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Johann Flögel (1834–1918) and the birth of comparative insect neuroanatomy and brain nomenclature

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ABSTRACT

Johann H.L. Flögel (1834–1918) was an amateur scientist and self-taught microscopist in Germany who 130 years ago pioneered comparative arthropod neuroanatomy. He was fascinated by innovations in optical instrumentation, and his meticulous studies of the insect supraoesophageal ganglia were the first to use serial sections and photomicrographs to characterize the architecture of circumscribed regions of brain tissue. Flögel recognized the interpretative power resulting from observations across various species, and his comparative study of 1878, in particular, provided a baseline for subsequent workers to evolve a secure nomenclature of insect brain structures. His contributions stand out from contemporary accounts by virtue of their disciplined descriptions and emphasis on identifying comparable elements in different taxa. Here we give a biographical sketch of his life and summarize his remarkable achievements.

1. Introduction

A stable anatomical nomenclature originates from a set of clearly defined terms, the subsequent alterations of which result from new data rather than the whims of an investigator. Novel methods, new insights about developmental processes, and functional studies can all redefine previously named structures. However, as is evident from the plethora of terms used in vertebrate neurology (see, for example, the discussion by Swanson, 2000), alternate terms denoting the same entity hinder communication and slow the progress of science. Insect brain research has been more fortunate in that the invention of names has overall been relatively free of ambiguity. From the outset, names were used that signified familiar constructs, such as "the beam" ("Balken" in German) for a structure that was massive and which appeared to support elements above it. This early clarity was the achievement of a nearly forgotten scientist from Germany: Johann Flögel, a self-taught microscopist who a hundred and thirty years ago pioneered comparative neuroanatomy.

2. Biographical sketch

Johann Heinrich Ludwig Flögel was born in 1834 in Glückstadt/Holstein, in northern Germany. He trained as an administrative lawyer, and later pursued a modest career as a municipal notary public and tax official ("Kirchspielvogt") in Bramstedt, near the coastal city of Kiel. Apparently, his duties left him enough spare time to pursue serious scientific research. In 1889, due to administrative government reforms, he chose early retirement from his office and (at the age of 55) settled in Ahrensburg, not far from Hamburg. He became what is known as a "Privatgelehrter" – a self-motivated researcher funded by private means – who developed a passion for studying natural phenomena. Two studies of the microscopy of diatoms resulted in him becoming a member of a maritime survey of the Baltic Sea. He purchased microscopes and telescopes, all built according to his own specifications, so he could indulge in both meteorological and microscopical observations (see the portrait in Fig. 1, left). He published on cloud formation, the aurora borealis, and the microscopic structure of hail and snow. All of these studies were recognized as highly professional and they earned him an honorary doctorate in 1875 from the University of Kiel. His studies were reported in contemporary Proceedings of the Royal Microscopical Society (1883, p. 969), which reviewed the design of his specially constructed darkroom and his novel use of photography to capture photographic images of histological preparations and commented on his use of paraffin wax for embedding. In 1885, he was made an honorary Fellow of the Royal Microscopical Society of London on the basis of his anatomical studies, which are summarized here.

Flögel was intrigued by minutiae. Of the living, he favored the insects, because they offered extraordinary and microscopic detail. At first glance, his neuroanatomical publications seem modest, a mere two papers. However, they are pivotal to almost all

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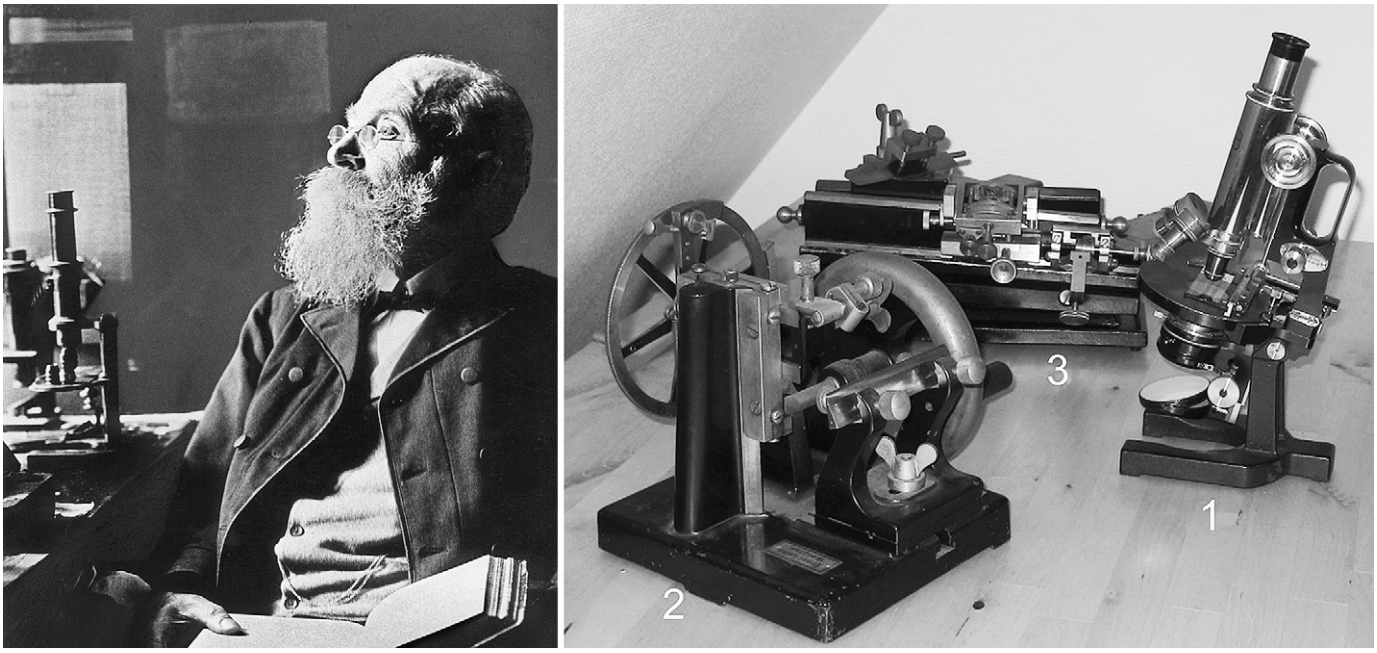

Fig. 1. Left: Johann H.L. Flögel, circa 1910, with one of his microscopes (reproduced from the original portrait kept in archives of Zoologisches Museum, Universität Hamburg, Sign. Ie6). Right: The "tools of the histologists trade" at around end of the 19th century. Zeiss Jena Microscope (1) equipped with an Abbe condenser, water and oil immersion lenses, a Minot-Blake rotary microtome from 1899 (2) for serial sections, and a Thoma sledge or sliding microtome from 1881 (3) for obtaining single sections of gelatin- or nitrocellulose-embedded tissue.

subsequent work on the insect brain. The first of his two papers, published in 1876 and titled *Über den feineren Bau des Arthropodengehirns* (The fine-structure of the arthropod brain), was an expanded transcript of his demonstration to the 49th meeting of the renowned *Gesellschaft Deutscher Naturforscher und Ärzte* (Society of German Naturalists and Physicians) on September 21, 1876. There, he exhibited for the first time, to a group of distinguished anatomists, the sectioned brains of insects, describing their partitioning into circumscribed centers that were comparable to those of other (vertebrate) animals. In his oral presentation, he used the negatives of micrographs he had taken of the brain sections; following his talk, the audience was invited to inspect his preparations directly under a microscope. While his 1876 publication consists only of a text, his second paper, published in 1878, is a comparative study of the brains of many different species showing that each consists of homologous centers (Figs. 2 and 3). It is this second account (Flögel, 1878) that provides the basis of terms used today in English translation and which inspired many subsequent studies during the last two decades of the 19th Century.

3. Flögel's histological techniques

Flögel's research was the first to use serial sections for studying the insect central nervous system, a method of analysis enabled by the recent invention of the microtome by Wilhelm His, around 1866–69, after he assumed the Chair of Anatomy at the University of Basel (His, 1870; Mall, 1905). By the time Flögel embarked on his investigations the staining of serial sections and reconstruction of internal anatomies had been popularized by Albert von Kölliker's Würzburg School of Zootomy (Schiebler, 1982) and in medical research was becoming an essential tool for studying all manner of tissue (Hopwood, 1999). Flögel used the most up-to-date tools of the trade, some precursors of technological developments in the 1880 and 1890s (Fig. 1, right). The method he used most was to fix the whole heads of insects in isobutyl alcohol, carefully dissect the brains out of the head capsule, and then stain them *in toto* before dehydrating the specimens and infiltrating them with hot paraffin wax. He must have been a masterly histologist, for he managed to embed and section even the minute brains of rustflies (Psilidae) as well as those of eyelash mites, *Demodex folliculorum* (Flögel, 1891).

Flögel experimented with various methods, such as a tissue dye called Berlin blue and osmium vapor for fixation. As his papers reveal, he was clearly less pleased with these than picrocarmine, which he prepared by mixing carmine obtained from macerated cochineal cactus scales (*Dactylopius cacti*) with picric acid and ammonia, to provide a water-soluble stain. Flögel also employed haematoxylin, which was an alcohol-soluble dye obtained from the "bloodwood tree" (*Haematoxylum campechianum*) used in conjunction with ferric chloride to stain nuclei (Merck Index, 1996). Flögel's microtome, possibly based on that published in 1866 by the near-by Kieler physiologist Victor Hensen (see also Bracegirdle, 1978; loc cit. p. 130, Fig. 22), achieved serial sections that were less than 10 microns thick, which he mounted on glass slides prepared with gum arabic (Flögel, 1883b). After removing the wax with benzene, he made photomicrographs – his crucial innovation – to show circumscribed regions of tissue (Flögel, 1883c). This was the neuropil (which he called the "Punktsubstanz" using Leydig's 1855 terminology) that is distinct from the more basophilic somata that covered the brain. Flögel was not able to reveal photographically the fibrous organization of the neuropil, nor its axon bundles. However, his 1876 and 1878 texts describe his observations of fibers. He characterizes what we now know as olfactory glomeruli as dense ball-like tangles of fibers ("Ballen" in German) and he even suggests that the apparent homogeneity of the mushroom body lobes is likely due to their composition of unusually thin parallel processes, which we now know to be true. He also described, but did not name, five distinct regions of the protocerebrum (a term introduced later by Viallanes, 1887) in front of and lateral to the mushroom body lobes. And although he noted the occurrence of discrete tracts connecting different brain regions, their relationships were unresolved. This would remain so until the introduction of reduced silver stains by Cajal and Sánchez (1915), and later by Sánchez 1933 and Power (1943, 1946); the latter using Bodian's (1937) method, the reliability of which is unsurpassed.