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Protistology

A brief history of ciliate studies (late XVII - the first third of the XX century)

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Summary

The most prominent protistologists who worked with ciliates from the Leeuwenhoek time up to the beginning of the XX century are mentioned. Their achievements in ciliatology and especially in taxonomy of ciliates are briefly discussed on the basis of the original literature and reviews, published during the last 150 years.

Key words: ciliates, history of ciliatology, protists

Ciliates were among the first living microscopic organisms to be discovered and described by A. Leeuwenhoek (Dobell, 1932) and have attracted much scientific interest ever since. Apart from a plethora of studies devoted especially to representatives of this group, some ciliates are favourite model objects used in diverse investigations in the fields of cytology, molecular biology, genetics, biochemistry and physiology. Despite of a number of publications dedicated to the history of protistiology (Calkins, 1901; Cole, 1926; Brodsky, 1937; Corliss, 1978, 1991,1997; Kuznicki, 1982; Entzeroth, 1994; Geus, 1994; Leadbeater and McCready, 2000; Vickerman et al., 2000; Fokin, 2001a; Wolf and Hausmann, 2001; Kuznicki, 2003), the major historical stages of development of ciliatology are still not enough reflected in modern literature. Especially it is true for the development of ciliatology in Russia and some other Eastern European countries. The present article attempts to fill this blank at least in part.

Early studies of the world of protists were triggered by the invention and progress of microscopes in the first half of the XVII century. However, at first microscopes interested only a few physicists, astronomers and philosophers (Sobol, 1949). "The invisible world of living creatures" waited for its researcher. More than half a century since the invention of the microscope had passed, before such a man appeared: a manufacturer from Delft and a self-taught optician Antony van Leeuwenhoek (1632-1723) (Dobell, 1932; Corliss, 1975, 2002). Though he had no scientific education, it was Leeuwenhoek who made the first reliable observations of live ciliates. He described them, as well as many other microscopic objects, in his letters to the London Royal Society starting from 1674 (Dobell, 1932; Corliss, 1975). Leeuwenhoek was also the first to draw a ciliate (apparently, *Nyctotherus*), from the frog's

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gut (1683). Those observations, amazing for their time, were made with the use of very simple microscopes, in fact, magnifying glasses, which, however, allowed a remarkably high magnification (up to 300 times). Leeuwenhoek introduced a lot of technical innovations and was probably the first to achieve in his microscopes the illumination effect resembling the present-day "dark field".

Judging from his detailed descriptions, Leeuwenhoek dealt with *Carchesium, Chilodonella, Coleps, Colpidium, Cyclidium, Dileptus, Kerona, Paramecium, Vorticella* and a number of other ciliates (Corliss, 1975). He did not only mark morphological details of the "animalcules" observed but also measured them, described their reproduction, retractivity and apparently some conjugation stages.

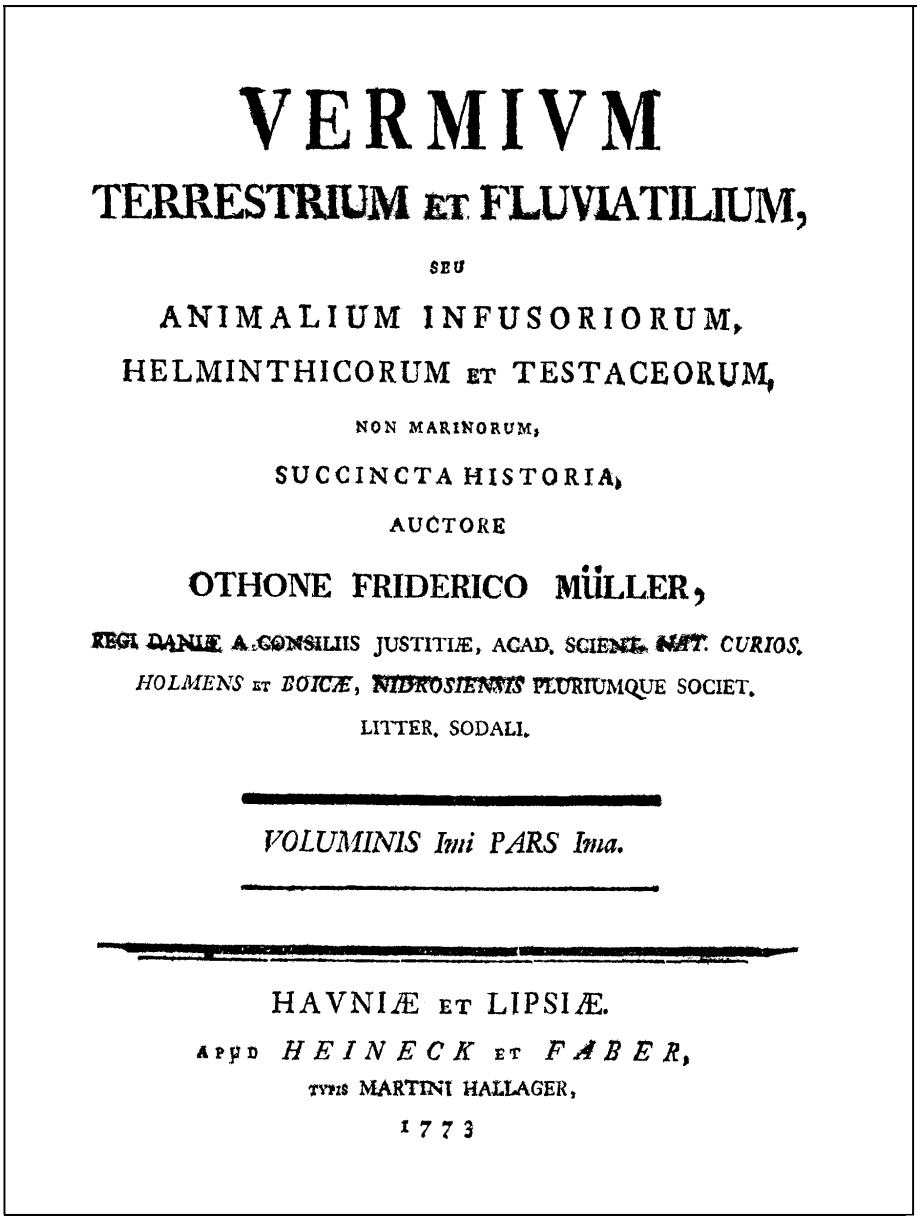
At the same time, however, the "invisible world" attracted several more researchers. For instance, in 1678 Ch. Huygens (1629-1695) described several ciliates in a letter to his brother (Dobell, 1932). Buonanni (1638-1725) was the first to publish a drawing of a ciliate (apparently, *Colpidium*) in 1691 (Cole, 1926). Two year later King sketched several protists, including *Euplotes* (Corliss, 1991).

The middle of the next, XVIII, century was dominated by the ideas of Carl Linneaus (1707-1778), the father of modern taxonomy and biological nomenclature. Being a botanist, he had little concern for water "animalcula" and did not trust the microscope. Only the 12th edition of his *Systema Naturae* (1767) included protists (four genera), two of which were personified as *Volvox* and *Vorticella*. The rest of Protozoa were huddled into two other genera, whose names, *Chaos* and *Furia*, told their own tale. "Mysterious living molecules, to be understood by our descendants", that was how Linnaeus characterised ciliates (Sobol,1949). However, as early as in 1703 an anonymous author published a drawing of, unmistakably, a paramecium (Woodruff, 1945; Wichterman, 1953). The same ciliate was investigated by L. Joblot (1645-1723), who produced in 1718 a pioneer description of ciliature, nuclei and contractile vacuoles in ciliates. In 1752 J. Hill (1717-1775), in his famous "History of Animals", gave the "slipper-shaped" ciliate its present name, *Paramecium*. He is the author of many other names, including *Cyclidium* and *Enchelys*. Unfortunately, Hill's priority has not been retained, because his descriptions were made 6 years before the January of 1758, since which time, according to the International Codex of Zoological Nomenclature, generic names are accepted as valid. Also in 1744-1748, A. Trembley (1700-1784), renown for the study of the hydra, investigated division in "funnel-shaped polyps" (ciliates from the genus *Stentor*) and described reproduction in *Epistylis, Carchesium* and *Zoothamnium* (Kanaev, 1972; Corliss, 1991).

Altogether, quite many XVIII century scientists described and made sketches of ciliates and other tiny animals, unicellular or multicellular (flagellates, amoebae, rotifers, trematode larvae), then considered as "infusoria" (see Kutorga, 1839). S.S. Kutoga (1805-1861), one of the first Russian scientists to study ciliates, wrote in 1839: "this discovery [of infusoria] excited all the researchers, and everybody in possession of a microscope hastened to enjoy the sight of perpetual movement of this invisible world". Among the researchers fascinated by "infusoria" were Baker (1698-1774), who described *Lacrymaria* in 1753, and Wrisberg, who first applied the term "infusoria" to protists (1765). In 1769 Ellis (1710-1776) experimentally induced extrusion of trichocysts in *Paramecium*, and in 1796 Guanzati first described cysts in a ciliate, belonging presumably to the genus *Amphileptus* (Corliss, 1991). Somewhat earlier (1754) Joblot described the contractile vacuole and noted the characteristic position of cilia in different ciliates.

Scientific achievements of O.F. Müller (1730-1784), a famous Danish zoologist and the first systematist of ciliates, deserve special mention (Corliss, 1986). His outstanding monographs "Vermivm terrestrium et fluviatilium seu animaliun infusoriorum, helminthicorum et testaceorum" (Müller, 1773) and "Animalcula infusoria fluviatilia et marina" (Müller, 1786) contain about 300 species descriptions of bacteria, protists (mostly marine and freshwater ciliates) and small multicellular animals. Müller described ciliates from marine sand, scuticociliatids, gymnostomatids, tintinninds, oligotrichs, suctoria, the colonial *Ophridinium*, the marine loricate *Folliculina*, and made notes on their ecology and physiology. In naming the animals discovered he adhered to the binominal nomenclature rules, and many Latin names of ciliates are still followed by the letters O.F.M. Müller should be credited with the correct interpretation of the conjugation phenomenon in ciliates as a sexual process. More than 100 years had to pass before protozoologists (Balbiani, 1861) finally accepted this notion. Noteworthy, Müller considered protists as the most simply organized living creatures, a view supported by the natural philosophers – Lamarck, Schweigger, Oken – who relied on Müller's works.

The first Russian protozoological research dates back to the late XVIII century. A zoological-physiological dissertation of M.M. Terekhovsky (1740-1796), "On Linnaeus' Chaos infusorium" (1775), was defended in the University of Strasbourg (Sobol, 1949). On the basis of long-term successive experiments with different infusions, the author proved in 88 paragraphs of his dissertation that ciliates "as all animals, originate by way of reproduction from antecedent parents". Thus, as early as in 1775, Terekhovsky confuted the wide-



VERMIVM
TERRESTRIUM ET FLUVIATILIUM,
SEU
ANIMALIUM INFUSORIORUM,
HELMINTHICORUM ET TESTACEORUM,
NON MARINORUM,
SUCCINCTA HISTORIA,
AUCTORE
OTHONE FRIDERICO MÜLLER,
REGI DANIÆ A CONSILIIS JUSTITIÆ, ACAD. SCIENT. NAT. CURIOS.
HOLMENS ET BOICÆ, NIDROSIENSIS PLURIUMQUE SOCIET.
LITTER. SODALI.

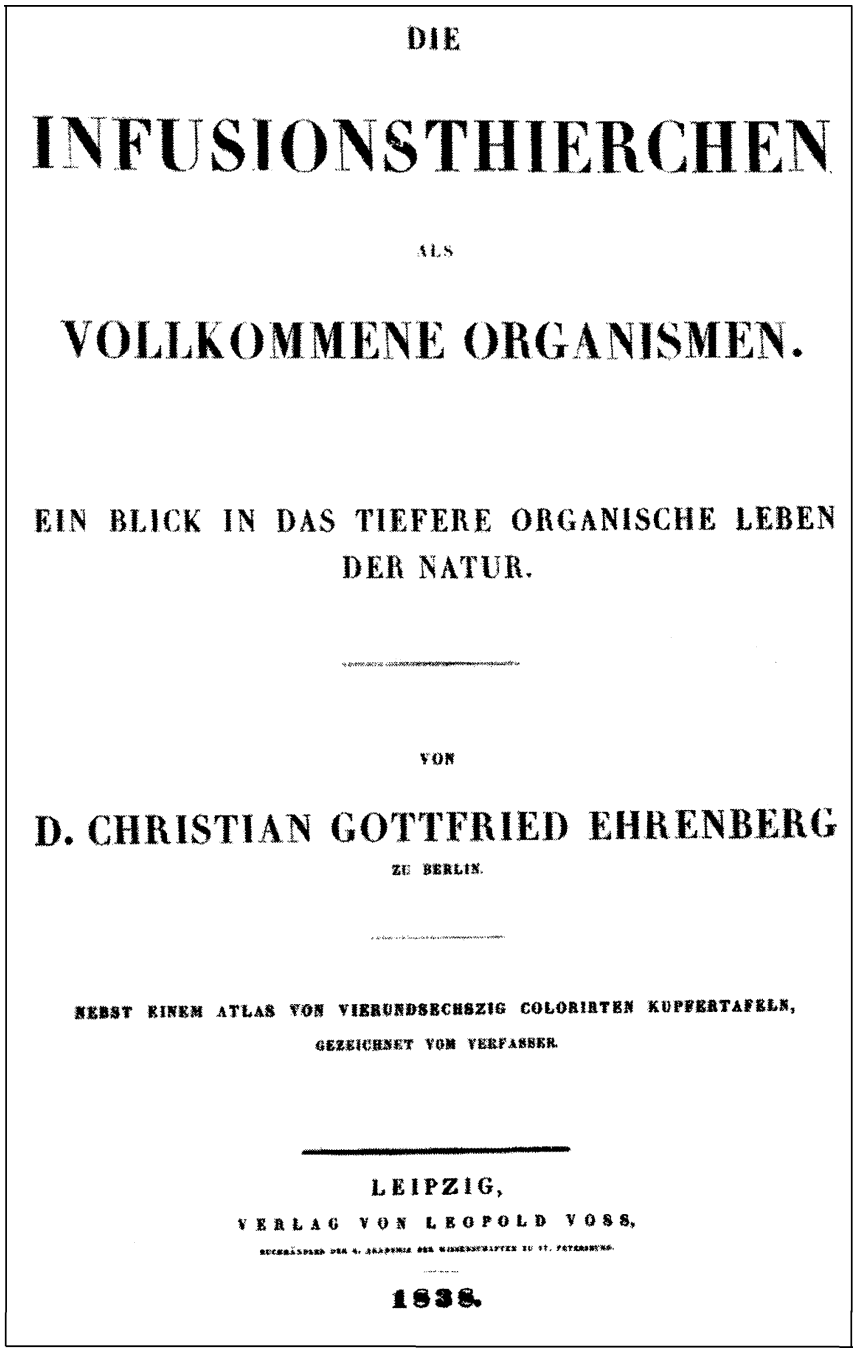
VOLUMINIS Imi PARS Ima.

HAVNIÆ ET LIPSIÆ.
APUD *HEINECK ET FABER*,
TYPIS MARTINI HALLAGER,
1773

spread theory about spontaneous generation of ciliates, giving an infallible proof of their animal nature. The main works of L. Spallanzani (1729-1799) on this topic saw light in 1765 and 1776. These problems stirred the scientific world even in the first half of the XIX century. "Let those destined to study the nature deeper determine whether these water animalcula belong to worms, or to insects, or to some other animal class", – wrote Terekhovsky in the conclusion of his dissertation. – "Let them also, following Hill and Müller, determine more precisely their genera and species" (Sobol, 1949). This task was to be accomplished in the next century.

The XIX century brought about an unheard-of interest in protists, that manifested itself in two main directions. Firstly, descriptions of new protistan species and their morphological studies continued, which was associated with a broader geographical range of studies and further improvement of microscopic techniques: the invention of the Chevalier complex object lens, the Lister microscope and the Ross correction eye-lens (see Karpov, 2001). Secondly, after the "critical mass" of species descriptions had been accumulated and comparative taxonomic studies began (Corliss, 1992), attempts at classification of protists on the basis of characteristics of their groups became possible.

The next prominent researcher and systematist of ciliates after O.F. Müller was, undoubtedly, Ch. G. Ehrenberg (1795-1876), who started his scientific career in the first quarter of the XIX century. After publication of a fundamental monograph "Infusionsthierchen als Vollkommene Organismen" (Ehrenberg, 1838), containing descriptions of more than 350 species



DIE

INFUSIONSTHIERCHEN

ALS

VOLLKOMMENE ORGANISMEN.

EIN BLICK IN DAS TIEFERE ORGANISCHE LEBEN DER NATUR.

VON

D. CHRISTIAN GOTTFRIED EHRENBERG

ZU BERLIN.

NEBST EINEM ATLAS VON VIERUNDSECHSZIG COLORIRTEN KUPFERTAFELN, GEZEICHNET VOM VERFASSER.

LEIPZIG,

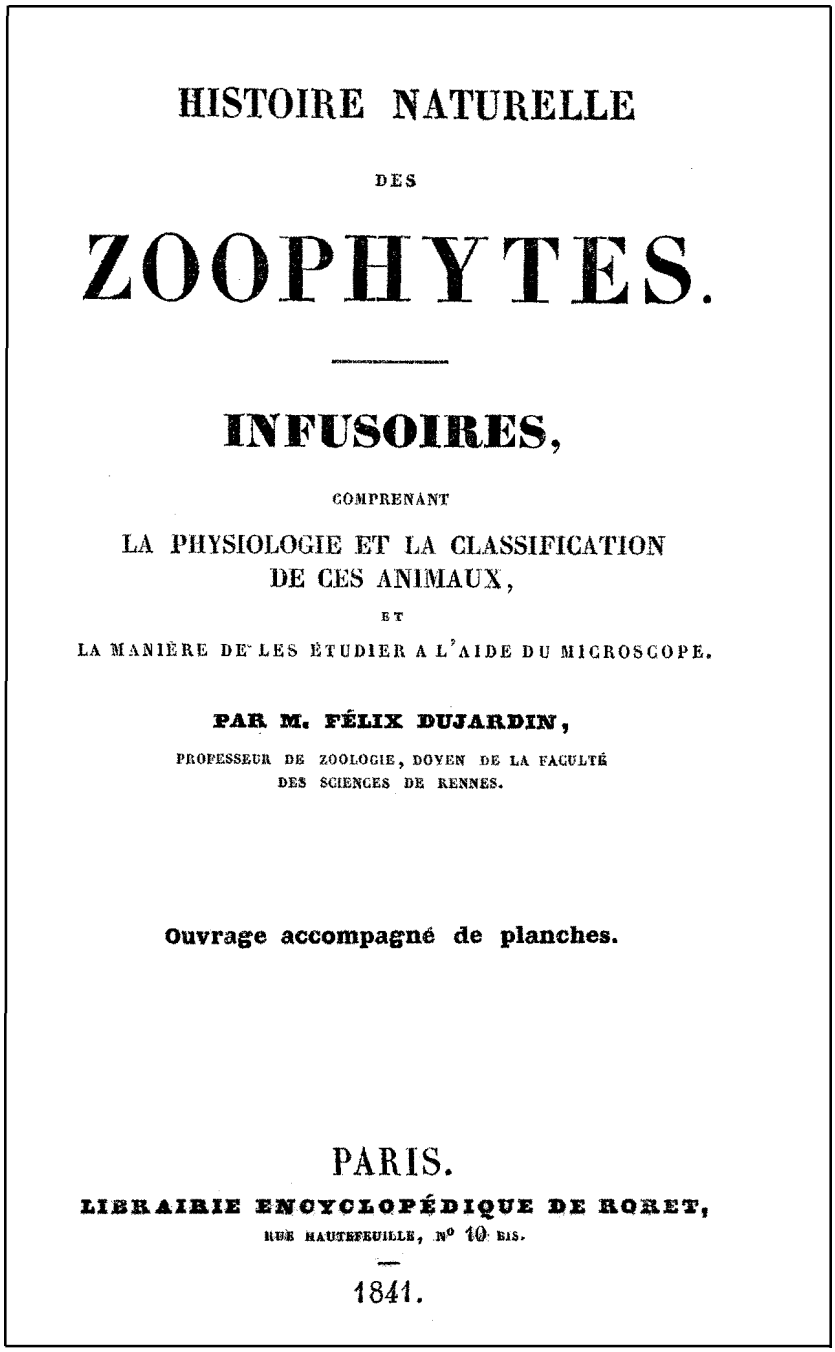
VERLAG VON LEOPOLD VOSS,

BUCHHÄNDLER DER K. AKADEMIE DER WISSENSCHAFTEN ZU ST. PETERSBURG.

1838.

of "infusoria" (as understood at that time), numerous brilliant illustrations and elaboration of "polygastric" theory of their organisation, Ehrenberg became a protozoological authority beyond exception. As a matter of fact, it was owing to his efforts that this latter discipline emerged within the framework of zoology. At the same time, Ehrenberg's view on infusoria as on "perfect" animals (possessing, in miniature, all the features of multicellular ones) certainly retarded the studies of Protozoa, a term coined by G.A. Goldfuss (1782-1848) (Goldfuss, 1817). Ehrenberg's theory, elaborated prior to the publication of the basics of the classical cellular theory (1838-1839) of T. Schwann and M. Schleiden, reflected a "common-sense" approach to functioning of a living organism. Presence of cercariae and rotifers among the "infusoria" of those days also made one look for features of a similar organisation in ciliates, and, of course, such features were found. Ehrenberg "discovered" in infusoria the digestive tract (including teeth and various glands), musculature, sexual organs, eyes and anlages of the nervous system.

Ciliate classifications in early XIX century were in fact modifications of those by J.-B. Lamarck and G.



HISTOIRE NATURELLE

DES

ZOOPHYTES.

INFUSOIRES,

COMPRENANT

LA PHYSIOLOGIE ET LA CLASSIFICATION
DE CES ANIMAUX,

ET

LA MANIÈRE DE LES ÉTUDIER A L'AIDE DU MICROSCOPE.

PAR M. FÉLIX DUJARDIN,

PROFESSEUR DE ZOOLOGIE, DOYEN DE LA FACULTÉ
DES SCIENCES DE RENNES.

Ouvrage accompagné de planches.

PARIS.

LIBRAIRIE ENCYCLOPÉDIQUE DE RORET,

RUE HAUTEFEUILLE, N° 10 BIS.

1841.

Cuvier, who did not study "infusoria" themselves and relied on O.F. Müller's material. For instance, Lamarck in 1815 placed "infusoria" into two first classes of his classification (animals having no organisation and animals close to polyps). Cuvier (1817) put "infusoria" into a separate class, which he divided into two orders: Rotiferes (rotifers) and Infusoires homogenes (wherein all protists were placed). In the book by Schweigger (1820) (Kutorga, 1839), infusoria *sensu* Müller were put into the class of zoophytes, divided into two orders: those consisting of "simple matter" (infusoria) and "heterogeneous" (polyps).

According to Ehrenberg, infusoria (Polygastrica) belonged to zoophytes (or radiata), where they made up two classes: agastrous (amoebae, flagallates, diatoms) and gastrous (ciliates and some actinophorans). The latter group included 4 divisions, with only two characters serving for delimitation: the position of the cytostome and that of the cytoproct, which resulted in an extremely artificial classification. A Russian follower of Ehrenberg, S.S. Kutorga, who compiled a "Natural History of Infusoria" (1839) from the German author's material and some original additions, nevertheless, placed ciliates into the class of articulate

animals. Within this class, he believed them to be closest to Entozoa (internal animals or helminths). The division "infusoria", according to Kutorga, consisted of two orders. The first, Vibratoria, comprised agastrous forms (amoebae and flagellates) and gastrous forms (ciliates). The second order, Rotatoria, included rotifers. The same classification of ciliates was supported by another Russian scientist, P.Ph. Goryaninov (1837), who placed them, however, into zoophytes (Fokin, 2001a).

Though Ehrenberg's interpretations of ciliate organisation were incorrect, his drawings were astonishingly accurate. His studies of geographical distribution of "infusoria" from North Africa, Arabia, Germany, European and Asian parts of Russia for a long time remained the chief source of information on zoogeography of protists. Ehrenberg took part in an expedition to Russia undertaken by A. Humboldt in 1829, thus becoming the first investigator of ciliates in the vast expanses from St. Petersburg to Barnaul. He was very productive and prepared over 120 publications in the field of protozoology during the long life granted to him.

F. Dujardin (1801-1860) was Ehrenberg's junior contemporary. Besides his considerable achievements in the studies of amoeboid organisms (incidentally, it was he who offered the term Rhizopoda), Dujardin also studied ciliates. He was the first to "rebel" against Ehrenberg's theory (Dujardin, 1841). However, his classification, dividing ciliates into symmetrical (*Coleps*) and asymmetrical (all others) proved almost as artificial (see Schewiakoff, 1896). Suggestions that Protozoa consist of a single cell were also made by Meyen and Barry (see Calkins, 1901). By the 1860s, when the division of animals into multicellular and unicellular had been accepted by C.T.E. Siebold (1804-1885) and some others, and the term "cell" clearly defined (H. Moll, F. Leydig and M. Shultze), Ehrenberg's theory was considered outdated. In fact, by that time unicellular animals were already divided into two classes: Rhizopoda and Infusoria (Siebold, 1845), the latter being understood since that time as Ciliata, unicellular animals with cilia (Perty, 1852). At the same time investigations of E.G. Balbiani (1825-1899) started. We owe him the correct evaluation of the sexual nature of conjugation phenomenon in these protists (Balbiani, 1861).

A considerable advance in ciliate studies was made in the 1850s by E. Claparéde (1832-1871) and J. Lachmann (1832-1860). On the basis of original meticulous observations of long standing these two scientists published, a treatise in two volumes: "Les Infusoires et les Rhizopodes", where they distinguished Suctoria as a separate group and divided the rest of the Ciliata into 10 families: (Claparéde and Lachmann, 1858-1861). Noteworthy, these researchers at first considered ciliates to be multicellular, attributing them to the Coelenterata. A. Pritchard published a large review on ciliates (Infusorial Animalcules) in England a few years before (Pritchard, 1852, 1853).

Almost at the same time (1859) the classification of F. Stein (1818-1885) saw light. It was to play a major role in the development of ciliatology in both the XIX and the XX century. Stein took ciliature as the basis of classification and divided Ciliata into 4 orders according to the distribution of cilia: Holotricha, Heterotricha, Hypotricha and Peritricha. Flagellata and Suctoria were also included, in the rank of orders. Curiously, in one of the first macroclassifications of living organisms (Haeckel, 1866), where unicellular animals were already united into the kingdom Protista, ciliates were placed into Articulata, that is, they were again imagined to be multicellular.

Having studied ciliates for decades, Stein described many new genera and species. His classification included as many as 23 families and 107 genera. Stein's painstaking research of the orders Hypotricha and Heterotricha was summed up in two monographs (Stein, 1859, 1867). However, this brilliant series was left unfinished (Stein, 1883). Acineta-theory proposed by Stein (1849) was based on inaccurate observations upon development of peritrichs and suctorians, suggesting the existence of ciliate embryos. It was soon confuted by Cienkowsky, Metchnikoff, Lachmann, Balbiani and Kölliker (see Calkins, 1901; Kuznicki, 1982).

Further development of ciliate studies was closely connected with several scientists: O. Bütschli and R. Hertwig in Germany, E. Maupas in France and W. Kent in England. Born from 1842 to 1850, they belong to the same generation and pursued similar directions of research, but their impact on science was different.

O. Bütschli (1848-1920), called by Dobell "an architect in protozoology" (Dobell, 1951) and by Corliss, "a giant among giants" (Corliss, 1978), began to study ciliates in 1871. Though he was a zoologist of broad interests, it was in protozoology that he left the greatest trace. Curiously, Bütschli's interest in ciliates and his fundamental knowledge in this area apparently arose from self-education: for almost 4 years (1871, 1873-1876) he worked alone in a private laboratory in his native Frankfurt (Novikov, 1922; Fokin, 2004). In 1876 Bütschli published a treatise where the functions of ciliate nuclei were correctly interpreted for the first time after the conjectures of Ehrenberg, Dujardin and Claparéde and the transformations of nuclear apparatus during conjugation were elucidated. For this study he used own data of the nuclear reorganisation process for more than 10 species of ciliates (Bütschli, 1876). It should be noted that Engelmann arrived at the same

conclusions simultaneously and independently, proposing the term "reorganization" for conjugation changes of the nuclear apparatus (Engelmann, 1876).

Besides the ciliates' sexual process, Bütschli studied their physiology and morphogenesis, life cycles and cytology. The latter investigation area led to analysis of protoplasm structure, where Bütschli applied his knowledge of colloid and physical chemistry. His theory of alveolar cytoplasm structure created in 1890s was widespread even in the first quarter of the XX century (Bütschli, 1892; Novikov, 1922; Hartmann, 1929).

For 42 years Bütschli was professor of zoology in Heidelberg. One cannot help mentioning that many young people, who studied and worked in Heidelberg at different times, "passed through" his protozoological school. Among them were the renown German and Russian protistologists and cell biologists: F. Blochmann, R. Lauterborn, R. Goldschmidt, C. Hamburger, W.T. Schewiakoff, S. I. Metalnikoff, N. K. Koltzov, S.V. Awerintsev and A. S. Schepotiev (Goldschmidt, 1956; Fokin, 2004).

The peak of Bütschli's career as a protistologist was the three-volume treatise on Protozoa (1880-1889), with the third volume (953 pages!) almost exclusively devoted to ciliates (Bütschli, 1887-1889). It was in this treatise that Bütschli proposed his classification of the Ciliata. This class was divided into two subclasses (Ciliata and Suctoria). The former consisted of two orders, established according to the structure of the cytostome and the pharynx (Gimnostomata and Trichostomata), while the latter comprised two groups in the rank of suborders, according to presence or absence of the adoral row of cilia (Aspirotricha and Spirotricha). Spirotrichs, in their turn, were split into four groups following Stein. On the whole, Ciliata included 25 families and 142 genera. It was the state-of-the-art classification of that time, with a complex of characters taken as a basis and with orders and families being more or less natural groups (Schewiakoff, 1896).

E. Maupas (1842-1916) was not a professional biologist, but the trace he left in ciliatology is quite considerable. In 1880s he published a brilliant series of articles on karyology, sexual process and reproduction in ciliates (Maupas, 1883, 1886, 1888, 1889). R. Hertwig (1850-1937) was known not only a protistologist but also as an experimental embryologist. Having apparently inherited curiosity of protists from his teacher, E. Haeckel, Hertwig studied radiolaria, ciliates and actinophores. As a ciliatologist, he is remembered as the author of a very profound research devoted to ciliate conjugation (Hertwig, 1889). Like Bütschli, Hertwig was a brilliant pedagogue and educated many prominent protistologists. W.S. Kent (1845- 1908) was a versatile zoologist, ciliates being only one of the many groups that excited his interest (Esteban et al., 2002). His most important contribution to ciliatology was the publication of a fundamental series of three volumes: "A Manual of the Infusoria" (Kent, 1880-1882) and the description of a considerable number of peritrichan and suctorian species. The latter were put by Kent into a separate group Tentaculifera (Corliss, 1978).

Approximately at the same time ciliate studies commenced in the New World. In late XIX century the most prominent figure among ciliatologists of the USA was A.S. Stokes. He published a substantial review on the ciliate fauna of the United States and wrote manuals on microscopic studies (Stokes, 1888, 1894, 1896). A bit earlier J. Leidy (1823-1891) produced there several publications on free-living and parasitic ciliates, though he was mainly an "amoeba man" (Corliss, 2001).

In Russia in the second half of the XIX century there was a researcher, whose range of interests and profundity of thought equalled those of the best representatives of the Western European School - L.S. Cienkowsky (1822-1887). He was the graduate of the St. Petersburg University and later (unfortunately, only for a short time: 1854-1861), its professor, an outstanding Russian scientist (of Polish origin), one of the founders of Russian protistology (Raikov, 1959; Fokin, 2001a; Kuznicki, 2003).

His discourse "On the structure of the simplest living organisms" was presented to obtain the docent position in 1847 (Raikov, 1959). His doctoral dissertation "On the lower algae and ciliates" (Cienkowsky, 1856) contained studies of various protists (also ciliates *Enchelys, Stylonychia* and *Vorticella*) and convincingly demonstrated that protists consisted of a single cell and thus had no organs ascribed to them by Ehrenberg. Cienkowsky introduced the microscope into the teaching practice in Russian universities. He discovered and described several dozens of protists and traced the life cycles of many of them. He was one of the first to study cyst formation in ciliates. He experimentally showed impossibility of spontaneous generation in protists (Cienkowsky, 1859). In his public lectures Cienkowsky popularised the idea about the connections between uni- and multicellular animals. He was the first to pay attention to the phenomenon of symbiosis in lower organisms (Raikov, 1959). Life circumstances did not allow him to found a protistological scientific school of his own. During the second part of his scientific career (in Odessa and especially in Kharkov), L.S. Cienkowsky switched to microbiological research (Metelkin, 1950). However, his protistological ideas and works inspired a number of students and followers (A.S. Famintzin, A.O. Wrzesniowski, M.S. Voronin and K. S. Merezhkovsky). It may be, partly, under the influence of Cienkowsky that I.I. Metchnikoff (1845-1916) began his scientific career with ciliate studies, publishing a number of original observations (Metchnikoff, 1864, 1865).

COLUMBIA UNIVERSITY BIOLOGICAL SERIES. VI.

THE PROTOZOA

BY

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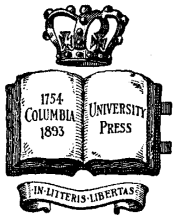
"Lies dieses Buch, und lern dabey,
Wie gros Gott auch im Kleinem sey."

D. G. L. Huth: Rösel von Rosenhof.



New York
THE MACMILLAN COMPANY
LONDON: MACMILLAN & CO., LTD.
1901

Among the above scientists, K.S. Mereschkowsky (1855-1921) was the one to study ciliates most systematically (in the beginning of his scientific career: 1877-1886). He was the author of the first (after E. Eichwald's series dating back to 1844-1860s (Eichwald, 1844, 1860) and several J. Wiesse's studies) faunistic reviews on the protists of Russia: "Studies of the protozoans of the Russian North" (Mereschkowsky, 1878), "Materials to the ciliate fauna of the Black Sea" (Mereschkowsky, 1880) and "On some new or little-known ciliates" (Mereschkowsky, 1881).

Noteworthy, there were two women among Russian ciliatologists of the last quarter of the XIX century, a very rare instance in the science of those days. They were Yu. I. Andrusova (1863-1942) and S.M. Pereyaslawzeva (1849-1903), who studied the ciliate fauna of the Black Sea (Andrusova, 1886; Pereyaslawzeva, 1886). A.S. Famintzin (1843–1918), a well-known physiologist of plants and the student of L.S. Cienkowsky, also repeatedly turned to studies of protists, ciliates in particular (Famintzin 1889, 1890).

In late XIX century intensive investigations of

ciliates were conducted in the universities of Warsaw, Kiev and Odessa. The Warsaw University (in 1862-1869 the Principal School) was for a long time (1864-1889) home to a well-known Polish protozoologist A.O. Wrzesniowski (1837-1892). He produced a number of papers on morphology, ecology and systematics of ciliates (Kuznicki, 1982). Chronologically the peak of ciliatological studies in Warsaw falls to the time when the zoolomical cabinet was under the supervision of his successor, Prof. P.I. Mitrofanov (1857-1925). Besides faunistic research (Eismond, 1890), a considerable attention of the Warsaw researchers was paid to ciliate cytology (Przesmitsky, 1894; Sosnowsky, 1897; Kudelsky, 1898; Mavrodiadi, 1913).

A voluminous study on morphology and biology of tentaculate ciliates was published by N.A. Keppen (1888), a researcher from Kiev. P.P. Butschinsky (Odessa) investigated the protistan fauna of the limans (Butschinsky, 1895). W.M. Havkin, one of Metchnikoff's students in the Odessa University and later a well-known bacteriologist, laid the foundations of studies of bacterial endobionts of ciliates, when working in the Pasteur Institute (Hafkine, 1890).

In the autumn of 1894 ciliatology in Russia received a considerable reinforcement: W.T. Schewiakoff (1859-1930) returned to Petersburg from Germany. Schewiakoff graduated from the Heidelberg University, where he had studied under the supervision of Prof. O. Bütschli (Fokin, 2000, 2004). While still in Germany, he started a successful research of ciliates (Fokin, 2000, 2001b). After graduation he travelled round the world (1889-1890). The main objective of this 10-months trip was the study of geographical distribution of freshwater protists, ciliates in particular. Materials of the voyage became the basis of the monograph (Schewiakoff, 1893), which three years later was awarded the Brandt academic prize. Immediately after coming back to Russia, Wladimir Timofeevich defended the Master's dissertation "On the biology of protozoans", published as a voluminous article. Two of the three chapters were devoted to morphology and distribution of ciliates (Schewiakoff, 1894).

Two years later W.T. Schewiakoff presented the study "Organisation and systematics of Infusoria Aspirotricha (Holotricha auctorum)" (Schewiakoff, 1896) as a doctoral thesis. It was a brilliant conclusion of a series of monographs started by F. Stein. A fruit of ten years of observation and thought, the treatise (408 pages of text and 7 large tables of excellent drawings) included a comparative-anatomical description of ciliate morphology, the analysis of a number of biological and physiological characters of the group, their geographical distribution and a detailed discussion of classification and phylogenetical connections of holotrichs.

Schewiakoff's classification was somewhat different from that suggested by Bütschli. For instance, he considered Holotricha as a more natural group, undeserving division into the Gymnostomata and the Trichostomata in the rank of orders. All Ciliata were divided by Schewiakoff into two orders: Spirotricha and Aspirotricha. Their composition was, naturally, altered. The order Aspirotricha, thought of by Schewiakoff as a more primitive one, comprised Holotricha *sensu* Stein with some additions. This order was divided into 3 suborders according to the structure of the cytostome and the pharynx: Gymnostomata, Trichostomata and Astomata. Altogether, the order Aspirotricha *sensu* Schewiakoff comprised 19 families, 80 genera and 181 species. Some of Schewiakoff's taxonomic groups are still retained in the modern classification of Ciliophora (Schewiakoff, 1896; Lynn and Small, 2000).

Since Schewiakoff's arrival the St. Petersburg University became the largest Russian protozoological centre. His students often paid tribute to the scientific topic of their teacher. Among them there were well-known XX century scientists S.I. Metalnikoff, A.K. Lin'ko, S.V. Awerinzev, V.A. Dogiel, A.S. Schepotiev and I.K. Dembovsky (later on the founder of the Polish Academy of Sciences).

Early XX century saw a considerable expanse of the composition and geography of the ciliatological community. Besides the above scientists, their students and junior colleagues entered the scientific stage. An important role in consolidation of scientific forces, exchange of fresh information and recruitment of new researchers was played by the first international protozoological journal "Archiv für Protistenkunde" (1902), founded by F. Schaudinn (1871-1906), as well as by the first protozoological textbooks (Calkins, 1901; Doflein, 1901). In Russian a similar function was performed somewhat later by the "Russian Archive for Protistology", which, unfortunately, existed only for 8 years (1922-1929).

G.N. Calkins (1869-1943) was the first professor to read a special course "Protozoology" and to head a department of this name. He studied physiology and cell cycles of protists, working mostly with paramecia (Corliss, 1998). In 1912 his textbook (Calkins, 1901) was translated into Russian (Calkins, 1912) by V.S. Elpatievsky, a zoologist from Moscow.

F. Doflein (1873-1924), the student of R. Hertwig, had very broad scientific interests that also included studies of epibiontic ciliates Chonotricha (see Jankowsky, 1973). It was he who distinguished ciliates into a separate type Ciliophora (Doflein, 1901). Another German protozoologist, M. Hartmann (1876-1962), a trainee of R. Hertwig in Munich (but also worked in Heidelberg), published a "Practicum on Protozoology" (Hartmann, 1907). At first Hartmann dealt with systematics and comparative morphology of different protists, including ciliates, later concentrating on

theoretical issues (Hartmann, 1929; Mollenhauer, 1998). Studies of sexual process in protozoans and the analysis of organisation of their nuclei interested Hartmann throughout his long scientific life (Hartmann, 1952, 1955). The same direction of investigations was actively developed by one of Hartmann's closest colleagues, K. Bêlař (1895-1931), whose first book devoted to the nucleus of protozoa (Bêlař, 1926) promised a brilliant scientific future, which was, unfortunately, tragically unrealised. It is hard to underestimate the influence of the above scientists on the development of ciliatology. The same fully applies to the most extraordinary figure in ciliate systematics and faunistics of the first third of the XX century, A. Kahl.

A teacher in a gymnasium and an amateur who studied ciliates as a hobby, A. Kahl (1877-1946) published his first work when he was 49 years old (Kahl, 1926). During the following 9 years the series "Animal world of Germany" and "Animals of the North and the West Seas" he published more than 1000 pages of species description, identification keys and drawings. This study, made by Kahl alone without any help, reflected, in fact, the whole bulk of data on free-living and ectocommensal ciliates known at that time (Kahl, 1930-1935, 1933, 1934a, 1934b). He also revised the classification of Ciliophora and suggested its new version incorporating the best achievements of Stein, Bütschli, Schewiakoff and Chatton – an incredible work of a lonely enthusiast!

The first quarter of the XX century in France also witnessed the emergence of outstanding ciliatologists: E. Chatton (1883-1947) and E. Fauré-Fremiet (1883-1971). Both were born in 1883 and both used extensively the method of impregnating the ciliate cortex with silver elaborated by Chatton and Lwoff (1930). Chatton, who mostly studied marine and symbiotic forms, should be credited with the discovery of the desmodexy rule, the establishment of the main division types of protists and the understanding of the autonomous nature of the process of kinetosome multiplication in ciliates. In suggesting the terms pro- and eukaryotes, he was the first to fully recognise the evolutionary distance between bacteria and other organisms. A number of ciliatological studies were made by Chatton in collaboration with A. Lwoff (1902-1994), the future Nobel Prize winner (Chatton and Lwoff, 1935; Soyer-Gobillard and Schrevel, 2003), who was related to a famous Russian painter V.A. Serov.

Fauré-Fremiet mostly investigated freshwater free-living protists (Corliss, 1998b). He used the features of ciliate cortical morphogenesis, discovered by his colleague, for analysis of evolution and phylogeny of Ciliophora. He paid special attention to the processes of stomatogenesis in different ciliate groups, which later enabled him to create a new variant of this phylum's classification (Fauré-Fremiet, 1950).

Besides the traditionally strong German and French ciliatological schools, at the beginning of XX century in some other countries protozoologists worked with ciliates as well (C. Dobell, J. Gelei, B. Klein, M. Popoff, B. Petschenko, I. Dembovsky, I. Lipsi, B.L. Bhatia). Early XX century witnessed the emergence of a remarkable constellation of American scientists. C. Kofoid (1865-1947), employed at the University of Illinois at the same time as G. Calkins, studied parasitic and endocommensal protists. He also investigated ciliates from the rumen of domestic ruminants and Entodiniomorpha from elephants, tintinnids, and "neuromotor" apparatus of ciliates and flagellates (Corliss, 1998a). H. Jenning (1868-1947) was another outstanding protozoologist of that generation. A specialist in behaviour and physiology of protists, he worked predominantly on ciliates. Jennings was one of the first to start investigations of genetics of Ciliophora (Jennings, 1929) and to use *P. bursaria* as a model object (Jennings, 1939). L. Woodruff (1879-1947), the first student of Calkins, also studied exclusively ciliates, addressing himself to the problems of cytology and life cycles. Besides, he published a number of articles on the history of zoology, including the history of paramecia studies (Woodruff, 1926, 1938, 1945).

The beginning of the XX century in Russia was marked by further development of St. Petersburg protozoological school. V.A. Dogiel (1882-1955), its brightest representative, became an acknowledged leader of Russian protozoology of the Soviet time (Fokin, 2001c). As a ciliatologist, he investigated the representatives of the family Ophryoscolecidae and studied this group very thoroughly (Dogiel, 1923, 1927; Fokin, 2001c). His numerous students also researched ciliates (Gassovsky, 1916, 1918; Rammelmeier, 1925; Poljansky, 1928; Strelkov, 1928; Furssenko, 1929; Bogdanowich, 1930; Cheissin, 1930; Zhinkin, 1930).

Interesting investigations on cytology, faunistics and physiology of some Ciliophora were published in the first quarter of the XX century by S.I. Metalnikoff (1907, 1911; Metalnikoff and Galadjiev, 1916), N.K. Koltzov (1911), B.A. Swartchevsky (1912, 1928), L.L. Rossolimo (1916, Rossolimo and Perzewa, 1929) and some others. Extensive ecological-faunistical studies of ciliates were started on Lake Baikal by N. Gajewskaja (1927, 1933).

The middle and the end of the XX century were so eventful in the history of ciliatology and involved so many researchers and such a broad scope of investigations that this period calls for a large review of its own. In this brief article I have to confine myself to the above.

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