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Flight muscle histolysis in *Lasius niger* queens

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ABSTRACT. The foundation of new ant colonies often involves a solitary phase for the newly mated queens. These queens are subject to high food stress during this period that can last several weeks or months until the appearance of the first workers. The food stress is mainly associated with egg laying, larval feeding, and the queens' own metabolism. The flight muscles of ant queens are histolyzed during early colony foundation, a process that was first described by Charles Janet more than a century ago. We here document this breakdown process in *Lasius niger* queens using careful dissections and histological examination. As we have the war-surviving original sections of Janet in our possession, we were able to include part of his original data in this paper. Our study also provides a calibration ladder for future investigations on flight muscle histolysis in ants. We describe the process, its stages, and discuss the allocation of nutrients from histolysis and the speed of histolysis related to the duration of colony foundation.

Keywords	Flight muscles, Histolysis, Histology, Colony foundation, Nutrient allocation
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INTRODUCTION

For most ant species, reproduction and dispersal involve a nuptial flight during which the virgin alate females and males fly away from their natal nest and mate in the air (Peeters & Molet 2010; Cronin et al. 2013). This flight at the same time ensures a high genetic crossbreeding between sexuals from neighboring colonies, and the dispersal of the founding queens over a considerable distance (Hölldobler & Wilson 1990). Soon after mating, the males die, whereas the inseminated females start the foundation of a new colony. Their wings are no longer needed and are therefore torn off shortly after the nuptial flight. The young queens then set off in search of a place to raise their first batch of worker offspring.

According to species, the founding stage can last several weeks to several months. During this period, the foundress will be subject to an intense food stress, that is particularly high because of the need to obtain nutritive resources for her own metabolism as well as for the laying of eggs and the feeding of the larvae. In the ancestral

condition, the foundress needs an external supply of nutrients to rear her first batch of worker offspring, and therefore must regularly forage for food outside the nest. This unspecialized foundation is known as 'non-claustral' and predominates in most early diverged ant subfamilies (Peeters & Ito 2001; Keller et al. 2014; Peeters 2020). In contrast is 'claustral' foundation, in which the young queen permanently stays in her new nest, and rears her first offspring only with her own internal nutrient reserves. The latter type of colony foundation without external food supply is possible thanks to the queen's large metabolic reserves such as fat and specialized storage proteins accumulated before leaving the natal nest (Keller & Passera 1989; Wheeler & Buck 1995). This behavioral and developmental innovation is coupled to a miniaturization of the workers that accelerates their development and reduces their feeding cost (Peeters & Ito 2015). In addition to the specialized fat and protein reserves, the flight muscles of the foundresses will contribute as they will be recycled by histolysis, thus providing the queens with a considerable protein supply.

Insect flight is powered by the fast-moving antagonistic longitudinal and dorsoventral (also known as transverse) indirect flight muscles that occupy a large portion of the thorax (Dudley 2000). Flight muscle histolysis is a widespread phenomenon, often forming part of the trade-off between dispersal and reproduction (also known as flight-oogenesis syndrome; Johnson 1969; Marden 2000), and has been reported in various insect taxa such as planthoppers, water striders, aphids, crickets, firebugs and termites (Denno et al. 1989; Kaitala & Huldén 1990; Tanaka 1991; Kobayashi & Ishikawa 1994; Socha & Šula 2006; Zhang et al. 2021). Flight muscle histolysis in ant queens was first documented by Charles Janet in 1906. The fire ant (*Solenopsis invicta*) later became the model species used to understand the triggering factor(s) of this process. Juvenile hormone was first proposed as the initiating factor (Barker 1979) but was later invalidated by Azizi et al. (2009). According to the latter study, it appears that the initiating factor should be in the sperm or a chemical component associated with it. Additionally, Davis et al. (1989) showed evidence that one or more humoral factors are responsible for the initiation of flight muscle histolysis in winged fire ant females.

A wide variety of foundation strategies exists in ants (Cronin et al. 2013; Peeters 2020). Nevertheless, to date, flight muscle histolysis has been studied only in species with claustral founding. Several preliminary observations on Poneroid ants (*Pachycondyla crassinoda*), however, showed that flight muscle histolysis also occurs in species with non-claustral foundation (see below). According to the phylogenetic position of the early diverged clade of the Poneroid and Formicoid groups with respect to the other crown-ants (Moreau et al. 2006; Barden et al. 2020; Keller & Peeters 2020), we assume that flight muscle histolysis probably appeared early during ant evolution and diversification. Interestingly, the flight muscles occupy a large volume in the thorax of ant queens (e.g. 41 % in *Euponera* and 52 % in *Cataglyphis* according to Peeters et al. 2020) and thus represent a significant nutritive resource for the queens during solitary foundation. A modification of the speed and efficiency of histolysis may therefore influence foundation success and help define the dynamics of colony foundation among species. We here document the process of flight muscle histolysis in *Lasius niger*, a Formicoid species in which the queens are typical claustral founders, and provide a calibration ladder that can be used for future studies on flight muscle histolysis in ants.

Charles Janet was the leading pioneer in the histological description of the internal anatomy of social insects (Billen & Wilson 2008) and was the first to document flight muscle histolysis in ant queens. Between 1906 and 1907, he published four articles on flight muscle histolysis in the queen of *L. niger*, as well as a book in which he provided a highly accurate and detailed description of the process (Janet 1906, 1907a,b,c,d). Janet's original histological sections were almost completely destroyed during a bombardment in the second world war. Only 91 of the fragile glass slides survived this catastrophic event, and through a most remarkable coincidence are currently in our possession (see Billen & Wilson 2008). As Janet's work was done in the late 19th and early 20th century, his publications were illustrated with drawings only (Fig. 1). As we are in the privileged position of having access to his remaining original work, we are able to share his pioneer data in the present paper.

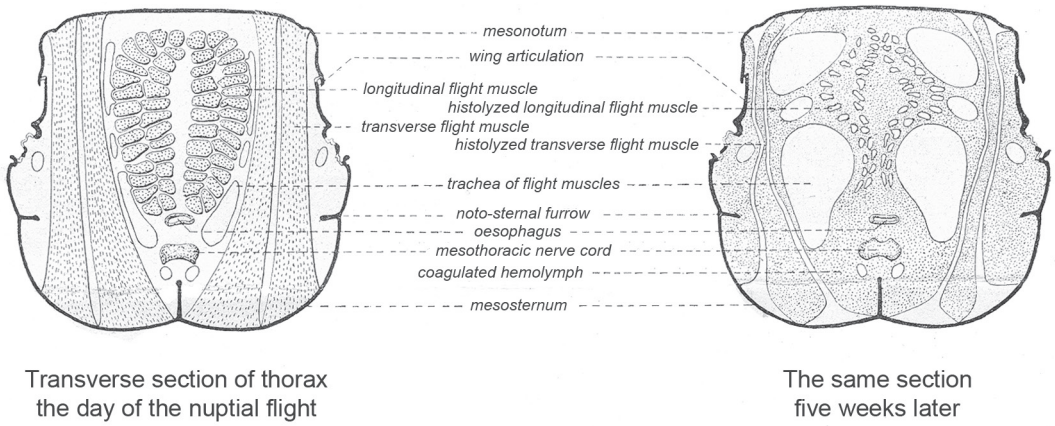

Fig. 1. Example of Janet's excellent illustration of flight muscle histolysis (modified from Janet, 1907a: original drawing but with explanation translated into English from the original French).

MATERIAL AND METHODS

On 22 June 2020, immediately after the nuptial flight, many dealate queens of *L. niger* were running on the ground in the city of Rennes (France). We collected a few hundred of them and maintained them individually in test tubes with water storage, in darkness, at 25°C, and without any food supply. Starting on the first day of sampling (age 0 days), up to 24 days after the nuptial flight, eight queens were fixed every three days in ethanol 80% for later dissection, and two queens were fixed in glutaraldehyde for histological examination.

Images of both longitudinally and transversally split thorax at the various age categories were obtained by making cuts with a sharp razor blade along the central body axis for longitudinal views, while transverse cuts were made at the level of the forewing articulation. Pictures were acquired using a Canon EOS M50 camera equipped with a Canon 60 mm f/2.8 coupled with a Raynox MSN-202 lens. The individuals were photographed while immersed in alcohol. Z-stack images were taken for each individual and combined using the software Zerene Stacker.

For histology, similarly cut thorax parts were fixed in 2% cold glutaraldehyde in a buffer of 50 mM Na-cacodylate and 150 mM saccharose. After postfixation in 2% osmium tetroxide in the same buffer and dehydration in a graded acetone series, tissues were embedded in Araldite® and sectioned with a Leica EM UC6 microtome. Semithin 1 µm sections for light microscopy were stained with methylene blue and thionin and viewed in an Olympus BX-51 microscope.

All longitudinal images in this paper are shown with the anterior side to the left.

RESULTS

Among the 91 still existing original glass slides of Janet's sections, we found seven slides with almost calligraphic labels that are directly connected to the study of flight muscle histolysis in the queen of *L. niger*, although these unfortunately only deal with the later stages from day 24 onward. They all clearly show the degenerated flight muscles. Four of these slides form part of an originally probably much larger series of transverse sections through the thorax at 2-day intervals, and show individual sections of remarkably high quality (Fig. 2). Three other slides illustrate how Janet experimented with various staining methods to illustrate the process of histolysis in the best possible way (Fig. 3). One of the latter slides mentions that the thickness of the paraffin sections was 25-30 µm, which explains how he could collect the series of an entire thorax on a single glass. Although Janet's papers only included drawings, the availability of the original sections allowed us to match one of his drawings with the very section from which it was made (Fig. 4). This showed that Janet applied some ar-

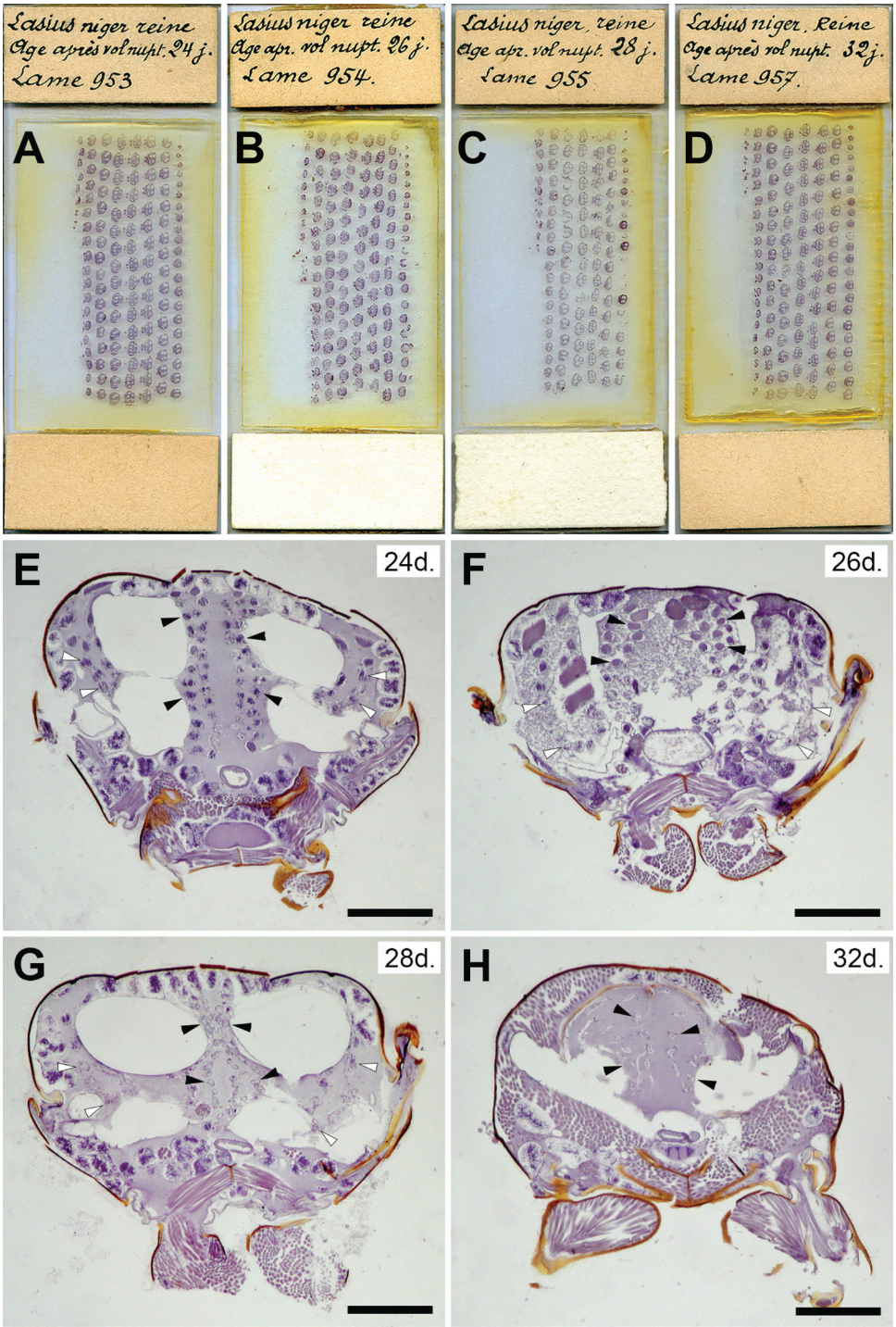

Fig. 2. A-D. Four histological slides of Janet's age-dependent study of flight muscle histolysis. Each slide contains the serial transverse sections through an entire thorax. The hand-written labels say "*Lasius niger queen. Age since nuptial flight 24/26/28/32 days. Slide 953/954/955/957*". The text of the labels is written on fairly thick cardboard, a blank piece of the same cardboard is glued onto the opposite side of the slide to allow easy piling up of slides. **E-H**. Selected view of a section from each of the slides. Black arrowheads indicate histolyzed longitudinal flight muscles, white arrowheads indicate histolyzed transverse flight muscles. Scale bars 0.5 mm.

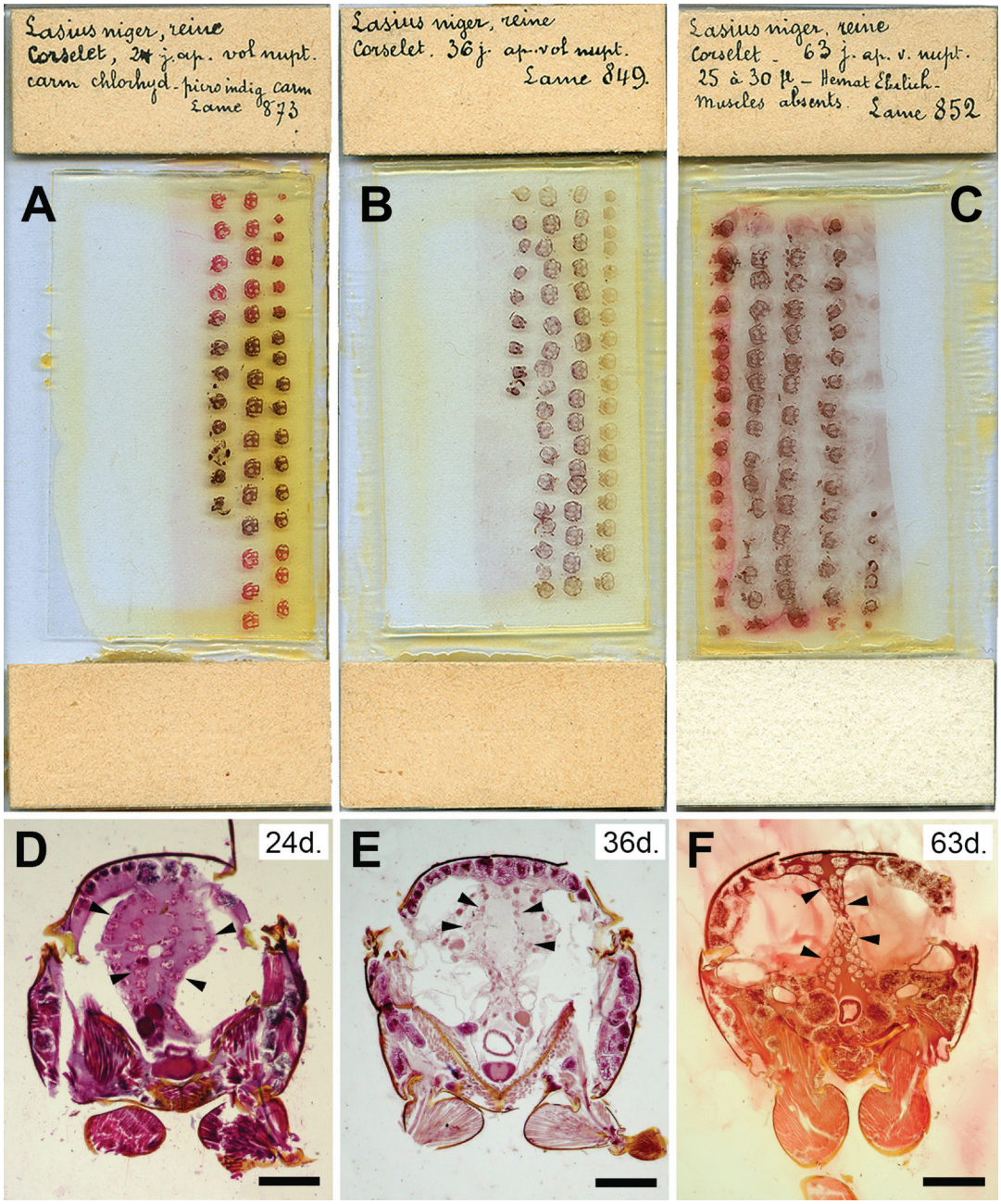

Fig. 3. A-C. Three histological slides of Janet, showing his experimenting with various staining methods to best document flight muscle histolysis. Each slide contains the serial transverse sections through an entire thorax. The hand-written labels say "*Lasius niger queen thorax. Age since nuptial flight 24/36/63 days. Slide 873/849/852*". Additional information on **A** states "*carmine-picroindigocarmine staining, chloral hydrate (?)*", that on **C** states "*section thickness 25-30 µm, Ehrlich's hematoxylin. muscles absent*". **D-F**. Selected view of a section from each of the slides, black arrowheads indicate histolyzed longitudinal flight muscles. Scale bars 0.5 mm.

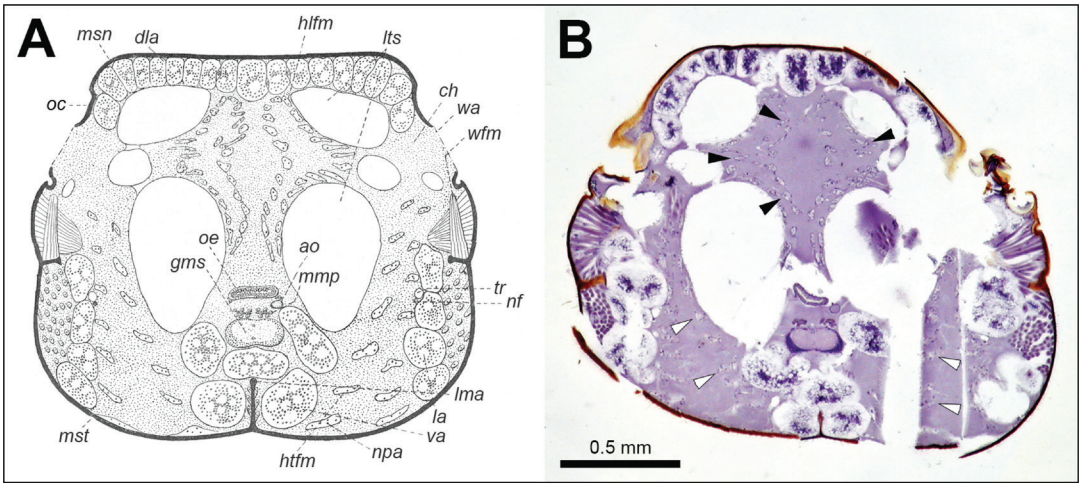

Fig. 4. A. Detailed cross section drawing of a queen mesothorax 32 days after the nuptial flight (fig. 39 in Janet 1907d) and **B**. the original section from which he made this drawing (black arrowheads show histolyzed longitudinal flight muscles, white arrowheads show histolyzed transverse flight muscles). Note Janet's artistic idealization when making the drawing, e.g. the mesonotum is drawn more straight possibly to compensate for the partly broken right side of the section; the wing folding muscles are drawn in more detail than visible on the section. The original explanations have been translated into English. abbreviations: ao: aorta, ch: coagulated hemolymph, dla: dorsal layer of adipocytes, gms: ganglion mesothorax, hlfm: histolyzed longitudinal flight muscles, htfm: histolyzed transverse flight muscles, la: lateral adipocytes, lma: longitudinal mesothoracic apodeme, lts: longitudinal tracheal sacs, mmp: motoric muscle prosternum, mst: mesosternum, msn: mesonotum, nf: nerve fiber, npa: nucleus primordial adipocytes, oc: oenocytes, oe: oesophagus, tr: trachea, va: ventral adipocytes, wa: wing articulation, wfm: wing folding muscles.

tistic idealization when making the drawings, but at the same time illustrate the magnificent quality of his paraffin-based histological sections considering the technical equipment he had to work with more than a century ago.

Our own results clearly confirm Janet's observations of degeneration of the flight muscles (Fig. 5), almost all of the muscular content being depleted during the 24 days following the mating flight. Dissection pictures offer broad and natural views of the patterns that the muscles take during the histolysis process (Fig. 6 A-I and Fig. 7 A-I). We can also note the extreme dilatation of the oesophagus in several queens at advanced ages (Fig. 6 F-H and Fig. 7 G, I). In addition, histological sections bring accurate views, allowing us to see the details of the breakdown at the level of the muscle fibers and myofibrils (Fig. 6 J-R, Fig. 7 J-R, Fig. 8). Longitudinal sections illustrate the fast transformation of intact myofibrils with regular sarcomeres to a kind of disorderly soup. Sarcomere length is 2.31 ± 0.1 µm at day 0, 2.59 ± 0.41 µm at day 3 and 2.52 ± 0.11 µm at day 6; at day 9 and later, individual sarcomeres can no longer be recognized (Fig. 8). Longitudinal sections also illustrate how this disorderly soup gives rise to ovoid sarcolytes (Fig. 6 O) and later on also fat globules (Fig. 6 P-R). Cross histological sections show the fiber diameters gradually decrease, indicating that the fibers are emptied of their contents (Fig. 7 J-R). We can also note on these cross sections that tracheal branches remain intact during muscular breakdown (Fig. 7 M-R). Moreover, the fiber positions inside the thorax stay unchanged during the entire process.

Most queens displayed colony foundation in a relatively similar way. The first eggs were already noticed as soon as three days after the mating flight and their number increased until the hatching of numerous larvae. After 21 days the number of eggs has decreased more than the number of larvae has increased, which indicates oophagy. The first larvae hatched between 15 and 18 days after the mating flight and spun their cocoon between 21 and 24 days after the mating flight (Fig. 9).

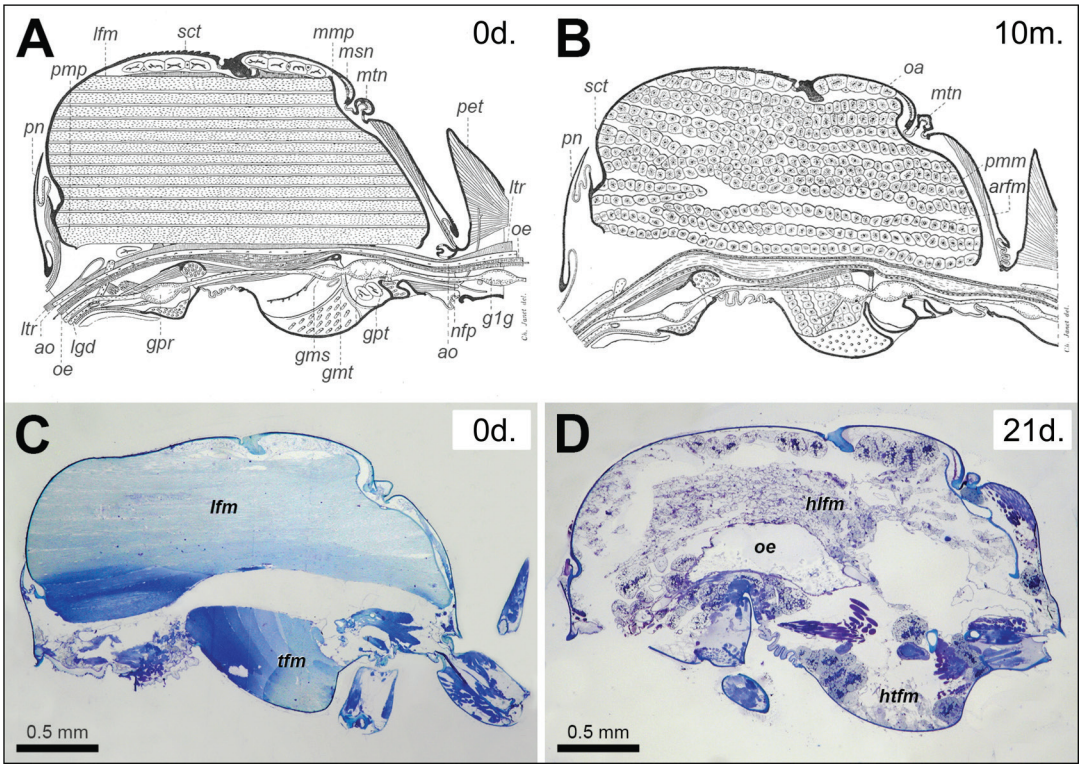

Fig. 5. Longitudinal section drawings of the queen thorax on the nuptial flight day (**A**, fig. 1 from Janet 1907d) and 10 months later (**B**, fig. 40 from Janet 1907d). **C**,**D**. Our semithin sections showing fully developed (0d.) and degenerated flight muscles (21d.). Only part of the original explanations have been translated into English abbreviations (Janet's original drawing in A contained 72 explanations): ao: aorta, arfm: adipocytes replacing flight muscles, g1g: ganglion 1st gastral segment, gms: ganglion mesothorax, gmt: ganglion metathorax, gpr: ganglion prothorax, gpt: ganglion petiole, hlfm: histolyzed longitudinal flight muscles, htfm: histolyzed transverse flight muscles, lfm: longitudinal flight muscles, lgd: labial gland duct, ltr: longitudinal trachea, mmp: meso-metanotal phragma, msn: mesonotum, mtn: metanotum, nfp: nerve fiber petiole, oa: old adipocytes, oe: oesophagus, pet: petiole, pmp: pro-mesonotal phragma, pn: pronotum, sct: scutum, tfm: transverse flight muscles.

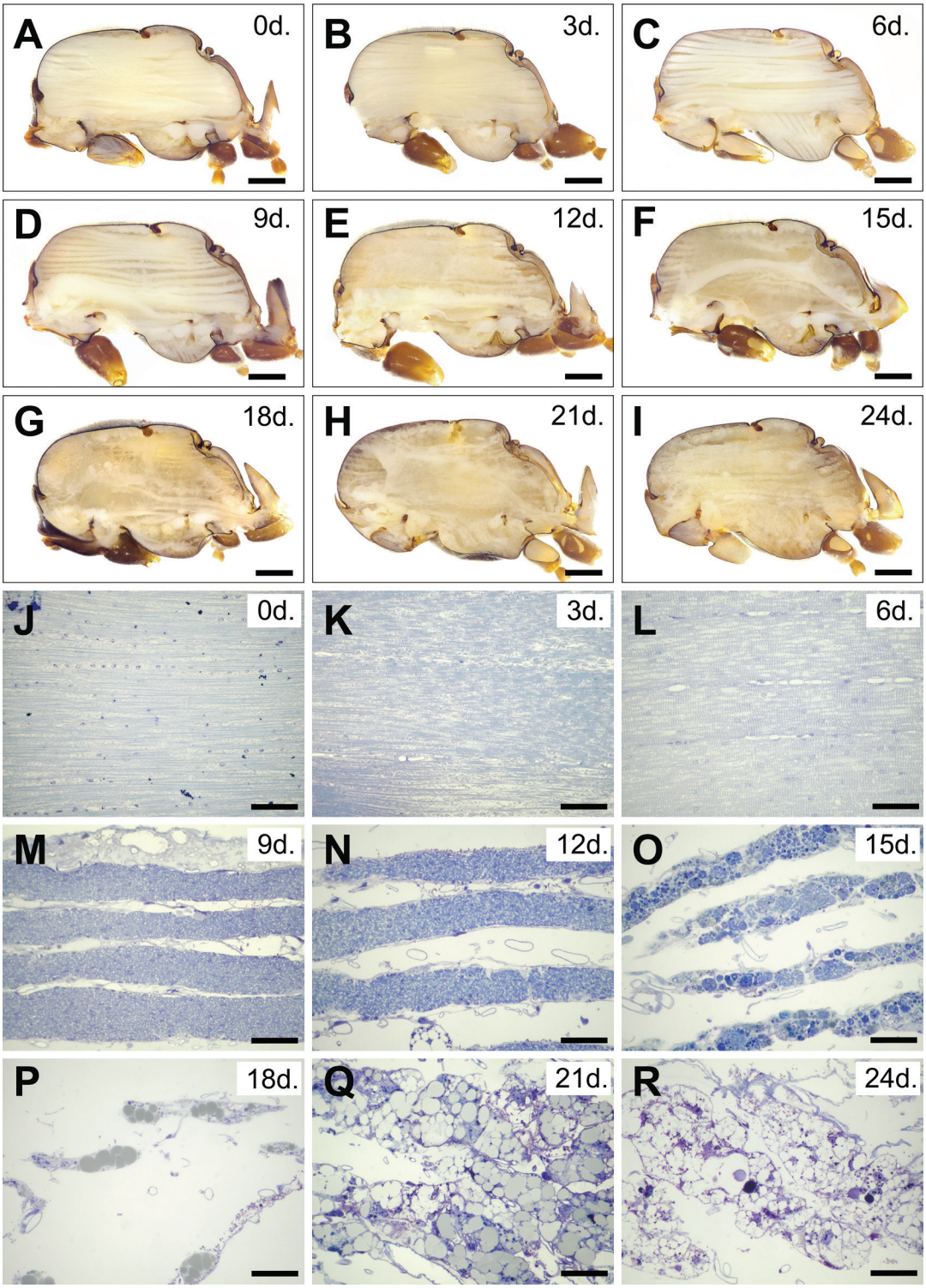

Fig 6. Progressive stages of flight muscle degeneration at 3 day intervals starting from the day of the nuptial flight. **A-I**. Dissection views of longitudinally split thorax. Scale bars 500 μm. **J-R**. Histological details of longitudinal sections through the dorsal longitudinal flight muscles at the same ages. Scale bars 50 μm.

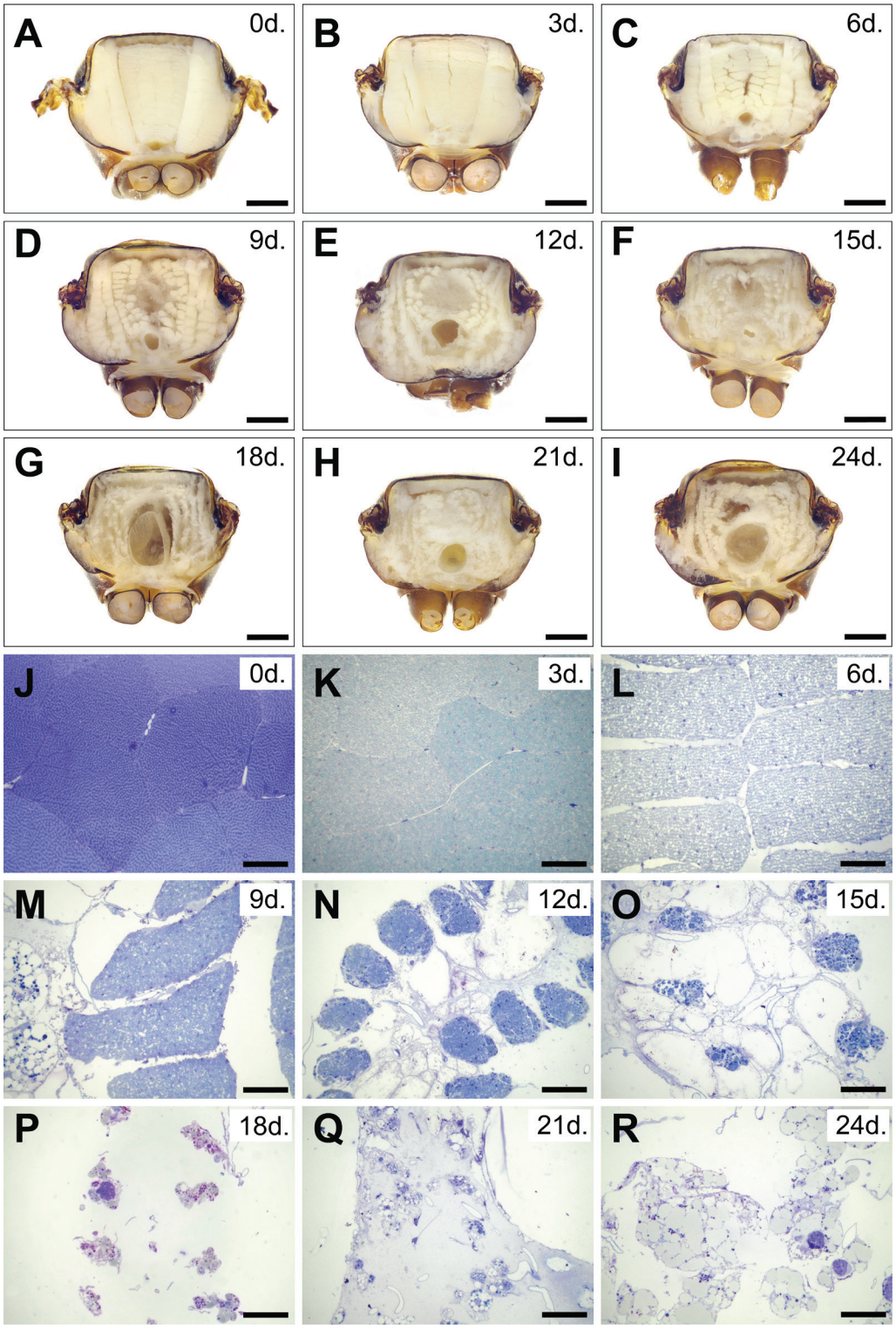

Fig. 7. Progressive stages of flight muscle degeneration at 3 day intervals starting from the day of the nuptial flight. **A**-**I**. Dissection views of transversally split thorax. Scale bars 500 µm. **J**-**R**. Histological details of cross sections through the dorsal longitudinal flight muscles at the same ages. Scale bars 50 µm.

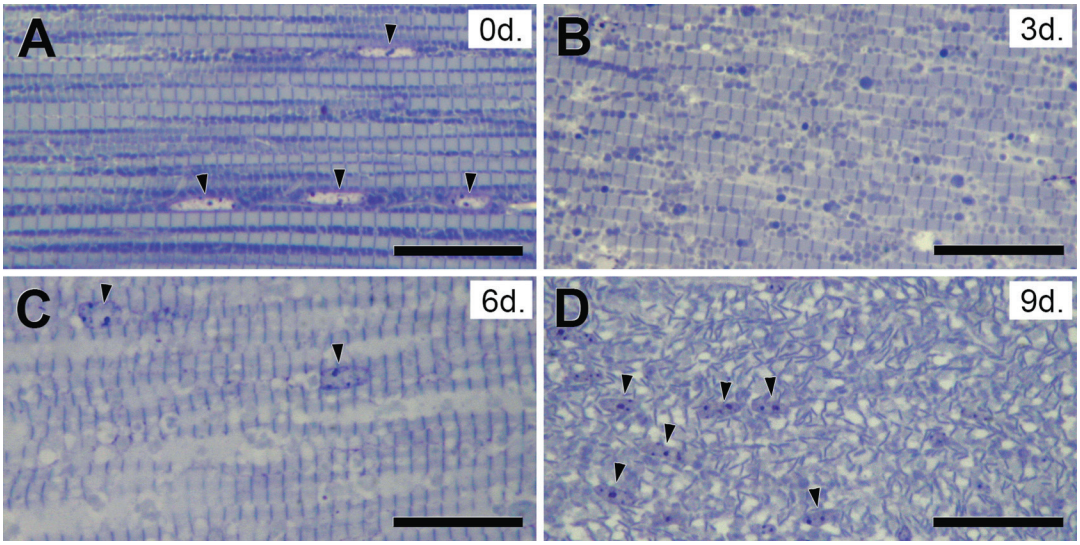

Fig 8. Details of the dorsal longitudinal flight muscles showing sarcomere disruption after 1 week (at ages >9 days, sarcomeres can no longer be recognized). Arrowheads indicate nuclei. Scale bars 20 µm.

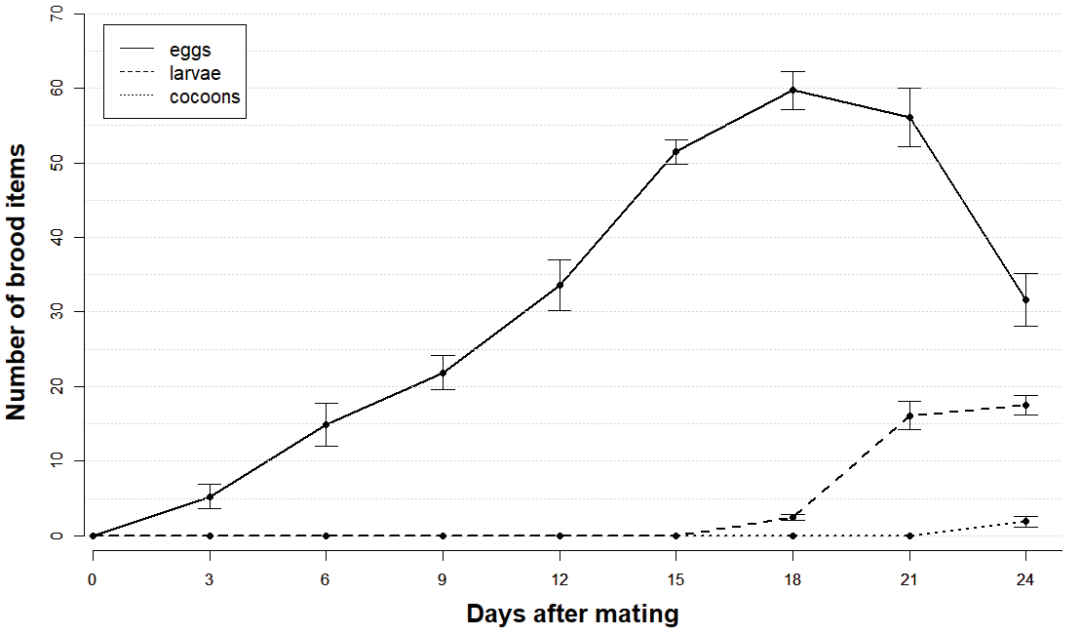

Fig. 9. Mean brood production of eight *Lasius niger* queens during the first 24 days of colony foundation under laboratory conditions. Day 0 corresponds with the day of the mating flight. Ranges indicate standard errors.

DISCUSSION

Main steps of flight muscle histolysis

Our histological results were highly congruent with the drawings published by Janet a century ago (Fig. 5). From Janet (1907d) and according to our own results (Figs 6-8), the histolysis process can be divided into several main steps (summarized in Table 1).

At the initial stage, the flight muscle fibers are swollen and squeezed together (0-3d.), leaving space only for nerve fibers and tracheal branches. Subsequently, while the beginning of flight muscle histolysis could be seen as soon as two hours post-insemination in the most peripheral fasciculi (Jones et al. 1978), the first clear evidence of the histolysis process is the decompaction of these muscles (6d.).

The following step is the dislocation of the myofibrils in the flight muscle fibers (9d.). The sarcomeres become disorganized, and, mixed with nuclei and interfibrillar cytoplasm, they constitute a kind of sarcomere soup which is only delimited by the muscle fiber's cell membrane or sarcolemma. Sarcomere length as measured in the still functional flight muscles of our *L. niger* queens is in the same range as reported for termite flight muscles, in which an increase in sarcomere length occurs prior to their degeneration (Zhang et al. 2021). This increase in sarcomere length might be due to a compaction of the fibers which could be in line with the increase of space between the fibers that occurs after 6 days.

Then follows the release of fiber content into the hemolymph. Firstly, the muscular substance remains a time in its soup shape in which the big proteins of the Z-discs that constitute the sarcomere limits become unrecognizable (12d.). This soup then ends up as ovoid sarcolytes before being released into the hemolymph (15d.). Once the muscle fibers are emptied or almost emptied of their initial content, the fibers fill up with numerous fat globules produced by adipocytes. While these adipocytes' activities begin during the foundation stage, they continue after the emergence of workers and thanks to the food retrieved by the workers, the queens will therefore build up a large storage of nutrients in their thorax (see Fig. 1 in Wheeler & Buck 1996). According to Janet (1907d), these reserves will be partially used later on, by queens of established colonies, to resume egg-laying after hibernation before the workers begin harvesting abundant food. Finally, after all muscular components have been released into the hemolymph, the entire content of the muscle fibers will have been replaced by adipocytes which now occupy a large part of the thorax and will remain there throughout the life of the queen.

Interestingly, the wing folding muscles of the mesothoracic wings (metathoracic wing muscles being vestigial in ants) show the same process as the main flight muscles but later and slower (Janet 1907d).

Table 1. Summary of the main processes of flight muscle degeneration at 3-day intervals starting from the day of the nuptial flight.

Day	Main processes
0	Muscle fibers are intact
3	No clearly visible degeneration
6	Decompaction of the muscle fibers
9	Disorganisation of sarcomeres forming a kind of soup
12	Z-discs can no longer be recognised
15	Formation of early sarcolytes in muscle fibers (i.e. globules of muscular content)
18	Almost all muscular content of fibers has been released; the earliest adipocytes appear
21	The amount of adipocytes increases
24	Adipocytes take a large space in the thorax and their density will continue to increase until all free spaces are filled

Nutrient allocation

During colony foundation, foundresses are subject to three major energetic and resource costs being (i) egg production, (ii) larval feeding, and (iii) the queen's own metabolism. All these needs are associated with three key macronutrients which are carbohydrates (sugars and glycogen), lipids, and proteins. Before leaving their natal nest, winged queens of claustral species store an amount of these three elements in the abdominal fat body, which will be subsequentially depleted over the founding period. In contrast to the fat body, flight muscle histolysis releases proteins and some carbohydrates (Wheeler & Buck 1996). So far, however, their precise utilization remains unclear and the extent to which histolysis products are involved in these three needs remains unknown.

Ants are reported to mainly use carbohydrates as a source of energy (Markin 1970; Martin & Lieb 1979). Thereby, the carbohydrate released by histolysis and the fat bodies can serve as energy source for queens. However, the use of protein and lipid as metabolic fuel by ant queens cannot be discarded. Teulier et al. (2016) showed that several hymenopteran species have the ability to use proline as metabolic fuel for flight. This amino acid which is abundant in collagen can be oxidated alone or coupled with carbohydrate-derived substrates, which significantly enhances carbohydrate oxidation (Teulier et al. 2016). Martin and Lieb (1979) while studying three ant species, showed that, although *Formica ulkei* exclusively oxidises carbohydrate, *Atta colombica* can metabolize both carbohydrate and lipid, and *Pogonomyrmex californicus* exhibits an energy metabolism based upon lipid oxidation. Martin and Lieb had therefore shown that the patterns of fuel utilization are selected according to the feeding ecology and dietary regime of species rather than their phylogeny.

According to Wheeler and Buck (1992), when larvae of *Solenopsis xyloni* stop their feeding stage to start metamorphosis, they contain on average almost 14% of carbohydrates, 37% of lipids, and 49% of proteins. Proteins are therefore an essential resource for larvae (e.g. Vinson 1968; Markin 1970; Brian & Abbott 1977). Interestingly, proteins can be transmitted from queens to larvae through trophallaxis and eggs. Stomodeal trophallaxis is usually known to share liquids previously stored in the crop. LeBoeuf et al. (2016), however, showed evidence of endogenous proteins in trophallactic fluid, involving secretion of cells lining the foregut or glands connected to the alimentary canal (e.g. pharyngeal, mandibular, labial glands). In addition, already in 1907, Charles Janet commented on the exosmosis of the nutrients from histolysis in the pharyngeal pouch, allowing queens to redistribute protein contents to larvae (Janet 1907d). The redistribution of proteins to larvae by trophallaxis therefore seems to be a possible mechanism. However, in the present study, we recorded that muscle fibers are already substantially emptied of their muscular content when larvae hatched (18d).

In another way, oophagy by larvae was much more often recorded. Although the composition in protein, lipid and carbohydrate of ant eggs is still unknown, according to the general composition of egg in insects, proteins constitute 40–50%, lipids 30–40%, and carbohydrates around 10–30% (Němec 2002; Giron & Casas 2003; Geister et al. 2008; Sloggett & Lorenz 2008; Tigreros & Davidowitz 2019). In addition, Voss et al. (1988) showed the existence of trophic eggs containing higher quantities of proteins than fertile eggs. Moreover, there is some evidence that metabolites released by flight muscle histolysis can be used for oogenesis (Nair & Prabhu 1985; Tanaka 1993; Wheeler 1996; Socha & Šula 2008). During flight muscle histolysis, the large amount of protein released could therefore be used by queens to allow the production of a large number of eggs and trophic eggs that will later become part of the larval diet.

We noticed an extreme dilatation of the oesophagus in several queens at advanced ages. This was also briefly noticed by Janet (1907d), though he did not further comment on it. This phenomenon was equally shown in queens of mature colonies in several species and is involved in the storage of liquids (Casadei-Ferreira et al. 2020). This dilated oesophagus is presumably associated with the large space that the ovaries take up in the abdomen, compacting the crop which usually fulfills this function of storing liquids (Petersen-Braun & Buschinger 1975). In the context of colony founding, this dilatation of the oesophagus could be involved in the redistri-

bution of trophic eggs to larvae. Indeed, trophic eggs can be eaten directly by larvae or ingested by the queens and subsequently redistributed to larvae. The contents of the queen's oesophagus could thus be enriched with substances useful for the development of the larvae as demonstrated by LeBoeuf et al. (2016), as well as with proteins resulting from muscle histolysis.

Nutrient release and duration of the nest foundation period

At 25°C, the foundation of a *L. niger* colony takes almost 40 days until the first workers appear. The first cocoons are spun on average 25 days after the nuptial flight. These data were reported by Kipyatkov and Lopatina (2015) and are fully corroborated by our observations on brood dynamics in the present study (Fig. 9). The major part of nutrients released by flight muscle histolysis is already completed 24 days after the mating flight (Figs 6, 7). Interestingly, the spinning of the first cocoons during colony foundation means for the foundress the end of a period of strong selective pressures for food, since some workers will hatch a few weeks later without needing food supply anymore. The colony's survival chance being dependent on the number of first workers (Porter & Tschinkel 1986), the coordination of the period of nutrient release by histolysis and the end of the feeding pressure by the spinning of first cocoons represents a selective advantage for the foundress. Indeed, such coordination maximizes the available nutrients during the feeding stage of larvae and consequently allows an increase in the numbers of first workers, increasing therefore the colony's chances of success. Nevertheless, the development time varies among ant species (Kipyatkov & Lopatina 2015) and therefore, the nutritive needs occur at different times of the foundation according to species. It therefore would be interesting to investigate the speed of flight muscle histolysis in species with other founding strategies and with a significantly longer development time. Preliminary observations, however, indicate that the histolysis process could begin at the same time and take the same time in all species independent of their founding strategy and development time. This assumption is supported by some dissections of *Pachycondyla crassinoda* queens, which is a phylogenetically distant species (Moreau et al. 2006) with a development time of almost 90 days (A.M. unpublished, see also supplementary Fig. S1). The histolysis process therefore may be similar among ant species, though the specific development time may considerably depend on whether the queen can or cannot rely on flight muscle histolysis to produce her first workers. This could therefore play a major role in the determination of the founding strategy of queens between non-claustral and claustral species.

Interestingly, from the time data associated with histolysis according to Janet (1907d) and direct comparison of his sections (Figs 2-4) with our data in the present study (Figs 5-7), it seems that the process of histolysis of Janet's queens was slower than in the queens we observed. After the initial stage, Janet described the next stage 12 days after the mating flight. At this age, he reported the fibrils as almost untouched, although slightly contracted, which corresponds to what we observe already six days after the mating flight. At 18 days, Janet observed in some muscle fibers a homogeneous mass formed by the disorganization of sarcomeres that we observe after nine days (Fig. 8D). At 24 days, Janet described the climax of histolysis with numerous dissolved sarcolytes, which we observed between 15 and 18 days (Figs 6, 7). Therefore, the time between the formation of the homogeneous mass of sarcomeres and their release in the hemolymph appears similar in both cases, but seems to have started later in Janet's study. This difference may be explained by the different conditions in which queens were kept. Janet indeed kept his queens in polygynous groups of several dozen queens (sometimes more than 50) at an unspecified temperature, while we kept them single at a constant temperature of 25°C. The metrosis and the temperature could therefore influence the speed of the process. Flight muscle histolysis in ants in general has so far been poorly studied, and numerous aspects still need to be clarified in the huge diversity of ant species as well as the modification of these processes when queens experience different environmental conditions.

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