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Social insect histology from the nineteenth century: The magnificent pioneer sections of Charles Janet

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Abstract

Charles Janet (1849–1932) was the leading pioneer in the histological description of the internal anatomy of social insects, in particular of ants and wasps. Because many of the original Janet sections still exist, this article is able to illustrate the amazing skills through some selected pictures taken from this more than a century old material, and thus to pay tribute to this French founder of insect morphology.

Keywords: Social insects; Histology; Microscopy; History; Charles Janet

1. Introduction

In the history of social insect research, the first microscopical approach dates back to Francesco Stelluti in the 17th century, who described the structures of the honeybee using Galileo's newly built microscope (Baccetti, 1986). Other microscopical descriptions of the honeybee followed within a few decades with the works by Robert Hooke and Jan Swammerdam (Cobb, 2002). The excellent work of these and other researchers was based on the precise and skilful dissection work. A new dimension in the morphological study, however, was introduced with the development of histological sectioning techniques. Today's knowledge on the internal anatomy of social insects without any doubt finds a most solid basis in the extraordinary sectioning work of Charles Janet that started at the end of the 19th century (Billen, 1994).

2. Janet's life and career (Berland, 1932; Casevitz-Weulersse, 1988)

Charles Janet (Fig. 1) was born in Paris on 28 June 1849. He grew up in the village of Saint-Vit near Besançon in the Doubs Department, and obtained a degree as ''engineer of arts and manufactures''. From childhood, he developed a pronounced interest for insects, with ants and wasps his favourites (his brother Armand was to become a renowned lepidopterist). After a few jobs in industrial companies, he started in 1877 a life-long career at a broom factory, J. Dupont & Cie, located in Beauvais, northern France.

In 1895, he stopped his work as engineer in the factory, and became a member of the Council, which gave him more time to spend on his beloved insects. With an engineer's precision, he described the development of a hornet nest from its very beginning (Janet, 1895), and was the very first to report on the liquid food exchange between adult and larval wasps (Janet, 1895, 1903), years before the term trophallaxis was coined for the phenomenon by Wheeler (1918). His behavioural observations also made him famous for the construction of artificial plaster ant nests (Janet, 1897b), later named after him, which attracted a great deal of attention at the 1900

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Fig. 1. Charles Janet in 1899 at the age of 50 (Archives de la Société Entomologique de France).

World Exposition in Paris. We equally remember Janet for his reports on the biology of social parasites and commensals in ant nests (Janet, 1897a). In 1900, he obtained the degree of ''docteur ès Sciences'' at the University of Paris (Janet, 1900).

Janet's reputation was permanently established by his high-precision descriptions of the internal structure of social insects, with special focus on ants and wasps. Among other studies, he conducted a very detailed description of the internal petiolar anatomy (Janet, 1894a), and discovered the process of histolysis of the flight muscles in founding ant queens (Janet, 1907). His detailed and precise descriptions of the exocrine system were of invaluable help for the identification of the anatomical origin when the first pheromonal substances were discovered (Wilson, 1959, 1962; Wilson and Bossert, 1963). His histological work on the exocrine system of ants, especially of *Myrmica rubra,* also included the description of some previously unknown glands, such as the antennal base gland (Janet, 1894b), the pygidial gland and the gonostylar glands (Janet, 1898a), the prothoracic gland (Janet, 1907) and, in males, the penial ring gland (Janet, 1898a). Not only the glands themselves attracted Janet's attention, he also studied the anatomical organization of their discharge mechanism (Janet, 1898b), as usually provided with very detailed and precise accurate illustrations (Fig. 2). The accuracy of this work was confirmed by later studies that were done with far more advanced techniques and equipment (Billen, 1982; Schoeters and Billen, 1996). It is unlikely that much of the early work on pheromones could have been accomplished without Janet's research published half a century earlier.

In 1911, his entomological work came to an end, with 64 papers published during 19 years (Casevitz-Weulersse, 1988). He remained very active in research afterwards, but turned his attention to geology. Among other distinctions, Charles Janet was President of the French Zoological Society in 1899, and became honorary member of the French

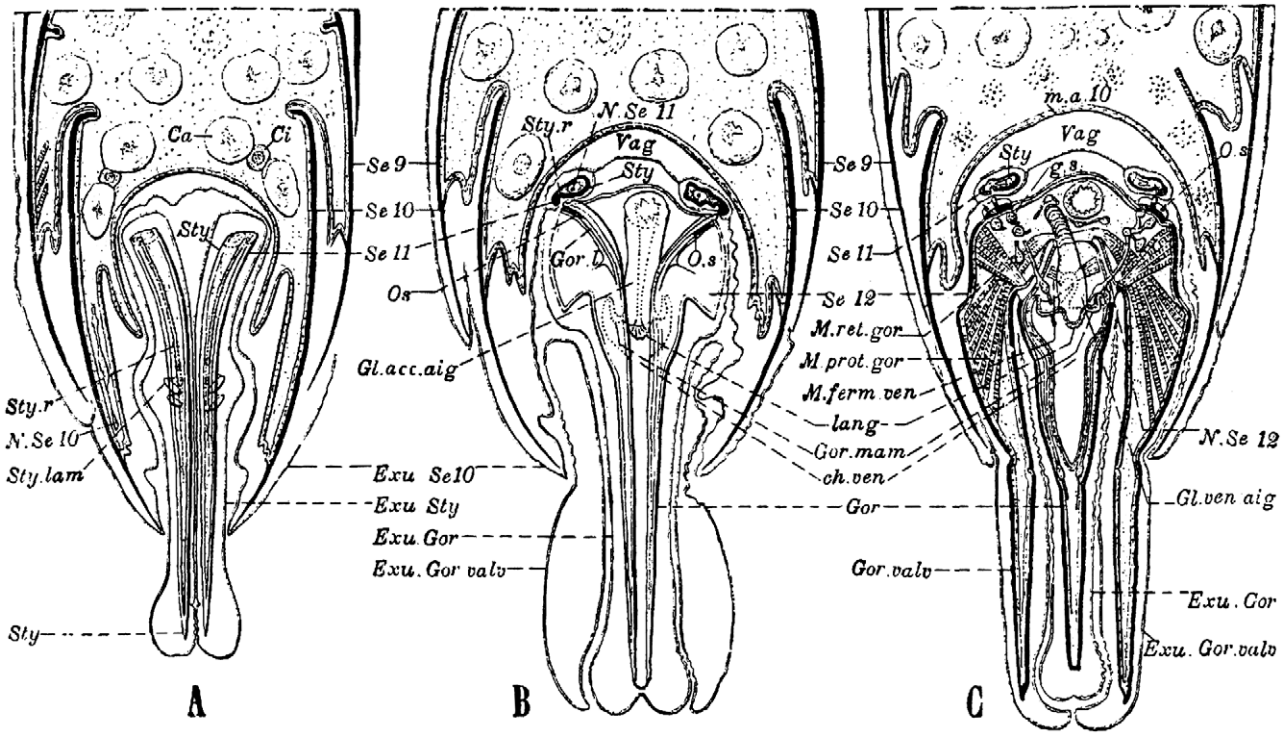

Fig. 2. Example of Janet's detailed drawings, showing the anatomical organization in the region of the sting base of a *Myrmica rubra* worker (from Janet, 1898b).

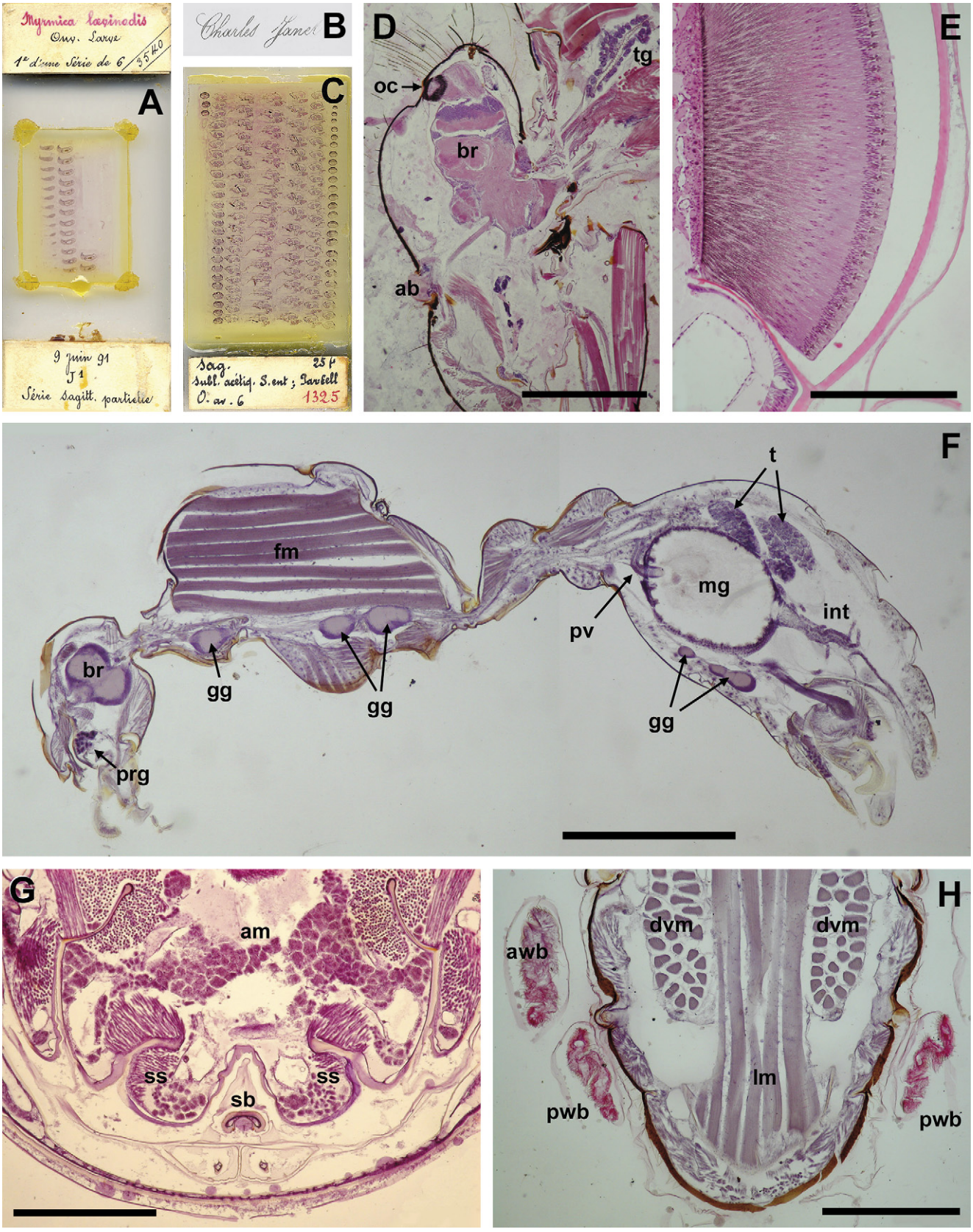

Fig. 3. (A) Example of a histological slide with sections through a worker larva of *Myrmica laevinodis,* showing the precision of Janet's labelling (the date "9 juin 91" refers to the year 1891!). (B) Janet's engraved name as it appears on some slides. (C) Slide with serial longitudinal sections of 25 μm thickness through the entire head of a honeybee worker. (D) Detail of Fig. 1C, showing one of the head sections. ab, antennal basis; br, brain; oc, ocellus; tg, thoracic labial gland. Scale bar 1 mm. (E). Section through compound eye of *Vespa crabro* pupa. Scale bar 500 μm. (F) Longitudinal section through adult male of *Myrmica* sp. br, brain; fm, longitudinal thoracic flight muscle; gg, ganglia; int, intestine; mg, midgut; prg, propharyngeal gland; pv, proventriculus; t, testis. Scale bar 1 mm. (G) Cross section through the abdominal tip region of a *Vespa crabro* queen. am, abdominal muscles; sb, sting base; ss, sting sheath. Scale bar 1 mm. (H) Section through the thorax of a bee or wasp (the slide unfortunately lost its label). awb, anterior wing bud; dvm, dorsoventral flight muscle; lm, longitudinal flight muscle; pwb, posterior wing bud. Scale bar 1 mm.

Entomological Society in 1921. He also carried the prestigious title of laureate of the Institut de France, and was chevalier of the Legion of Honour. He died on 7 January 1932 at Voisinlieu near Beauvais at the age of 82.

3. Janet's histological sections

Janet's morphological work is of an astonishing high quality for his time. He was one of the very first researchers who studied the internal anatomy of social insects through histological sections, and his drawings based upon them were rendered with unerring accuracy (e.g. Janet, 1898a,b). Good fortune has saved at least part of his original sections, which after a remarkable odyssey became available to us. After his death in 1932, the Janet sections were bought by the microscope manufacturer F. Lemardeley in Condé-sur-Noireau in Normandy. From there, they went to father Pierre Frémy, who was a priest-teacher at Saint-Lô College and specialized in Cyanobacteria. He died from his injuries of the Saint-Lô bombardment during the Second World War in June 1944, shortly before he was named corresponding member of the French Academy of Sciences (Jolivet, 1945). After father Frémy's death, the remainder of the Janet slides that had survived the bombardment, were inherited by Prof. Pierre Jolivet in Paris, who later handed them over, in two subsets, to us. The collection comprises 42 (with JB) and 49 (with EOW) glass slides; these 91 slides will be deposited in the Entomology Department of the Royal Belgian Institute of Natural Sciences in Brussels.

Compared to today's standard microscope slides of 76 × 26 mm, Janet used remarkably large glass strips measuring 87 × 37 mm. The thickness of the glass he used was quite variable, ranging from 0.98 to 2.03 mm, with even up to 10% variation in the thickness of the same glass measured at different positions (whereas nowadays microscope slides have a very uniform thickness of 1.00 mm). His hand-written labels are of a particular precision and beauty (Fig. 3A), while some of the slides had his name engraved in the glass in almost calligraphic writing (Fig. 3B).

The style and format of the publications of Janet's days unfortunately did not include methodological details. It therefore remains amazing how he managed to produce and study his sections with technical equipment that must have been rather primitive. As is commonly known, the cuticular exoskeleton of insects makes them hard to section without distortion and tearing in pieces, unless one uses resin embedding. As this was not available in Janet's days, he must have worked with fairly soft paraffin embedded material. He nevertheless managed to obtain good sections through entire adult insects, which may have been partly due to the rather high section thickness. Sometimes, a few technical details are provided in his hand-written labels, such as staining method and section thickness. Examples of the latter vary between 25 and 40 μm. Fig. 3C shows a slide with all 124 serial longitudinal sections through the entire head of a honeybee worker, with a detail shown in Fig. 3D. The indication "25 μm' should indeed approximate the section thickness, as this would correspond with a realistic head width of 3.1 mm. This particular slide moreover possesses exceptional beauty by itself, in terms of the section arrangement. Every morphologist knows that section surface slightly increases when making serial sections because of the pyramidal trimming, which occurs regardless of tissue size and makes the ribbons become more and more divergent. The series of the honeybee head in Fig. 3C, however, shows that section surface in the last part of the series *decreases* again when the embedded part of the head becomes smaller laterally, the last ribbons of the series becoming parallel again to the first ones! This reversal seems to be the result of a kind of "negative trimming" for the last part of the embedded block, which must have been very difficult to achieve.

Among other notable examples of Janet's excellent technical skills are his sections through the head of a pupal hornet queen with very clean images of the compound eye (Fig. 3E) and the longitudinal serial sections through an entire *Myrmica* male with excellent view of the central nervous system, the flight and petiolar muscles, and the gut (Fig. 3F). Also noteworthy are the cross sections through the abdominal tip in the sting base region of a *Vespa crabro* queen (Fig. 3G), as are the sections through the thorax of a bee or wasp pupal queen (the slide unfortunately lost its label) with the flight muscles and wing discs (Fig. 3H).

The histological slides of Charles Janet that we have available for study today, and that survived the Saint-Lô bombardment in 1944, probably represent only a very minor fraction of his entire microscopical oeuvre, as most illustrations in his publications appear not to be directly based on the sections saved. It is obvious, nevertheless, that the technical quality of his histological work combined with his skills in interpretation, illustration and description, have resulted in the basis upon which today's students of social insect morphology have been so fortunate to build.

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