



The original histological sections of myrmecophilous and termitophilous beetles of Erich Wasmann (1859–1931)

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Abstract

Through historical coincidence, we had the opportunity to study the original sections of myrmecophilous and termitophilous beetles that were made more than a century ago by the Austrian Jesuit priest Erich Wasmann. The collection contains 95 histological and 43 total mount slides, and includes serial sections through several entire beetles. The sections reflect Wasmann's technical skills to produce material for microscopical analysis, although inevitable limitations in section thickness resulted in only partial accuracy in his interpretation of anatomical organisation. Especially the recognition and description of exocrine glands remain rather limited, with most emphasis on the origin of secretions being attributed to the well-developed fat tissue instead. The collection will be transferred back to the Natural History Museum in Maastricht, Netherlands, to join the main Wasmann collection to which it belongs.

Keywords Histology · Microscopy · Guests · History · Exocrine glands · Mimicry

Introduction

The interspecific relations between social insects and their arthropod guests have long fascinated naturalists, with particular attention to the many beetle species that can be found in ant and termite nests. These ingenious invaders have managed to enter the nest fortress of the ant or termite colony by breaking the recognition code and getting access to the colony resources. This often includes advanced behaviour as well as the use of secretions from specialised glands that are highly attractive to their hosts, and their ability to participate in the hosts' food sharing system (Hölldobler 1967, 1970, 1971; Watson and Kistner 1972; Kistner 1979; Ikeshita et al. 2017; Hölldobler et al. 2018; Parker 2018; Hölldobler and Kwapich 2019; Parmentier 2020). Numerous papers have been published in this field, topped by a magnificent

overview in the recent book on “the Guests of Ants” by Hölldobler and Kwapich (2022).

A main pioneer and authority in the study of these myrmecophiles (ant guests) and termitophiles (termite guests) no doubt was the Jesuit priest Erich Wasmann (Fig. 1). Wasmann not only described hundreds of these symbionts, but also studied their behavioral interactions with their hosts (e.g. Wasmann 1886, 1897, 1915, 1920, 1925). In an attempt to find anatomical information that may help explain these interspecific contacts, he also made and discussed histological sections of many symbiotic beetles (Wasmann 1903). We here report on the original sections made by Wasmann more than 120 years ago, that we could study by accidental coincidence. In the period from 1963 to 1973, the late Prof. Jozef van Boven from Leuven University was curator of the Wasmann collection in Maastricht, and in that function must have had access to his histological sections. As Prof. Jacques Pasteels at nearby Brussels University (ULB, only 30 km from Leuven) in that period was studying termitophile beetles for his PhD (Pasteels 1968a,b, 1969), van Boven loaned the Wasmann sections to him. As the sections mainly contained material of myrmecophile species, however, they were never used and stayed all the time untouched in a drawer at Brussels University. It was only several years after his retirement that Pasteels when cleaning up his office in 2017 came across the old Wasmann sections again. He

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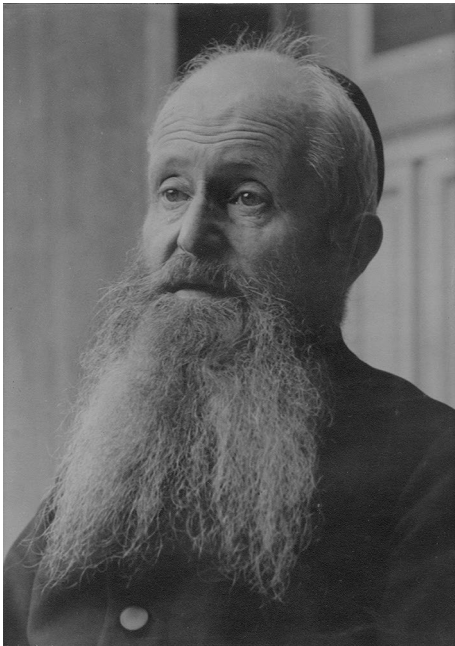


Fig. 1 Erich Wasmann at the age of 66 (photograph May 1925)

kindly handed them to one of us (JB, who in 1987 took over van Boven's position at Leuven University), thus bringing them back to Leuven from where he had received them half century ago. We now gladly take the opportunity to study this historical treasure before returning the sections again to the Wasmann collection in Maastricht.

Wasmann's life and career

Detailed accounts on Wasmann's life and career are given in two local journals in Dutch (Schmitz 1932; Terhal 1956) and by Stumper (1954) in French. Erich Wasmann was born on 29 May 1859 in the Austrian-Tirolean city of Meran (nowadays, Italy) as the fourth child of six. His father Friedrich was a painter who was born in Hamburg, Germany, but who moved at the age of 25 to the alpine environment in Meran because of his weak health. As Erich's older brother and sister died at very young age, he grew up in a family with three sisters. As a talented young student of 15, Erich Wasmann was offered a prestigious scholarship at the Jesuit school in the Austrian city of Feldkirch. Already after one year, 16-year-old Wasmann decided to join the Jesuit community, and therefore moved to Exaten (alternatively spelled as Exaeten) near Valkenburg in the southeastern Netherlands, as the Jesuit order at that time was banished from Germany and Austria. The monastery at Exaten also became the editorial office of '*Stimmen aus Maria-Laach*' ('*Voices from Maria-Laach*'), the journal that referred to the former Jesuit headquarters in Maria-Laach near Koblenz, Germany. The

Jesuits were welcomed by the Dutch bishops on the condition they would not actively participate in parish work. The remarkable result of this was that the German and Austrian priests could spend more time in study than would have been the case at home, resulting in very busy editorial activities for their journal.

Like his father, Erich Wasmann also had a weak health with lung tuberculosis and was therefore advised to spend much time in the open air. This brought him in contact with the magnificent fields and forests near the monastery, of which especially leaf-rolling weevils were the most appealing to him. Because of his fragile health, Wasmann did not receive the traditional training to become a missionary as his fellow Jesuit colleagues, but instead became a member of the editorial board of '*Stimmen aus Maria-Laach*' at the monastery. It was in May 1884 when a Jesuit priest brought the book "*Ants, Bees and Wasps*" of John Lubbock to Exaten that Wasmann's interest in the biology of ants was initiated. Before writing a commentary for the journal, Wasmann wanted to get a better background by studying ants himself, first in their natural habitat and later by building and observing artificial ant colonies with particular attention for slave-making species. His younger Jesuit colleague H. Schmitz, who participated in the field work, described the hard work of meticulously monitoring at least once a month 412 nests of the slave-making ant *Formica sanguinea*, with the amusing anecdote how Wasmann at the end of each inspection threw some sugar in the disturbed nests as a compensation for the damage he had created by opening them (Schmitz 1932). Wasmann soon became an eminent ant specialist himself, especially in the field of myrmecophiles and termitophiles. He actively corresponded with the leading myrmecologists of that time, particularly with August Forel. From him, and also from numerous Jesuit missionaries worldwide, Wasmann received countless samples of tropical myrmecophiles and termitophiles from Congo and East Africa, Madagascar, Sri Lanka, Indonesia, the USA and South America. He was the first to describe the phenomenon wherein myrmecophiles closely resemble the appearance of the host. He suggested that this was a form of tactile mimicry to deceive the host and would facilitate acceptance in the host colony. However, he did not dismiss the possibility that resembling ants could also function as a form of Batesian mimicry, fooling predators like birds that avoid aggressive ants (Wasmann 1925). This phenomenon was later coined as Wasmannian mimicry by Rettenmeyer (1970).

Soon after receiving his ordination as a Jesuit priest on 1 July 1888, Wasmann was sent to Prague University to study zoology (1890–1892). From 1899 to 1911, he lived in Luxembourg, where the editorial office of '*Stimmen aus Maria-Laach*' had then moved to. During this period without the extensive field work he was used to in Exaten, he could focus on writing up his findings and thoughts on philosophy and

Table 1 Survey of the microscopy material produced by Erich Wasmann

Species	Taxon	Number of slides	Group
Histological slides			
<i>Lomechusa emarginata</i> (Paykull, 1789) ^A	Aleocharinae	15	Myrmecophile
<i>Dinarda dentata</i> (Gravenhorst, 1806)	Aleocharinae	1	Myrmecophile
<i>Dorylomimus kohli</i> (Wasmann, 1902)	Aleocharinae	2	Myrmecophile
<i>Ecitogaster schmalzi</i> (Wasmann, 1900)	Aleocharinae	3	Myrmecophile
<i>Ecitophya simulans</i> (Wasmann, 1889)	Aleocharinae	5	Myrmecophile
<i>Lomechusoides strumosus</i> (Fabricius, 1792) ^B	Aleocharinae	36	Myrmecophile
<i>Phyllostinarda kohli</i> Wasmann, 1916	Aleocharinae	3	Myrmecophile
<i>Platyarthrus hoffmannseggii</i> (Brandt, 1833)	Isopoda	3	Myrmecophile
<i>Sympolemon anommatis</i> (Wasmann, 1900)	Aleocharinae	6	Myrmecophile
<i>Xenogaster inflata</i> (Wasmann, 1891)	Aleocharinae	19	Termitophile
Slide mounts			
<i>Dinarda dentata</i> (Gravenhorst, 1806)	Aleocharinae	4	Myrmecophile
<i>Displotera maderae</i> (Wollaston, 1854) ^C	Endomychidae	5	Myrmecophile
<i>Dorylomimus kohli</i> (Wasmann, 1902)	Aleocharinae	2	Myrmecophile
<i>Ecitogaster schmalzi</i> (Wasmann, 1900)	Aleocharinae	5	Myrmecophile
<i>Ecitophya simulans</i> (Wasmann, 1889)	Aleocharinae	2	Myrmecophile
<i>Forcipomyia braueri</i> (Wasmann, 1893) ^D	Ceratopogonidae	1	Myrmecophile
<i>Lasaeola tristis</i> (Hahn, 1833)	Theridiidae	1	Unassociated
<i>Leptogenys diminuta</i> (Smith, 1857) ^E	Formicidae	1	Ant
<i>Myrmecocatops latus</i> (Wasmann, 1897)	Tenebrionidae	1	Myrmecophile
<i>Myrmecorhinus pinniger</i> (Wasmann, 1897)	Curculionidae	1	Unassociated
<i>Ocyopus nitens</i> (Schrank, 1781)	Staphylinidae	1	Unassociated
<i>Periplaneta americana</i> (Linnaeus, 1758) (muscle)	Blattidae	1	Unassociated
<i>Phyllostinarda kohli</i> (Wasmann, 1916)	Aleocharinae	11	Myrmecophile
<i>Phyllostinarda xenocephala</i> (Wasmann, 1916)	Aleocharinae	1	Myrmecophile
<i>Rectinasus buxtoni</i> (Theobald, 1914)	Aphididae	1	Ant-associated aphid
<i>Sympolemon anommatis</i> (Wasmann, 1900)	Aleocharinae	3	Myrmecophile
Nematode from <i>Lasius alienus</i>	Nematoda	1	Nematode
(?) illegible label	–	3	

The collection comprises 95 histological slides and 43 slides with total mounds. Several species in Wasmann's time had a different species name than nowadays, the Table lists the current name with indication of the name appearing on the label as follows:

^A*Atemeles emarginatus* on original label

^B*Lomechusa strumosa* on original label

^C*Coluocera oculata* on original label

^D*Ceratopogon braueri* on original label

^E*Lobopelta diminuta* on original label

evolution. Wasmann has the great merit that he accepted Darwin's evolution theory although the Catholic Church had not generally accepted it. In 1911, the editorial office and Wasmann moved back to the Netherlands, to settle in the Ignatius college at Valkenburg, near to Exaten. Over the years, Wasmann built up a unique collection with over 1,000 ant and 200 termite species, and 44 insect boxes containing 2,000 species of myrmecophiles. He described 933 new species, mostly myrmecophiles and termitophiles, and published 290 papers on these symbionts, totaling over 7000 pages, in addition to 145 general entomology papers and 315

short communications (van Boven 1985). From 1950 until 1996, the University of San Francisco even published "*The Wasmann Journal of Biology*" as a tribute to the Austrian Jesuit.

In spite of his obvious knowledge and competence, Wasmann never had any teaching duties, and even declined an offer for a professorship at Frankfurt University in 1911. He was awarded an honorary doctoral degree in 1921 by the Swiss University of Freiburg, however, and received the prestigious "Wasmann-Festband" from the German Zoological Society with 30 contributions from worldwide



Fig. 2 Comparison of histological slides made by Janet (left) and Wasmann (right). Note the striking difference in size of the glass strips used



Fig. 3 Example of 8 consecutive histological slides containing the serial longitudinal sections through an entire adult male *Lomechusoides strumosus*. The hand-written labels specify this beetle was collected in colony 191 (probably of *Formica sanguinea*) in September

1898. Fixation was performed in alcoholic formaldehyde, staining of the 10–20 μm thick sections was done with Grunach's hematoxylin and eosin

authorities in honour of his 70th birthday in 1929. Health problems unfortunately became more and more frequent, and on 27 February 1931 Erich Wasmann peacefully died in the monastery at Valkenburg. In his will, Wasmann expressed the wish that his collection remained together, and appointed his fellow Jesuit H. Schmitz as its first

curator. The collection stayed in Valkenburg until it was moved in 1941 to the Natural History Museum in Maas-tricht. During the war, however, the collection was stolen in 1943 and transferred to Berlin. In 1945, it safely returned to its current location in Maastricht.

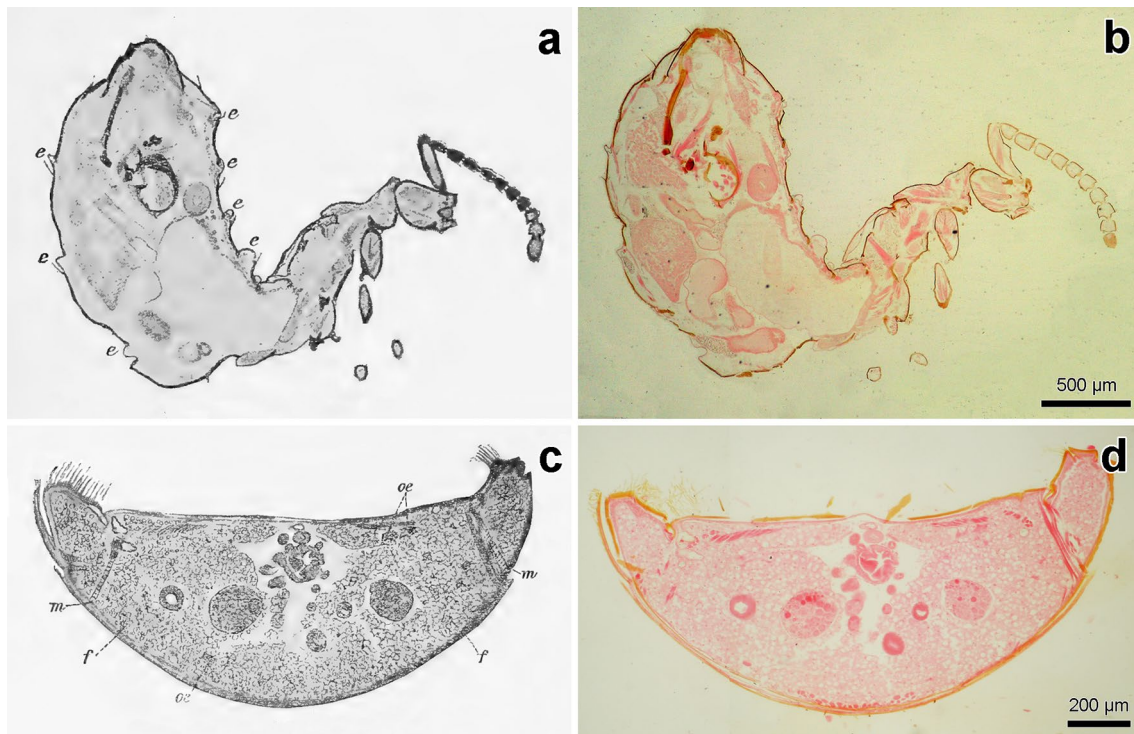


Fig. 4 Examples of Wasmann's illustrations (**a, c**) with the matching original histological sections (**b, d**). **a, b** Longitudinal section through body midline of young physogastric *Xenogaster inflata* male; *e* exu-

date buds (Fig. 24a in Wasmann 1903). **c, d** Cross section through abdomen of young *Lomechusa emarginata* male; *f* fat cells, *m* transverse muscles, *oe* oenocytes (Fig. 3 in Wasmann 1903)

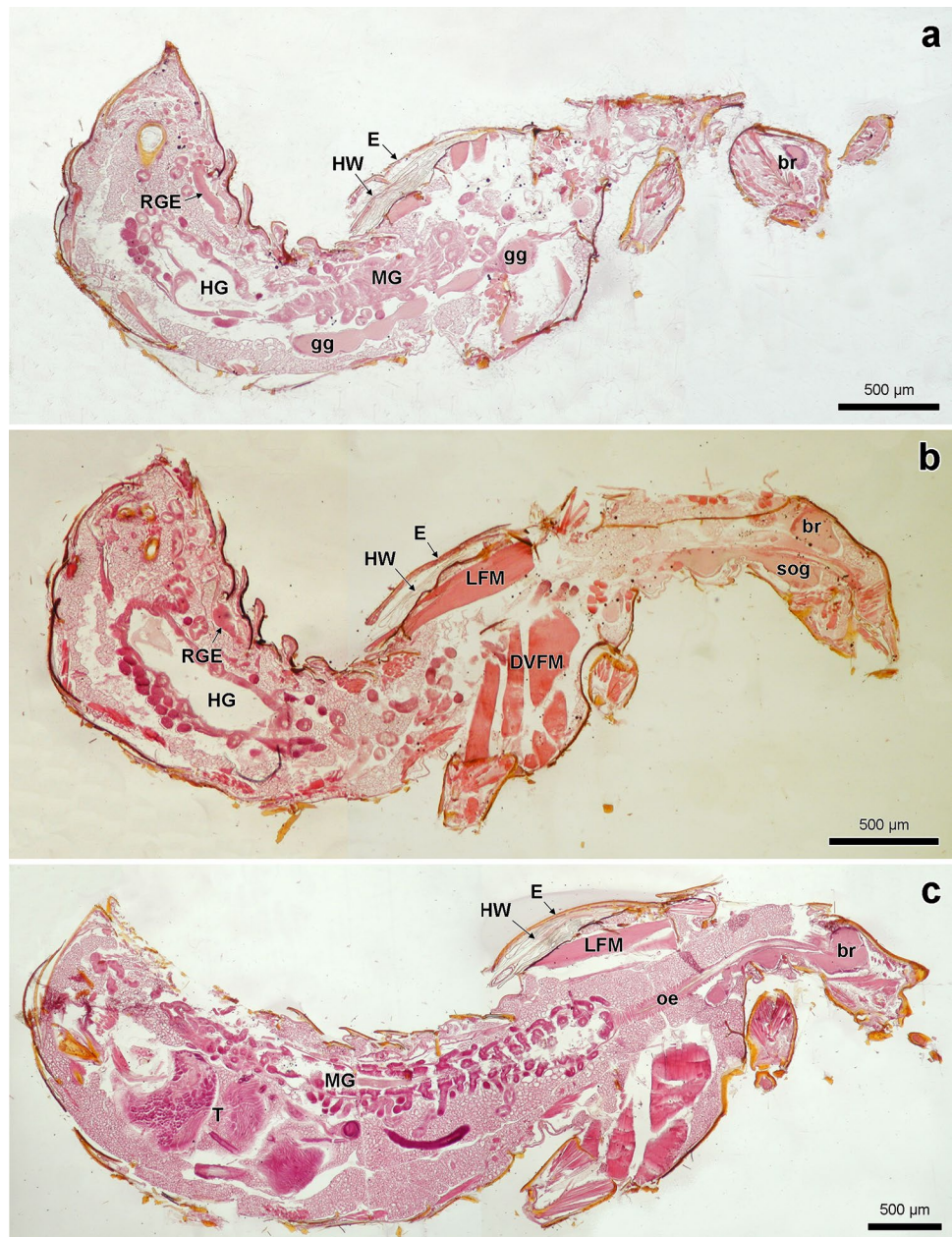
Technical description of Wasmann's histological sections

The collection we here describe consists of 138 glass slides, of which 95 had histological slides and 43 were slides with total mounts, a more detailed contents list is given in Table 1. Wasmann's own estimation of his histological work mentions about an overall number of 20,000 sections (Wasmann 1915). With an average of 20–30 sections per slide, his entire production may, therefore, be considerably larger than the slides we had available. The slides are in 9 cardboard folders that each contain a label "Wasmann collection Maas-tricht", which illustrates they did form part of the original collection before they were loaned to the ULB in Brussels in the early 1960s. The glass strips used are all today's standard commercial slides of 76 × 26 mm with a uniform thickness of 1.00 mm. This is remarkable as the illustrious French histologist Charles Janet, who lived in the same period as Wasmann, used considerably larger strips of 87 × 37 mm with up to 10% variation in the thickness of the same glass (Billen and Wilson 2008). Both pioneers provided their sections with almost calligraphic hand-written labels, Wasmann using commercial labels with blue or red decorations (we could not figure out any meaning for these colours), while Janet used more variable self-made cardboard labels (Fig. 2).

While Janet published several tens of papers with descriptions of his histological observations mainly in the period from 1893 to 1910, we are only aware of one significant and detailed publication with histological data of Wasmann in 1903 "Zur näheren Kenntnis des echten Gastverhältnisses (*Symphilie*) bei den Ameisen- und Termitengästen" (= "Towards a closer understanding of the real host behaviours (*symphily*) in ant and termite guests"), which is composed of 5 partial sub-papers. Including a Material and Methods section was uncommon in these days and Wasmann (1903) only provided a brief methodological account as a footnote on page 67: he embedded insects by immersing them during 1–3 days in a hard type of liquid paraffin at 50–60 °C, and for making sections used a Hatschek microtome. No information is provided about tissue fixation, the labels of some sections even indicated that some tissues were kept in ethanol for 10 years prior to sectioning (e.g. Figure 5b). Staining was mostly performed with hematoxylin (Delafield)/eosin, hematoxylin/Congo red, or haemalun (Mayer)/orange/eosin. Sometimes pre-staining with osmic acid was done. Information on section thickness can sometimes be found on the hand-written section labels, and usually is in the range between 10 and 20 µm.

The majority of the histological slides is formed by serial sections of mainly longitudinally cut entire beetles

Fig. 5 Longitudinal sections (anterior to the right) through adult *Lomechusa emarginata* (**a** and **b**; the specimen in **b** was preserved for 10 years in alcohol) and male of *Lomechusoides strumosus* (**c**). *br* brain, *DVFM* dorsoventral flight muscle, *E* elytra; *gg*: ganglia, *HG* hindgut, *HW* hind wing, *LFM* longitudinal flight muscle, *MG* midgut, *oe* oesophagus, *RGE* repellent gland epithelium, *sog* suboesophageal ganglion, *T* testes



of *Lomechusoides strumosus* (39 slides, formerly called *Lomechusa strumosa*), *Lomechusa emarginata* (15 slides, formerly called *Atemeles emarginatus*) and *Xenogaster inflata* (19 slides), comprising up to 8 slides for all sections of an entire specimen (Fig. 3). Wasmann classified social insect guests into five groups based on their biology and level of integration (Wasmann 1894). The myrmecophiles *Lomechusa* and *Lomechusoides* and the termitophile *Xenogaster* belong to the category of symphiles or true guests, which reach the highest level of integration of all guests. *Xenogaster* is a physogastric rove beetle with inflated membranous areas between tergites and sternites. *Lomechusa* and *Lomechusoides* are rove beetles characterised by yellow

tufts on the abdomen. The remarkable ability of symphiles to chemically deceive their host makes them particularly intriguing subjects for histological examination. As both Janet as Wasmann did not yet have the technical means to illustrate their publications with photographs of their histological sections using a camera, they included section drawings, although it must be said that Janet had considerably better artistic skills to produce highly detailed drawings. Of all 24 illustrations in Wasmann (1903), we managed to link only 2 with the matching original histological sections (Fig. 4). This low number, however, may reflect that we only had access to part of his entire histological work, and may also be explained because a number of the published

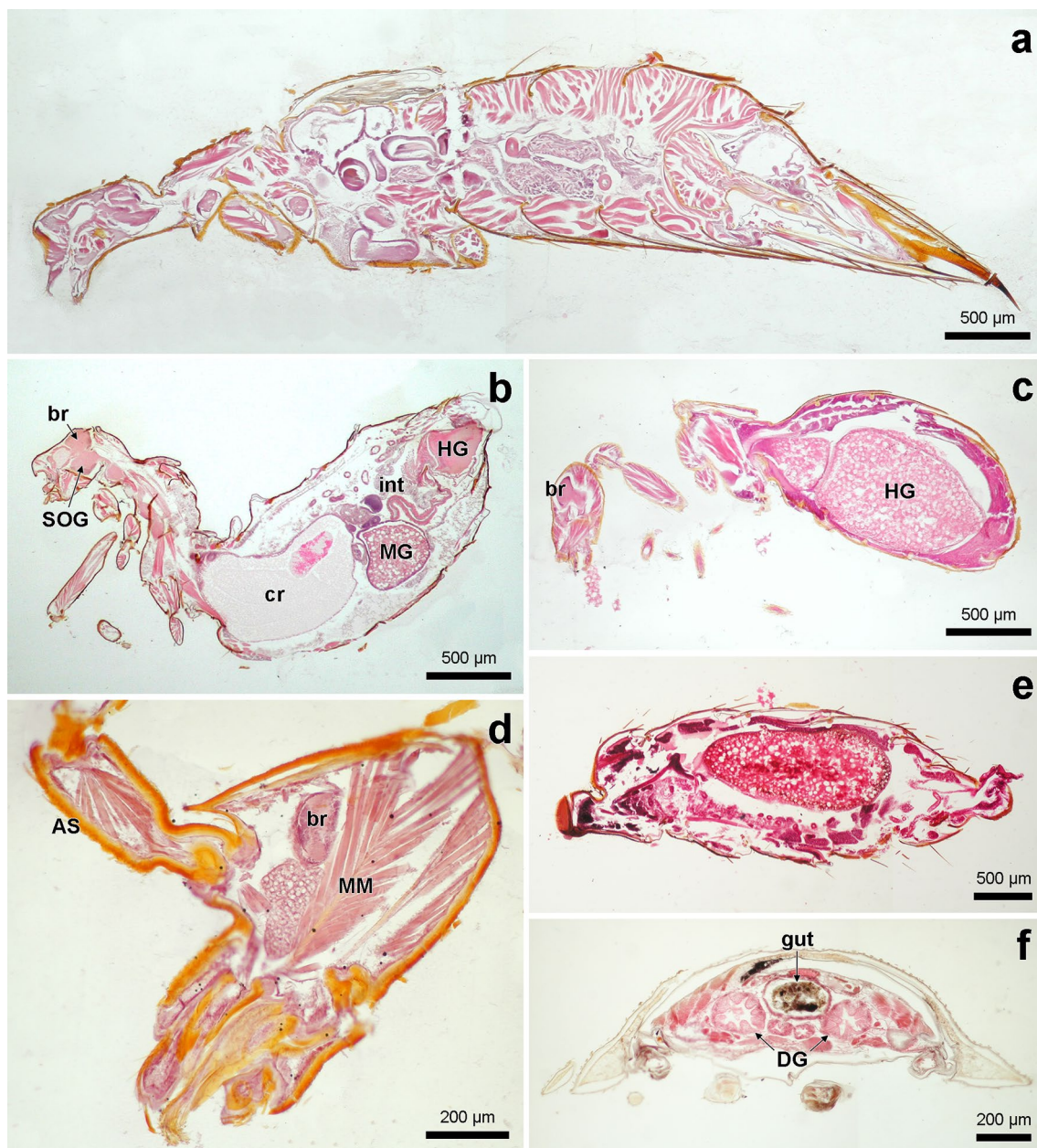


Fig. 6 Longitudinal (a–e, anterior to the left) and cross sections (f) of *Symplemon anommatis* (a), *Xenogaster inflata* female (b), *Dorylommimus kohli* (c), *Lomechusoides strumosus* male head with antenna articulation (d), *Ecitophya simulans* (e) and *Platyarthrus hoff-*

mannseggii (f). AS antennal scape, br brain, cr crop, DG digestive gland, E elytra, HG hindgut, HW hind wing, int intestine, MG midgut, MM mandibular muscle, oe oesophagus, SOG suboesophageal ganglion

drawings show just a single cell while others do not represent a view of a particular section but show schematic interpretations of anatomical structures (Fig. 8b).

In his 1954 ‘in memoriam’ contribution, Luxembourgian biochemist Robert Stumper (who became known for his discovery of the high contents of formic acid in the

formicine venom gland) gives an entertaining account on how he as a young boy was intrigued by the Jesuit priests in long black robes that walked around near their

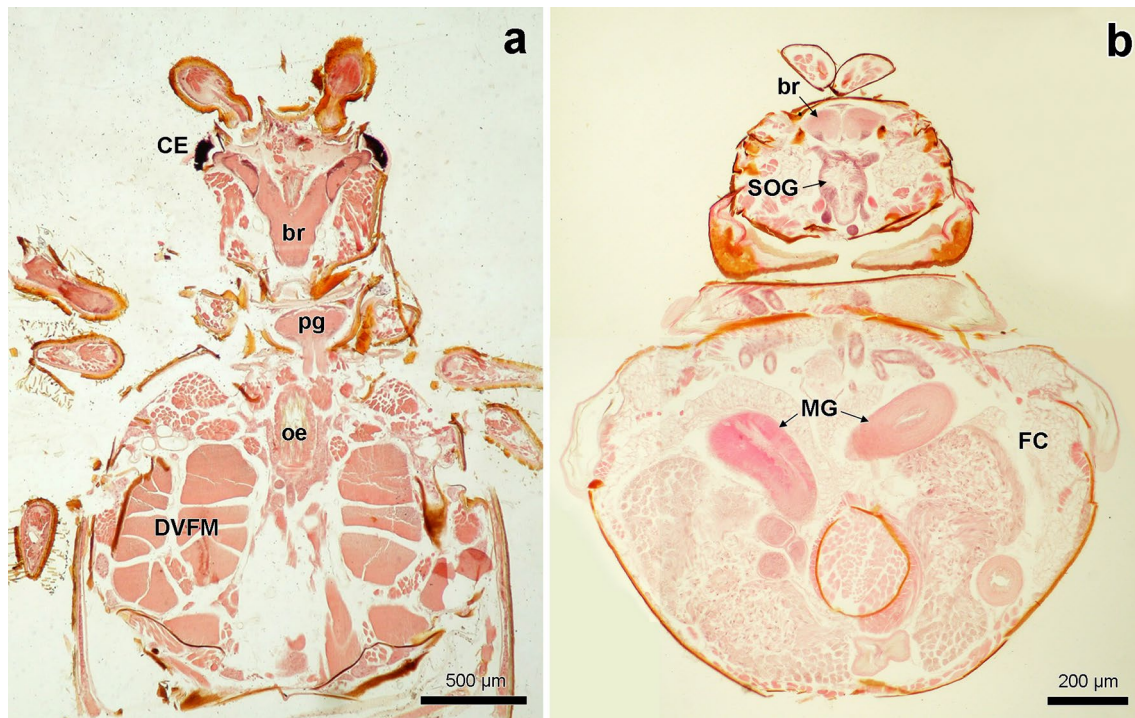


Fig. 7 Coronal plane sections of adult *Lomechusoides strumosus* female (**a**) and *Xenogaster inflata* male (**b**). *br* brain, *CE* compound eye, *DVFM* dorsoventral flight muscle, *FC* fat cells, *MG* mucus gland, *oe* oesophagus, *pg* prothoracic ganglion, *SOG* suboesophageal ganglion

monastery in Luxembourg. Especially the behaviour of one of them (Erich Wasmann) with a long grey beard who often turned stones in search for ants drew his special attention: Stumper describes how he was invited to visit his monastery room, in which Wasmann showed him a microscopy section. He also describes how Wasmann around 1893 went to Leuven, Belgium, to make himself familiar with histological techniques in the Carnoy Institute (= the University's Institute of Botany, where priest Prof. Jean-Baptiste Carnoy was an eminent specialist in cell biology and histological research). It is an amazing coincidence that Wasmann's sections 130 years after he learned in Leuven how to produce them temporarily came back to this city, before they will be returned to Maas-tricht to join the rest of the Wasmann collection.

Scientific description of Wasmann's histological sections

Our current understanding of the role of exocrine secretions in the interactions between the myrmecophilous beetles and their ant hosts is mainly based on the excellent papers of Jordan (1913), Pasteels (1968a, b, 1969) and especially Bert Hölldobler and co-workers (1970 for *Lomechusa pubicollis*; 2018 for *Lomechusoides strumosus*; 2019 for *Dinarda dentata*). In the most complex case of the subtribe

Lomechusina (*Lomechusa*, *Lomechusoides* and *Xenodusa*) four abdominal gland sets can be distinguished (see Fig. 11 in Hölldobler et al. 2018). The ant's initial aggressive behaviour fades away after its licking secretions of the epithelial appeasement gland complex that is formed by the thickened 8–10th tergal and sternal epithelia. Also, the nearby located paired secretory cell clusters of the postpleural glands play a role in this behavior. The paratergal lobes on segments 2–5 contain at their base as well as in their interior clusters of class-3 secretory cells that open through pores near the base of the numerous golden bristles. These gland cells represent the adoption gland that the ants lick prior to grabbing the beetles at their trichome tufts, lifting and carrying them into the ant nest. A large tergal gland between tergites 6 and 7 consists of large reservoir sacs at either side formed by the invaginated intersegmental membrane between both tergites with a massive differentiation of the epithelial reservoir wall, and two large clusters of secretory cells that open at the posterior side of the reservoir sac. This large composite tergal gland thus contains both class-1 and class-3 gland cells and acts as a repellent gland, that in *L. strumosus* contains benzoquinone, ethyl- and methyl-benzoquinone and n-tridecane (Blum et al. 1971).

Wasmann's histological work contains numerous serial sections of various species that offer good views of internal anatomy (Figs. 5, 6, 7). Whereas modern embedding techniques use polymer resins that allow making high quality

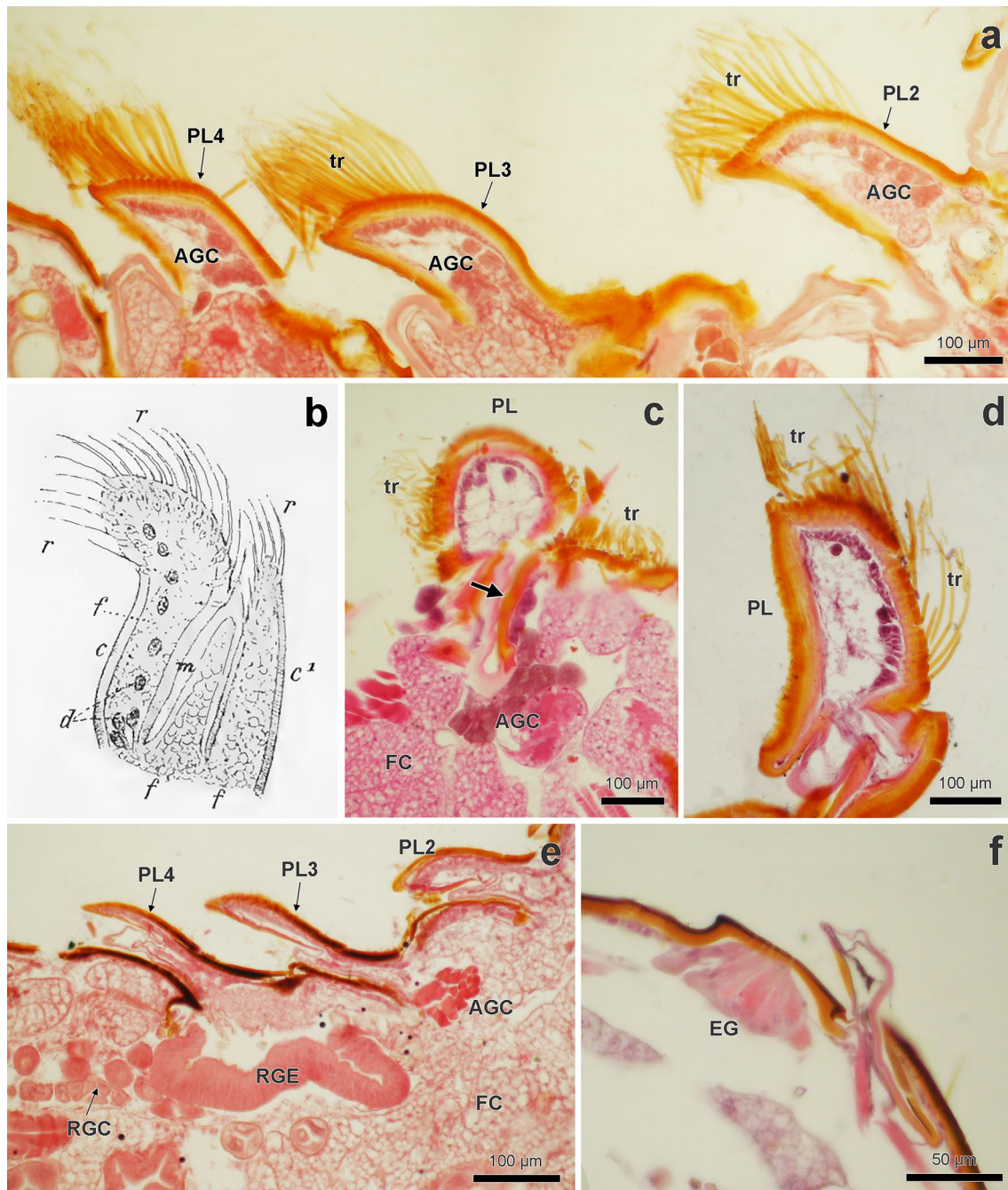


Fig. 8 Detail views showing exocrine glands (**a–d** *Lomechusoides strumosus*; anterior to the right): **a** Paratergite lobes (PL2–4) on abdominal segments 2–4 showing golden trichome hairs (*tr*) and secretory cells of adoption gland (AGC). **b** Wasmann's own interpretation of the paratergite lobes (Fig. 1 in Wasmann 1903) mentions about a 'membranous intermediate tip' (*m*) that acts as a duct to guide secretion to the exterior. Other abbreviations in his original drawing: *c*, *c1* chitinous bristle-carrying segmental tip, *d* dark gland cells with vesicles, *f* fat tissue with lipid droplets near apical tip, *r*

sensory bristle hairs with nerve cells at their base. **c**. The original sections reveal the 'membranous tip' is just the intersegmental membrane (arrow; see text). **d** Detail of paratergite lobe. **e** Terminal tergites of *Lomechusa emarginata* showing location of adoption gland (AGC) and repellent gland that comprises conspicuous epithelial sac (RGE) and more posteriorly clustered class-3 secretory cells (RGC). Note extensive presence of fat cells (FC). **f** Epithelial gland (EG) underneath the 5th tergite in *Xenogaster inflata* female

thin sections even through hard sclerotised insect tissue, Wasmann's material was embedded in paraffin and, therefore, was sectioned at a thickness between 10 and 20 μm . This inevitably compromised section quality and mainly allowed observation at low magnifications only, as proper image focusing of thick sections using higher magnifications could not be achieved. The use of paraffin moreover caused inevitable artefacts of torn cuticle, especially on sections of adult beetles. Most of the material we could study are aleocharine beetles which typically possess a tergal defensive gland. Although clearly visible on the sections of *L. emarginata* (Fig. 5a,b; 8e), it is surprising that no mention whatsoever is made of the tergal repellent gland in Wasmann's text description, as was also criticised by Jordan (1913). Also epithelial gland tissue in *Xenogaster inflata* (Fig. 8f) did not receive any attention in his reporting, which may be because it was not widely known in 1903 that gland tissue can have an epithelial appearance (as the classification of gland tissue into epithelial 'class-1' and clustered secretory cells 'class-3' was only published by Noirot and Quenenedey in 1974). On the other hand, Wasmann did recognise the existence of clustered 'class-3' gland cells, which he described on p.198 as 'unicellular gland cells' because they contain "einen Hof mit einem Sammelkanal in den Blaschen" (= "an area with a collecting duct connected to the vesicle") which clearly refers to what has later been designated as the end apparatus (Noirot and Quenenedey 1974).

Wasmann also reported that the paratergal lobes release their secretion through a 'membranous intermediate tip' that acts as a duct (m in Fig. 8b), although close examination of the original sections show this 'membranous tip' is just the intersegmental membrane (Fig. 8c). In spite of correctly recognising these cells as exocrine tissue, Wasmann minimises his own histological findings by considering the well-developed fat body as the main source of the secretion that attracts the ant workers. The clear demonstration of the involvement of the exocrine glands instead was first provided by Jordan (1913) and later confirmed by Pasteels (1968a,b, 1969), Hölldobler (1970) and Hölldobler et al. (2018). Noteworthy in this regard is the extremely vivid and at times even aggressive mutual criticism between Jordan (1913) and Wasmann (1915), in which Jordan refuted some of Wasmann's histological conclusions as simply wrong. Wasmann's reply contained 26 pages of an irritation-filled rebuttal! A translation of his cynical conclusion says "The unravelling of the secrets of *Lomechusa* and *Lomechusoides* should be done by meticulous studies that last many years instead of superficial observations. ... Literature does not exist to be ignored or to be wrongly cited. Science in this area will only make progress if it scrupulously builds on already known knowledge, otherwise it throws us back a quarter of a century." (Wasmann 1915).

Wasmann initiated the study of social insect guests and the importance of his pioneering contributions are immeasurable. He described numerous new species, hinted at evolutionary processes in this group (cfr. description of Wasmannian mimicry in Wasmann (1925) and his classification scheme in 5 types: synechtrans, synoeketes, symphiles, ecto- and endoparasites, trophobionts in Wasmann (1894)). He also characterised interactions with the host by close observation (cfr. food solicitation in symphiles, predatory behaviour in *Pella* (Wasmann 1920)), explored their variable host range (Wasmann 1920) and exposed unique facets of their biology (e.g. host switching "Doppelwirtigkeit" in *Lomechusa*, Wasmann (1915)). However, the extent of his influence on our understanding of their histology and their glands is more debatable. A closer examination of his histological slides and his interpretations demonstrated interesting discoveries (cfr p.70–71 with description of 5 types of excretion producing tissues), but also revealed inaccuracies in his work, partly due to the moderate quality of the slides.

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Data availability This review article deals with historical sections of more than 120 years old, that after publication of this paper will be returned to the Natural Historical Museum in Maastricht, Netherlands (as is clearly mentioned in the last sentence of the Abstract, and also in the main text). For this reason, a "data availability statement" is not really applicable.

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