication [11]. However, in 1897, Cohn reported that Auerbach obtained associate professorship on the 3rd May 1863, which could be a real date of academic procedures of Auerbach's habilitation, in which Cohn personally participated [2]. Auerbach was employed in the position of supernumerary Professor (*außerordentlicher Professor*) at the University of Wrocław in 1872 (according to Born) or in 1875 (according to Cohn) [2, 3].

After period of investigation of lymphatic vessels, he focused on studies on invertebrates [2, 3]. Leopold Auerbach was not resourceful in his relations with university administration [3]. Namely, he was never given even an assistant to help him [3]. Although he felt much solidarity with academic community, he was absolutely individual and autonomic in his surveys. He lived and worked “surrounded with glasses and tins (original phrase of Gustav Born authorship: *Mit Gläsern, Büchsen rings umstellt*)” at his own apartment at Agnesstrasse 2 (now Michał Bałucki street) in Wrocław [3]. It was the place, where he shared time for his medical practice and scientific explorations [3]. In a position of such a private professional activity, he overcame a hundred external obstacles, which most other researchers did not have even slight idea of [3]. In this perspective, his scientific achievements became even more stunning [2, 3, 5, 6]. Being himself of calm nature, here at home, Auerbach found silence and peace without feeling a tension of constant competition that can accelerate efforts of other scientists [3]. He had five children [2]. Actually, his cheerful, highly musical wife of extraordinary intellectual silhouette, Arabella Hess (4 August 1837–2 July 1896) added most of energy and enthusiasm to his life [2, 3]. She brought her husband a great relief in his hard work not only with music and other sorts of intellectual joy, but also made him involved in actions of charity as she inspired him with plenty of social projects [2]. On her immense, enthusiastic influence, a rather reserved Auerbach was elected to be an alderman in the Wrocław City Council and served as a member of the deputation for the administration of the All-Saints' Hospital in his hometown [2]. He was also active member of Silesian Society for Native Culture (*Schlesische Gesellschaft für vaterländische Cultur*) since 1850 [2]. With the death of his wife, in 1896, his creative work was completely stopped [3]. In summer of 1897, Auerbach started suffering from febrile seizures and soon he died on September 30, 1897 [2, 3]. He was buried in the same grave with his wife in the Jewish Cemetery at Ślężna Street (at the time Lohestrasse) in Wrocław (Breslau) [2, 3]. His celebrated friend Ferdinand Cohn mentioned that Auerbach received only few honors [e.g., Order of Red Eagle (*Roter Adlerorden*) IV Class] in disproportion to his numerous merits [2].

## Investigations in the field of gametogenesis and embryology of invertebrates

Auerbach published his first major study in the field of protozoa in the *Journal of Scientific Zoology*, in 1855 [11, 12], where he described cellular nucleus in the amoeba as a single living cell and demonstrated unicellularity of various types of amoeba in support of opinions of Albert von Kölliker [born Rudolf Albert Kölliker (1897–1905)] and Philipp Franz Balthasar von Siebold (1796–1866) who proved protozoans to be unicellular organisms [3, 12]. Auerbach conducted various studies on the eggs of the nematodes, e.g., observations within compression of the eggs of *Ascaris nigrovenosa* and *Strongylus auricularis* in process of cleavage [13, 14]. He further investigated development of nematodes from fertilization to note disappearance of the first nucleus of the fertilized egg cell from the fusion of two nuclei of gametes and its replacement with “dumbbell-shaped” figure of clear protoplasm with further classical steps of cell division [14]. Actually, Auerbach was the first to report that the primary nucleus emerged from fusion of two nuclei in the fertilized oocyte [3]. According to Gustav Born, “Auerbach deserves the credit for having provided the first scientific foundation for modern teaching on fertilization” [3]. Auerbach's findings and descriptions of germination were so detailed that recognized German zoologist Oscar Hertwig (1849–1922) got inspired by them particularly regarding *Toxopneustes lividus* (according to Lamarck's nomenclature from 1816, currently known as *Paracentrotus lividus*) [3]. In 1864, he deeply investigated formation of cysts of unicellular organisms of *Oxytricha pellionella* [15].

He wrote about impact of light on fertilized frog eggs in 1870 [16]. He also summed up nuclear changes in course of cell division, in 1876 [17]. On botanical ground, he wrote about cells and cell nuclei in a book edited by Ferdinand Cohn [18]. He closely evaluated changing patterns of distribution of threads of karyokinetic spindle of cellular nuclei in 1877 [19]. In the late period of his scientific activity, Auerbach focused on morphology of oocytes and spermatocytes [2, 3]. In this field, Auerbach was so prolific that Waldeyer advised the Prussian Academy to grant him a new Zeiss microscope with all modern aids and a good microtome in 1889 and soon Auerbach applied newer methods of paraffin embedding, microtome cutting and staining [3]. He provided characteristics of gametes regarding different chromatophilia of components of female germ cells and sperm, in 1891, to conclude that “male fertilization substance is a cyanophilic, the female fertility substance an erythrophile” [20–22]. He generalized that in all vertebrates the head of the mature spermatozoon is cyanophilic, while middle part of its tail is erythrophilic [23]. Since 1893, Auerbach was focused on development of spermatozoa of invertebrates [3]. He investigated sperm of *Dytiscus marginalis*, in 1893, to find conjugations of spermatozoa in pairs in the epididymis and to confirm Emil Ballowitz's (1859–1936) notice of double spermatozoa in this kind of beetle [23, 24]. He also tried to explain a theory of double staining, in his publication of 1894 [25]. In his last reports, he distinguished two types of spermatozoa of *Paludina vivipara*: hairlike-shaped (German: *haarförmigen*) and the worm-shaped (*wurmförmigen*) ones and the spermatogenesis of these fresh water (river) snails of *P. viviparus* species [26, 27].



Figure 1 – Medical Doctor Leopold Auerbach.

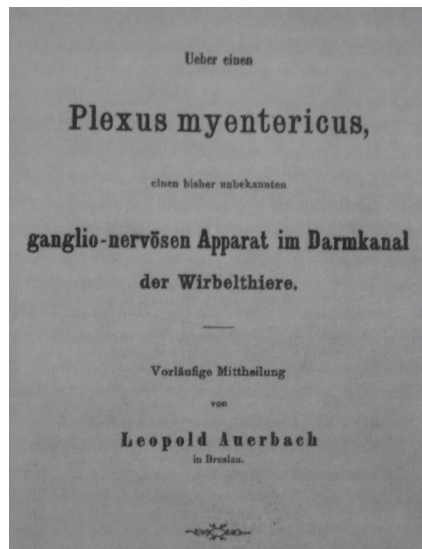


Figure 2 – Title page of Leopold Auerbach's report (dated on 1862) on plexus myentericus which brought him an eponymous fame in world medicine.

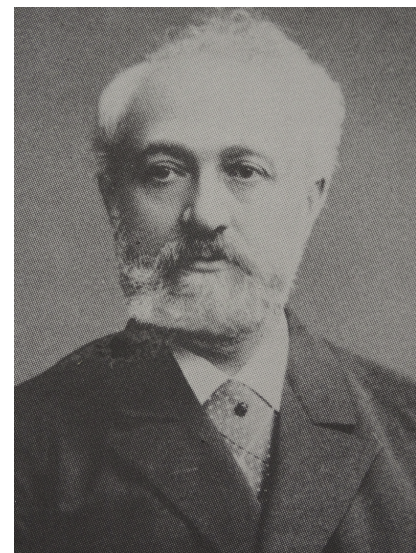


Figure 3 – Professor of Medicine Leopold Auerbach.

## Final remarks

As mentioned at the start of this paper, Leopold Auerbach was born and raised in Jewish family in Wrocław (Breslau at the time in German Empire) [2, 3, 5, 6]. He belonged to the ethnic minority of different culture and faith that suffered plenty of restriction and was severely

discriminated in centuries of European history [28, 29]. The access to education, particularly to University studies was an entrance for Jews to better life in support of enlightened academic community. University employment was recognized as a kind of ennoblement what was particularly evident in Breslau, where the University was founded as *Academia Leopoldina* (surprisingly having

the same initials 'AL' as name and surname of Leopold Auerbach) by Emperor Leopold I, in 1702, and located in a place of the former, medieval Piast castle and later imperial residence, that was completely rebuilt to form stunning baroque edifice in XVIII century (Figure 4) [30].



**Figure 4 – The view a baroque edifice of Wrocław University, which was built on remains of monarch's castle as Academia Leopoldina in XVIII century.**

In XIX century, the emancipation of German Jews took place in two ways, already described by Wilhelm von Humboldt in his memorial on *Judenordnung* [28, 29]. The first model – the path of revolutionary reforms – was adopted in the Grand Duchy of Berg and in the Kingdom of Westphalia, where anti-feudal reforms were introduced under the influence of the French Revolution so the provisions of the Napoleonic Civil Code (including the principle of equality of residents) were introduced. Characteristically, the first King of Westphalia, Jérôme Bonaparte – the youngest brother of Napoleon – first issued the Constitution of November 15, 1807, in which equality of inhabitants was proclaimed regardless of religion, and only by decree of January 27, 1808, special taxes paid by Jews were abolished [31]. In the Grand Duchy of Berg, equality was introduced by ordinance of July 22, 1808 and was associated with the need to enlist Jewish citizens in the army [31]. The Prussian Kingdom adopted a different model. Namely, equality was achieved through the top-down gradual abolishment of legal restrictions in various areas of life. The Kingdom of Prussia had the largest Jewish population among German states as 124 000 Jews lived there in 1816 with their large community in Wrocław [28]. Gradual legal emancipation of Prussian Jews was characteristically forced at times of weakening the Prussian Kingdom through internal unrest or in the event of a threat to the state by armed intervention from outside. Thus, the most important legal acts were issued during the Napoleonic Wars (the Emancipation Act of the Jews of March 1812), during the Spring of Nations and shortly before the unification of Germany [28]. According to Professor of History at Wrocław University and the Jewish Theological Seminary of Breslau (*Das Jüdisch-Theologisches Seminar Fränckel'scher Stiftung*), Heinrich Graetz (31 October 1817–7 September 1891), it is impossible not to notice numerous social practices that contradicted the letter of the law remained in social practice despite the lengthy emancipation process and

despite formal equality [28]. The Jewish emancipation was not controlled by revolutionary methods but executed and limited by administrative measures [28]. However, it was flawed by defective applying of the law due to emerging anti-Semitism [28]. The legal status of Jews living in Prussian Wrocław at the beginning of the XIX century was governed by the General Statute for Jews of April 17, 1797 (*General-Juden-Reglement für Süd- und Neu-Ostpreussen*). Jews were divided into two groups – protégés and tolerants –, special taxes paid by Jews were maintained, and a list of professions available to Jews (mainly related to services, including transport, trade, and craft) was established. Art. 12 of the Statute allowed the access of Jews to municipal government – but this was not implemented for a long time because of the opposition of the municipal government. Changes were brought by the City Act of November 19, 1808, which gave citizenship to every resident who met the census of possession and education – according to §15 and §23 this applied to property owners and entrepreneurs. This opportunity was also given to freelancers – including medical doctors and scientists – if they were the owners of the property [32]. Pursuant to §19 of the City Act, state, birth, and religion did not matter here [32]. Preparing for the liberation war from the domination of the French Empire, the Prussian Kingdom wanted the widest possible involvement of the general population in it. Representatives of the Jewish communities of Berlin, Königsberg and Wrocław submitted the request in this matter to King Frederick William III. To this end, the Act of March 11, 1812 – *Edikt betreffend die bürgerlichen Verhältnisse der Juden in dem preußischen Staate* –, was enforced [29]. The March Act equated to some extent the rights of tolerated Jews with the rights of other citizens (however, obtaining their citizenship required the fulfillment of many conditions), they gained the freedom to settle, buy and sell real estate, freedom to choose a profession, they could hold teaching positions, their position in the administration was to be decided by a separate Act (which, however, was never issued). Special taxes and fees, which were charged only to Jews, were abolished. Pursuant to §16 of the Act, military service was imposed on them, which caused lots of young Jews to fight in the ranks of the Prussian Army against Napoleon in Jewish troops [33]. The shape of this great reform was greatly influenced by the memorial of Wilhelm von Humboldt – head of the Department of Confessions of the Prussian Ministry of the Interior from July 1809. At the same time, it is impossible not to notice that the new rights of Jewish citizens were enumerated in the Act, and the subsequent practice of their application led to a narrowing of their content [33]. During the Restoration period, several reforms were withdrawn. In 1818, the government decided to exclude Jews from public service – they could no longer perform some functions in city councils and the function of judge. From 1831, they could not be mayors [33]. In August 1822, Jews were forbidden to occupy academic positions – at that time, Jews dealt almost exclusively with medicine and natural sciences [34]. Ultimately, in the years preceding the Spring of Nations, Jews could only serve as private Associate Professors at Prussian universities, and exclusively in medical faculties they could be

supernumerary Professors (German: *außerplanmäßiger* or *außerordentlicher Professor*). After the reactionary power of Frederick William IV – a supporter of departing from the provisions of the Emancipation Law of 1812 and the prohibition of military service for non-Christians – the Jewish public tried to stop adverse changes in the 1840s. Discussions were initiated in the press, Jews participating in the work of political organizations raised this problem, also at the forum of eight Provincial State Parliaments. The Silesian Provincial State Parliament appealed to the King to extend the principles of the Emancipation Law to the entire country – including the Grand Duchy of Poznań [35]. Liberal parties saw equal opportunity to increase social and cultural integration. Jews, who were rather the subject of government policy in Prussia, became a natural ally of progressive movements, and their importance increased with the number of inhabitants – in 1846, there were already 193 000 Jews in Prussia, and in Wrocław alone about 7000. In 1847, the first Prussian Parliament was convened, consisting of an aristocratic Upper and Lower Chamber, which included representatives of the nobility, middle class, and national minorities. In the Lower Chamber, the majority (which did not include young deputy Otto von Bismarck) wanted to admit Jews to all communal and state offices, except for religious matters, and to professorships at universities [36]. It was argued that Jews constituted a valuable part of German society – medical doctors, lawyers (though neither attorneys nor judges), and journalists [34]. As a result of parliamentary work, the Prussian government issued an Act of July 23, 1847, according to which Jews were admitted to those state positions that did not involve the exercise of police, judicial and enforcement powers; the value of their testimony in Court was equated with that of Christians; at the universities of the medical, geographical, natural and linguistic faculties, Jews were allowed to be Associate Professors, supernumerary and full Professors, but without the right to sit in the Senate, occupy the functions of Rector, Vice-Rector and Dean [34]. This rather conservative Act was not well received in the progressive circles. The following year, under the influence of revolutionary events, the Constitution of April 6, 1848 was adopted, whose §5 directly made the exercise of civil rights independent of religion. This was repeated in §12 of the Constitution revised by the King on December 5, 1848, stating that it recognized civil and political rights. It is impossible not to mention here the Act on the Cardinal Rights of the German Nation adopted in Frankfurt, which in Art. 5 proclaimed full equality [28]. After the fall of the Spring of Nations, pro-emancipation legislation was revised, but some of the achievements have survived – in particular, the Act of January 31, 1850 retained the general principle that the exercise of civil rights is independent from religion. In practice, Jews were not allowed to act as judges and Professors at universities, they were even removed from the position of junior high school teachers [36]. In general, it can be said that full equality in practice only remained in the field of civil rights. Political and civil rights returned to their pre-Spring of Nations status [36]. It is worth comparing this with the fact that we are talking about a period of rapid economic changes in which Jewish capital

played an important role in the development of banking, becoming the initiator in the creation of public credit institutions and German industry. Jewish capital was to play an important role in the construction of the railway network, in the developing industry of textiles, precious metals and in building of department stores. The Jewish working class was seen in manufactures and factories as a competition for Christian workers [28]. From ghettos, Jewish population blended into German culture, a process that was adopted with unjustified aggression and distrust of the part of the German society. It seems that religious motives played a smaller role in them, and economic reasons became the decisive component. At the time, the intellectual and religious life of the Jewish community flourished in Wrocław, and the Jewish Theological Seminary of Breslau was founded in 1854 there [28]. The way to formal equality in Prussia ended with the issue of the Act on equality of denominations in terms of citizenship and state of July 3, 1869 [37], lifting all remaining formal restrictions on the rights of the Jewish minority in the territory of the North German Union. At the same time, Jews were often elected to high positions in municipal governments. Thanks to the property census, they filled up to a quarter of places in the Wrocław City Council [28]. Despite formal equality after the reunification of Germany, some actual (though not legal) elements of discrimination have been preserved. This mainly concerned personnel policy – despite the very large number of Jews among lawyers, it was rare for them to take Court or senior administrative positions. A particularly apparent example of discrimination was the employment policy in the army. Their situation was greatly aggravated by the wave of Jewish migration from the eastern lands, which became the pretext for a broad anti-Semitic campaign in the Second German Empire [38]. The four new policy priorities were formulated for Jews by Chancellor Otto von Bismarck which included a ban on holding administrative offices by Jews and restrictions on “all immigration of foreign Jews”, which was followed with expulsion of 10 000 Polish Jews from Germany as recorded another one Leopold Auerbach (1838–1900), a lawyer who was born in Prague and worked in Vienna in his paper dated on 1890 [39]. As shown above, creative work, that determined progress of the whole civilization, did not rescue German Jews from oppression [36, 37]. Professor of Medicine at Breslau University, Leopold Auerbach did not experience the grim scenario of discrimination, but a gradual aggravation of persecutions culminated in tragic suicide death of his son, a world recognized physicist Felix Auerbach (1856–1933) and his wife Anna, in their magnificent, modernly designed villa in Jena, not a month after Adolf Hitler assumed the office of German chancellor [40, 41]. The heritage of Leopold Auerbach provided substantial impact in progress of the knowledge in the field of embryology at the time. As he is regarded mostly as a histologist because Auerbach discovered a histological structure of *plexus myentericus*, it is not surprising that as scientist shared his interests between histology and embryology or – to better say – his scientific activity naturally joined morphology and embryology. Indeed, histology usually goes with embryology and histologists all over the world are frequently fine

embryologists, as in the case of Alexandru Țupa (1886–1956) and Cornel Crișan (1895–1958), whose high moral standards together with overall humanistic attitude had profoundly beneficiary impact on medical education of generations of students [42]. Similarly, a silhouette of world-famous Leopold Auerbach has deserved at least one biographical record in *PubMed* repository as until 2020 there has not been any English written paper about him in any journal indexed in *Medline*. The example of Leopold Auerbach demonstrates how comprehensive interests of XIX century morphologists were and how essential part of their scientific output was made in the field of biology of invertebrates [2, 3].

### Conflict of interests

The authors declare that they have no conflict of interests.

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