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Biographical article

Jan Swammerdam on social insects: a view from the seventeenth century

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Summary. The Dutch microscopist Jan Swammerdam (1637–1680) carried out the first systematic scientific study of social insects. In the late 1660s and 1670s Swammerdam made a series of observations of bees, ants, wasps and hornets. His exquisite dissections and experimental studies, carried out with extremely primitive equipment, shaped much of our subsequent perception of social insect anatomy and its function. His behavioural observations and interpretations are striking by their accuracy and modernity.

Key words: Swammerdam, anatomy, reproduction, bees, ants.

Introduction

Modern science moves quickly, and there is an enormous pressure on researchers, old and young – but especially young – to focus on the most recent papers. And yet if we dig back further into science past, we can find results, commentaries and approaches that shed light on our current concerns. This paper is intended to show researchers how the ideas and discoveries of the Dutch microscopist Jan Swammerdam (1637–1680), underpin much of our current understanding of the anatomy, development and behaviour of social insects.

One of the most famous microscopists of the 17th century, Swammerdam's name is now largely forgotten by scientists, although his influence has recently been studied by historians, in particular the way in which he used the revolutionary technique of microscopic dissection, precise observation and experimentation as part of the seventeenth century "scientific revolution" (Wilson, 1994; Fournier, 1996; Ruestow, 1996). Swammerdam's name occasionally surfaces in apicultural magazines (e.g. Dade, 1972; Beetsma, 1979; Dodd, 1980), and his work has been discussed at a meeting of IUSSI (de Wilde, 1977), but he is rarely mentioned in academic journals (for example, he has only been cited once in this journal – Winston, 1980).

Swammerdam's work on social insects was published in two phases, first in his book "Historia Generalis Insectorum" (Swammerdam, 1669), which included a short set of studies dealing with the life cycle of bees and ants, and then in his posthumous work "The Book of Nature" (Swammerdam, 1737–38), which contains over 500 figures. This book is a treasure-trove of insect anatomy and behaviour and includes a summary of Swammerdam's work on bees, begun in 1673 and completed in 1676–80, "A Treatise on the history of Bees; or an accurate description of their origin, generation, sex, oeconomy, labours and use". The "Treatise" contains around 57,000 words and includes 60 figures.

Swammerdam was not the first to examine social insects with the twin techniques of microscopy and rigorous observation. The first known image made with a microscope, by Francesco Stelluti, was of three bees (Stelluti, 1625; for recent reproductions, see Crane, 1999, and Bignami, 2000). Subsequently, Robert Hooke turned his microscope on the bee sting (Hooke, 1665), while Francesco Redi took issue with the classical descriptions of social insects breeding from dead mammals (Redi, 1668). However, Swammerdam was the first to make in-depth studies of social insects, using a combination of careful observation, dissection and experimentation. As such, he played an important role in laying the foundations of modern biology in terms of both his results and the methods he used.

Anatomy

The most striking features of Swammerdam's work are his drawings of his dissections, carried out with the recently-invented single-lens microscope (only 1 mm in diameter) under extremely difficult conditions and using a variety of tools and techniques that he had to invent (Schierbeek, 1967). In particular, he did not have access to any differential staining techniques, and his treatment of his preparations did not go beyond using various solutions to dissolve fat or to harden certain tissues.

The earliest of Swammerdam's discoveries on social insects was that the insect that was widely assumed to be the "king" bee was, in fact, a queen. This had apparently been suggested in 1586 by the Spaniard Méndez de Torres (Crane, 1999), and some bee-keepers were already aware of the real situation, because as Swammerdam acknowledged, they also called the "King" a "good mother" (de Wilde, 1977). Nevertheless, by publicly dissecting a "king" bee in 1668 and showing that the insect had ovaries visible to the naked eye, and that the drone had testicles in his abdomen, Swammerdam was the first to assign gender to key members of the hive on a scientific basis (Swammerdam, 1669).

In the early 1670s, inspired by Malpighi's revolutionary anatomical monograph on the silk-worm (Malpighi, 1669; Cobb, in press), Swammerdam began dissecting under the microscope. As part of this radical new research programme, which helped to put an end to 2000 years of Aristotelian orthodoxy according to which insects had no internal structures to speak of, Swammerdam carried out a series of exquisite dissections of virtually every aspect of bee anatomy, many of which were only improved upon in the 20th century – many of his drawings stand comparison with those of Snodgrass (1956) in terms of their detail and accuracy. One of his most renowned figures was his illustration of the queen's ovaries (Fig. 1). This extraordinarily detailed drawing, accompanied by three pages of description and a 1000-word long legend, was backed up by an attempt to count the number of eggs present in the ovary – he calculated that there were around 5,100 eggs in the ovaries.

Swammerdam equally made the first precise descriptions of the mouthparts (Fig. 2) and of the sting and poison gland. In both respects his description was correct and highly detailed. For example, his dissection of the mouthparts included the cardo, which was frequently overlooked in drawings in the 20th century (Cole, 1944), while his description of the alternate movement of the stylets in the sheath represented a huge step forward compared to the simple external illustrations provided by Stelluti (1625) and Hooke (1665). Always keen to introduce a comparative aspect to gauge the generality of his findings, Swammerdam also described sex differences in the anatomy of the eyes, mouthparts, legs, sting, antennae and bristles, as well as studying similar structures in wasps and ants.

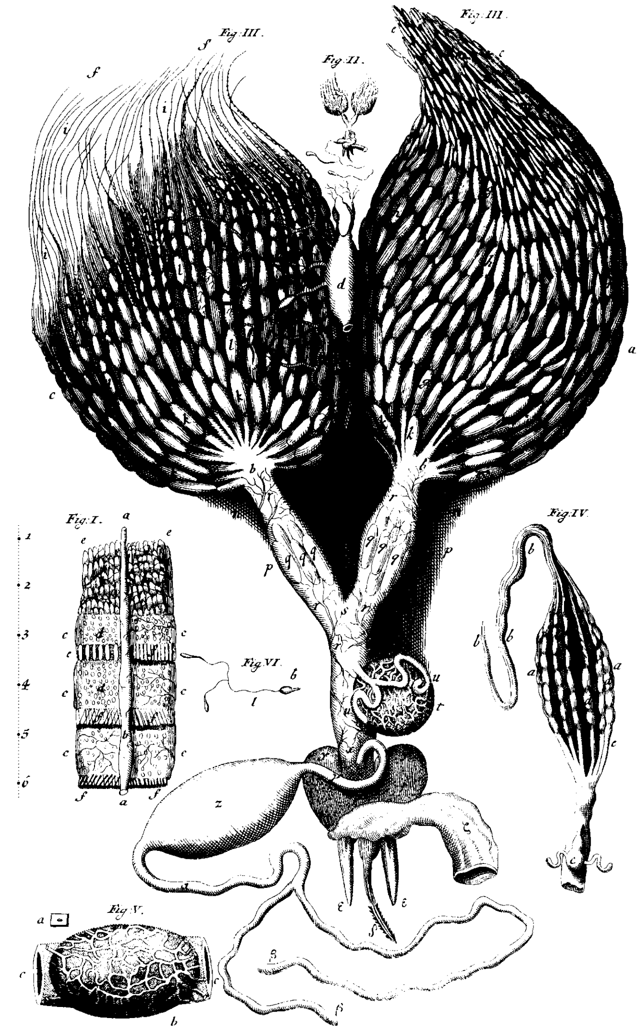

Figure 1. Drawings by Swammerdam from "The Book of Nature", Table XIX. The full original legend for this Table is around 1000 words long. Original figure titles: Fig. I: "The Bee's heart". Fig. II "The ovary of the Bee, of the size and form it appears to the naked eye." Fig. III: Queen ovaries. "This double ovary is composed of parts extracted from two different female Bees, viz. The part *a* from a full-grown impregated Bee; and the part *c* from another Bee less perfect, and not as yet impregnated." Fig. IV: "The ovary of a Wasp." Fig. V. "The egg of a Bee". Fig. VI: "The poison-bag of the Bee, of its natural size." © Bibliothéque Inter-Universitaire de Médicine, Paris

Reproduction and development

One of Swammerdam's major mistakes was to state that bees do not copulate, and that "the male Bees eject their sperm in the same manner as Fishes, who only shed it upon the spawn". To justify this argument he pointed to the different shapes of male and female genitalia and the smell produced by drones, which he put down to the "rank and strong odour" of their sperm, which could thus presumably act at a distance. This was a rare example of Swammerdam using rhetoric rather than experimentation to arrive at a conclusion. A generation later, Reaumur (1740) described Swammerdam's view as "very strange" and upbraided him for "thinking like the Ancients" rather than like a Modern on this question. However, Swammerdam did show that he was fully part of the new science: he suggested that it would be possible to test his hypothesis experimentally by seeing "whether the female Bee, enclosed in a little net made of fine thread, or in a small glass vessel covered with a piece of fine linen, or in a box with holes in it, could be impregnated by the bare scent of the male."

Swammerdam's key breakthrough was to rightly describe the egg-laying function of the queen, and the anatomical differences between queen, worker and male larvae and nymphs. At the time, this observation was far from banal: for example, Moses Rusden, bee-master to King Charles II of England, explained in his 1679 book "Further Discoveries of Bees" that young bees came from flowers (Meyer, 1939). Swammerdam's accuracy on this point was a consequence of

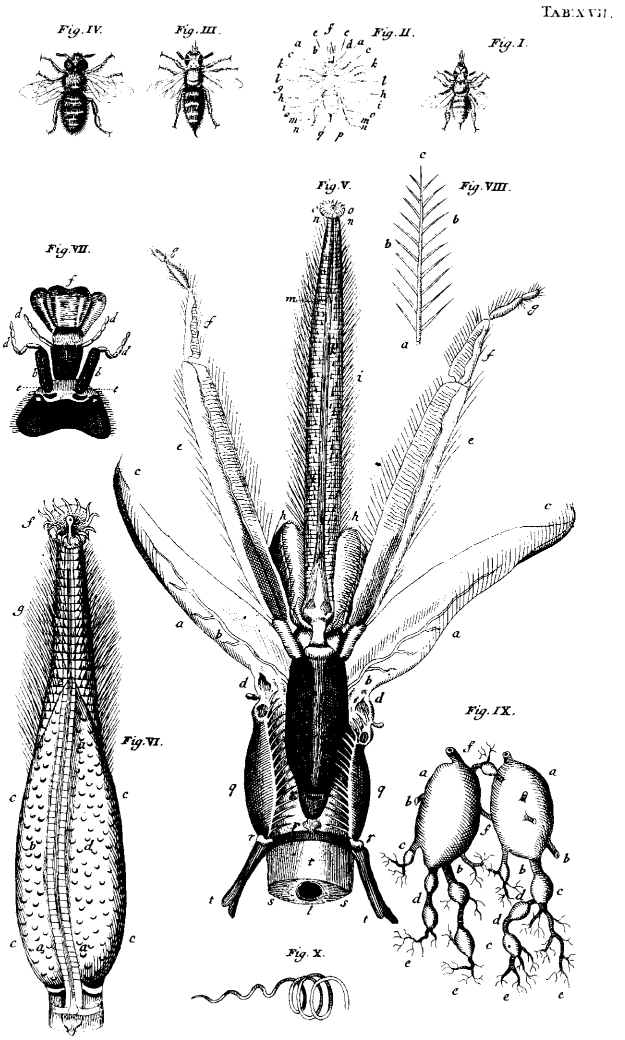

Figure 2. Drawings by Swammerdam from "The Book of Nature", Table XVII. Original title "Which represents Bees". The full original legend for this Table is around 1300 words long. Original figure titles: Fig. 1, Fig. II: "The common or labouring bee". Fig. III: "The female Bee, commonly, but improperly, called the king." Fig IV: male. Fig. V: "The proboscis of the Bee". Fig. VI: magnification of part kk in Fig. V. Fig. VII: "The proboscis of a wasp". Fig. VIII: "The hair of a Bee". Fig. IX: "The lungs of the Bee". Fig. X: "The pulmonary tube".

his revolutionary insistence that there was a continuity between the various stages in the insect life-cycle and that there was no "metamorphosis" in the sense of one individual being transformed into another, nor spontaneous generation. This was to be one of his decisive contributions to the history of biology.

Once again, Swammerdam proved his point by a combination of delicate dissection and careful observation. However, his understanding of insect development has often been misunderstood. In caterpillars, Swammerdam had correctly observed adult structures in the larval stage prior to pupation. On this basis he initially interpreted all development as simply being the product of the growth of already existing structures. This view, together with his early suggestion that an egg might contain a regressing series of descendants, encased like Russian dolls, gave rise to his subsequent reputation as the founder of "preformationism" (Cole, 1944). This was the idea, prevalent until the mid-18th century, that the adult is found perfectly formed inside the egg, and which was opposed to Harvey's theory of epigenesis (Roger, 1963). In fact there were two competing schools – the "ovists" and the "spermists", depending on which structure was thought to contain the preformed offspring. Swammerdam, however, died before this theory took hold. More importantly, his experimental method meant that as his research went on, he did not argue that all species show some kind of "preformation" – his findings simply did not support such a suggestion.

For example in the bee, unlike the butterfly, "weak and very tender" adult structures could be seen only in the nymph and not in the larva. Furthermore, rather than arguing that the adult bee simply grew out of pre-existing larval structures, Swammerdam was obliged to emphasise the *lack* of structural continuity between the larval and adult stages: the muscles underwent "incomprehensible changes" whereas the nervous system was "subject to very visible extensions, transmutations, contractions and even translocations". Once again, a sign of Swammerdam's modernity was that theory had to conform to empirical reality, and not *vice versa*.

Swammerdam described in great detail the anatomy and development of larvae and nymphs, including the feeding of royal jelly to queen larvae and the anatomy and mechanics of larval moulting. He also studied the tracheal system, which he stretched out by inserting a human hair. Being a 17th century scientist, he used himself as an instrument, eating larvae both raw ("very disagreeable", tasting of "rusty bacon") and boiled ("they have a somewhat more agreeable taste; but if one continues chewing them, the former taste prevails again.") Finally, he correctly observed and explained the changes in colour of young bees over the first few days of life, which he put down to the hardening of "those parts which are of a substance between horn and bone".

Sensory functions

Since the discovery of the microscope at the beginning of the century, the structure of insect eyes had intrigued scientists, although even Hooke (1665) had failed to discern the hexagonal form of the facets. In his work on the bee eye, Swammerdam not only showed this quite clearly, he also carried out a dissection of the eye, showing the various lamellae (Fig. 3), (inaccurately) imagined the consequences of the compound eye for the mechanisms of visual perception, and (more accurately) described the transmission of the visual signal from the "pyramidal fibres", via the "subjacent reticulated membranes" and the "transverse fibres" to the "cortical substance of the brain". He described the ocelli in bees, wasps and other flying insects, and noted that they were absent in the worker ants he studied. By painting over the eyes he demonstrated that they were indeed responsible for visual perception. He also ridiculed the idea that the hexagonal form of the hive cells is a consequence of the shape of the eye facets by pointing out that humans should therefore construct round buildings; this is apparently a response to his contemporary Leeuwenhoek, who, in one of his earliest letters to the Royal Society had made precisely this suggestion (Leeuwenhoek, 1673).

Swammerdam dissected the bee brain (Fig. 3, Fig. VI), showing the optic nerves projecting from the two compound eyes and the three ocelli. The two small parts of the brain figured as "Fig. VI ee" in Fig. 3 may be part of the mushroom bodies. Finally, Swammerdam also observed the clustering of worker bees around the queen, in particular during swarming, but also in the nest. To demonstrate that some kind of "strong scent" was involved, he removed the queen on a stick and observed the workers flying to her, even if she was placed some distance from the hive. The same technique was used nearly 300 years later, with the same objective, but without reference to Swammerdam's pioneering investigation (Morse, 1963).

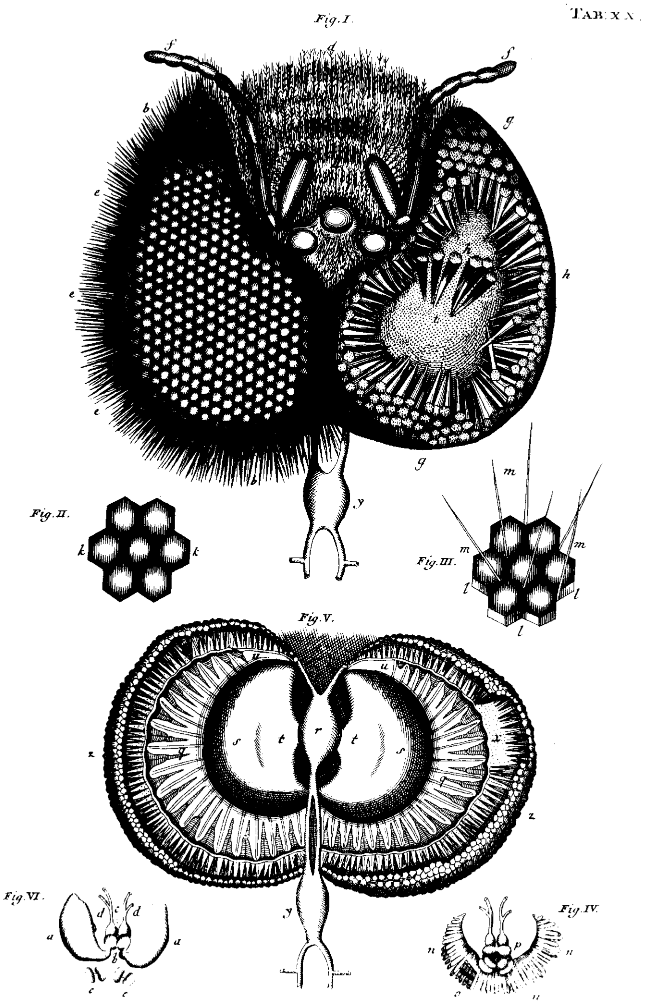

Figure 3. Drawings by Swammerdam from "The Book of Nature", Table XX. The full original legend for this Table is around 700 words long. Original figure titles: Fig. I: "The head of the Male Bee, with the parts belonging to it, especially the eyes, which are here represented much bigger than in nature." Fig. II: "The disposition or situation of the hexagonal divisions of the cornea." Fig. III: "A small portion of the Cornea, along with its hairs". Fig. IV: "The cortical lower fibres of the eye." Fig. V: "The eyes and brain, as they appear on beginning the dissection of them on the lower side." Fig. VI: "The brain more accurately displayed." © Bibliothéque Inter-Universitaire de Médicine, Paris

Experimentation

Swammerdam carried out a series of experiments to show that the pain caused by bee, ant, hornet and wasp stings comes from the poison gland, and not from the sting. He demonstrated the sucking action of the mouthparts by cutting a hornet in half between the thorax and the abdomen. He then fed the insect sugar water and showed that the liquid oozed out of the cut end of the thorax.

To study social behaviour, Swammerdam had to observe the colony directly. While this was relatively easy in the case of domesticated bees (he may have used glass hives; Crane, 1999), his study of ant behaviour meant he had to create what were apparently the first artificial nests: "I provided a large deep earthen vessel, and about six inches from the brim or verge of it, I put a bank or artificial rim of wax, and then on the outside of the circumference of this I poured water, in order to prevent the Ants confined in this enclosure from getting out. I afterwards filled the cavity of this dish with earth, and therein placed my little republic of Ants. It happened that in a few days the Ants laid their eggs in this vessel". He also attempted to rear larvae himself, but found that "without the assistance of the working Ants, […] I never succeeded". Intrigued by the way the workers cared for the brood, he moistened the soil and observed the way the colony responded by carrying larvae and pupae; he also reported field observations of ants carrying brood outside the colony, apparently to be warmed by the sun.

Colony organisation and reproduction

One of the few aspects of Swammerdam's work that has recently been cited (Wilson, 1971) is his description of five hives and queens in different situations. In each case, he counted the number of bees and brood present. His largest hive, which swarmed during his observations, contained 6468 worker larvae and pupae, 2433 workers in the swarm and 8494 workers in the original hive. He also counted the number of queens as nymphs and ready to eclose, as well as the number of different kinds of cells.

Although this kind of information was essentially anecdotal, it demonstrated the faith of the new science in precise observation and in numbers, and also revealed that Swammerdam's anatomical analysis of the composition of the colony was essentially correct. Furthermore, he reported that comparative studies with other social insects produced similar results, in particular with regard to males, which he noted had similar behavioural roles and anatomical peculiarities in bees and ants.

Having noted that all the social insect colonies he studied were mainly made up of sterile females, with occasional production of males and the presence of one or more reproductive females, depending on the species, Swammerdam tried to explain why this kind of social organisation should exist.

His views on this question changed with time: in his early study of ants, his description of the colony was marked by his mystical leanings (Cobb, 2000): "there is no superiority or pre-eminence among either Bees or Ants; love and unanimity, more powerful than punishment or death itself, preside there, and all live together in the same manner as the primitive christians anciently did, who were connected by fraternal love, and had all things in common." A step forward from contemporary "monarchical" models of insect society (Prete, 1991), this was nevertheless neither accurate nor particularly fruitful in terms of generating potential experiments.

In his later study on bees, Swammerdam's explanation of sociality was richer. Firstly, he noted that there was a clear reproductive division of labour within the colony: "the common Bees have no ovary, and therefore, like women who have lived virgins till they are past child-bearing, serve only the purpose of labour in the oeconomy of the whole body. These are thus by nature rendered incapable of doing any other business but that of nourishing and educating the young offspring".

Then he provided an explanation as to the function and driving force of sociality: "the cohabitation of Bees has no other end but to perpetuate their species; and thus, by the help of an exact order of production, to perpetuate their continuance." The focus of this "order of production", he argued, was the brood: "the actions of Bees of the three kinds, male, female, and eunuchs, spring from no other cause but from a vehement and ardent concern, by which they are carried to the generation, preservation, and raising of the brood, which, as it is alone the principle, so likewise it is the end of every thing the Bees do."

Swammerdam not only considered that reproduction was the factor that held the colony together, he also suggested that it was involved in causing conflicts: "As therefore it is generation alone by which the Bees are excited to all their actions, so this great cause, whenever it happens to be interrupted, is the sole motive from whence all the confusion at times observed in the hives arises". The kinds of "interruption" he described included queen sterility, or the presence of two queens in the hive, which gives rise to physical battles between the two individuals. He emphasised the importance of there being only one queen per hive, although he also noted that this is not the case in all social insects, and also noted an apparent relation between polygyny and reproductive ability: "This [polygyny] is manifest in Hornets and Wasps; for these insects suffer many females at once in the nest. It is proper to observe here this remarkable difference, that each of these females lay only a few eggs". The fact that Swammerdam focused on reproduction was as much a consequence of contemporary fascination with this great mystery as a result of his close observation of insect behaviour.

Conclusions

This brief survey of Swammerdam's work on social insects not only shows how he pioneered the study of their anatomy, it also indicates that his vision extended to describing and explaining their social organisation. His observations and interpretations, which are striking by their clarity and accuracy, show that, from the very beginning, the scientific study of social insects sought to go beyond mere description and to provide an explanation of sociality. Swammerdam's work shows the impact of the "scientific revolution" on the study of the natural world: using experimentation and new microscopic techniques, Swammerdam, like many of his contemporaries, made a key contribution to the development of biology. This article will have been worthwhile if it encourages all researchers, young and old, to occasionally take the time to study what the pioneers of our science actually wrote and discovered. In particular, Swammerdam's precious legacy of anatomical drawings and descriptions of behaviour deserve to be more widely known.

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