Molting Process in the Formosan Subterranean Termite (Isoptera: Rhinotermitidae)

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ABSTRACT This study describes the behavioral and histological changes that take place during ecdysis in the Formosan subterranean termite. The molting process was described in four distinct phases, starting with the peristaltic contraction of the abdomen to the complete shedding of the exuvium. Although individual termites still managed to go through the molting process when isolated from their nestmates, it required more time for the molting individual to complete the process than when aided by its nestmates. Histological observations were made on termites during the intermolt period, the premolting or fasting period, the pre-ecdysis and the ecdysis periods, and on newly molted individuals. Symbiotic protozoans were voided at the beginning of the premolting/fasting period. The detachment and reattachment of the muscles of the abdominal segments occurred during pre-ecdysis, and the leg muscle detachment and reattachment occurred during ecdysis. During pre-ecdysis, the abdominal cuticle had a wrinkled texture and two layers of cuticles were observed, one of which was the newly formed cuticle underneath the old one. Finally, the old tracheae were shed from the tracheal system and were pulled out from the spiracular openings of the mesothorax with the help of the nestmates. We concluded that, as social insects, the presence of nestmates during the molting of individual termites reduced the time necessary to complete the ecdysis, and the histological description of the molting process provides a template for further studies on the effect of chitin synthesis inhibitors on ecdysis in termites.

KEY WORDS ecdysis, *Coptotermes formosanus*, nestmate, aid, molting behavior

Coptotermes formosanus Shiraki is one of the most damaging termite pests because of its relatively large colony size and difficulty of control (Edwards and Mill 1986, Rust and Su 2012). Bait systems have been used for subterranean termite control, and chitin synthesis inhibitors (CSIs) are the active ingredients used in some bait products (Su 2003). CSIs target cuticle formation and disrupt the molting process, which has been a key to the success of CSIs in bait formulations (Rust and Su 2012). Because the molting process is linked to a particular time of the life stage of termites, the death of individuals exposed to CSIs is dose independent. This mode of action therefore allows the active ingredient to be transferred to most of the individuals of the colony before taking effect (Rust and Su 2012). Because termites are hemimetabolous insects, they undergo successive molts throughout their life span (for pseudergates) or until they reach a final caste (for soldiers and reproductives). Although molting is critical in the life cycle of termites, little is known of its process because of their cryptic nature. Providing novel information on the molting mechanisms in subterranean termites can help further improvements of control methods. Previous studies provided some elements regarding molting in termites, but most of the basic processes have yet to be described. Soltani–Mazouni and Bordereau (1987) described alterations of the ovaries and colleterial glands of molting neotenic and pseudergate individuals of *Kalotermes flavicollis* F. (Kalotermitidae), but did not provide a detailed description of the cuticular alteration during molting. Raina et al. (2008) described gut fauna voiding and the juvenile hormone and ecdysteroid titers during the molting process of *C. formosanus* workers, but provided no information on the structural changes during ecdysis. In addition, Raina et al. (2008) suggested that the molting termites need their nestmates' aid to finish ecdysis, which remained to be confirmed. Therefore, many aspects of the molting process in subterranean termites remain unclear.

In this study, we describe the ecdysis behavior of *C. formosanus* and examine whether termites need aid from their nestmates to complete ecdysis. We then observe the histological changes occurring during the molting process and determine key features of physiological alterations.

Materials and Methods

Termite Collection. Termites were collected from three colonies in Broward County, FL, by using

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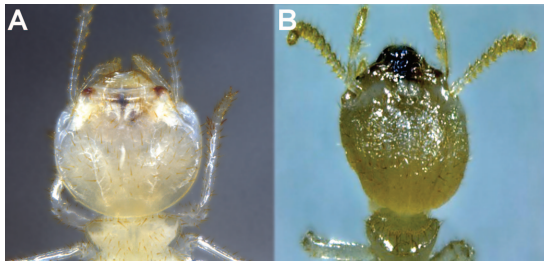

Fig. 1. (A) Termite in intermolt. (B) Mottled head capsule during pre-ecdysis indicates that termites are about to start ecdysis within 12 h. (Online figure in color.)

bucket traps (Su and Scheffrahn 1986), processed according to Tamashiro et al. (1973) and placed by groups of at least 3,000 termites in a plastic jar (diameter: 11.4 cm, height: 9.7 cm) containing 10 pieces of moist spruce wood slabs (*Picea* sp., each piece was 7.8 by 6.6 by 0.6 cm) and held at 28.8 ± 0.5°C before use.

Identification of Pre-ecdysis Individuals and Description of Molting Process. Raina et al. (2008) reported that none of the field-collected termites, presumably all being foragers, molted for 2 wk postcollection. Thus, the groups of ≈3,000 termites were kept in the laboratory for 2 wk before they were fed on filter papers stained with Nile Blue A (diameter: 8.8 cm, Nile Blue concentration: 0.5% wt:wt). According to Raina et al. (2008), termites stopped feeding approximately 6 d before ecdysis, and individuals that were about to molt could be identified by the lack of Nile Blue A in their body. After being exposed to a Nile Blue A-stained filter paper for 48 h, workers (undifferentiated larvae of at least the third instar) without blue color were collected and observed daily under a dissecting scope. Individuals in pre-ecdysis were identified by the mottled feature of their head capsule (according to Raina et al. 2008) (Fig. 1). Termites with pre-ecdysis features were individually transferred to a transparent plastic cylinder (interior diameter: 2.54 cm, exterior diameter: 2.94 cm, height: 0.9 cm, with smooth interior wall to prevent termites from crawling out). With the confined cylinder, the movement range of molting termites could be restricted within the field of view of the dissecting microscope, allowing the molting process to be recorded by a mounted video camera. To offer a color contrast with termites for better observation and to maintain the moisture, a moistened black filter paper was placed at the bottom of the cylinder. The dorsal cuticle of the molting termite was painted with a blue marker pen (Sharpie, Sanford ink industry, Oak Brook, IL) to differentiate the new from the old cuticle during ecdysis. Four workers that consumed Nile Blue A, and were identified as nonmolting individuals (intermolt), were transferred to the confined cylinder to allow interactions with an individual in pre-ecdysis. The experiment was replicated five times from individuals from a single colony to characterize the key features of the molting process, before extending the experiment to a larger sample size (see later in the text).

Effects of Nestmates on Molting Individuals During Ecdysis. In the treatment group, one pre-ecdysis worker was transferred to the confined cylinder without the presence of nestmates. In the control group, four workers that ingested Nile Blue A were transferred to the tube with a pre-ecdysis individual. The ecdysis process was recorded by using the dissecting microscope mounted with the video camera. Both experiments were replicated 15 times (five times per colony). Because it was difficult to determine the exact starting point of the pre-ecdysis, key behavioral features were determined to separate the molting process into four distinct phases to allow for quantitative analysis, starting with the peristaltic movements from the abdomen to the final extirpation of exuvium. The time required to complete a particular phase of the process for individuals with (control) and without nestmates (treatment) was compared with a Student *t*-test ($\alpha = 0.05$).

Histological Study on Individuals at Different Molting Stages. After termites were exposed to Nile Blue A-stained filter paper for 48 h, individuals without blue color were placed in a petri dish (radius: 4.6 cm, height: 2.1 cm) provisioned with moist filter paper for daily observation. The asynchronous molting time of termites made it difficult to determine the exact timing of the molting events. According to distinguishable physical features available, samples were collected at different times to help identify the sequence of molting events (Fig. 2). The time of ecdysis was defined as 0 h and pre-ecdysis (mottled head capsule) was defined as the time up to 12 h before ecdysis (0 to −12 h). The period that termites stopped feeding but did not reach pre-ecdysis was defined as the premolting or fasting period (−6 d to −12 h). The period 1 h after ecdysis was defined as newly molted phase. Because termites that acquired Nile Blue A were in their intermolt, they were used as control samples. Samples

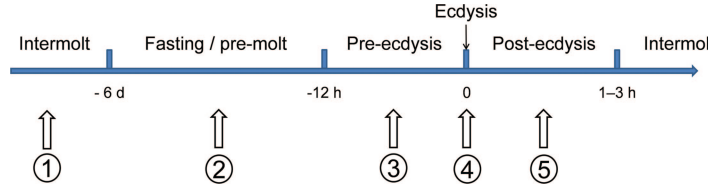

Fig. 2. Five types of samples were collected during the molting cycle, 1) termites in intermolt period, 2) termites in premolting/fasting period, 3) termites in pre-ecdysis period, 4) individuals undergoing ecdysis, and 5) newly molted termites with white mandibles and head capsule. (Online figure in color.)

from all phases (at least five per type of sample) were collected and subjected to histological preparation as described in the article by Chouvenc et al. (2009).

Head capsules and part of the legs of all the samples were removed before the samples were immersed into Bouin's aqueous fixing solution (75% aqueous picric acid, 20% formaldehyde, and 5% acetic acid) (Martoja and Martoja–Pierson 1967) for 7 d. Specimens were then dehydrated with successive baths of 75, 95, and 100% ethanol and 100% butanol. After dehydration, samples were placed into a container with 50% melted paraffin and 50% butanol for 6 h at 60°C. Because the melting point of paraffin is <60°C, the temperature setting could guarantee the melting of the paraffin and would not damage the tissues. Samples were then successively passed through three containers filled with 100% melted paraffin and were kept in each container for 24 h at 60°C to remove traces of butanol from the specimens, and finally embedded into melted paraffin blocks that were then held at room temperature for the block to solidify. Paraffin blocks were sectioned at 7 μm and stained using the Heidenhain Azan protocol (Gabe 1968). Stained sections were observed with a compound microscope and digital pictures were taken.

Results

Description of the Molting Behavior. The molting process was divided into four phases by distinguishable key behavioral features, and we investigated if the presence or absence of nestmates had any effect on the success of each phase.

Peristalsis (Phase 1). The first sign of the initiation of the ecdysis was the peristaltic contractions of the abdomen. Contraction pulses started from the tip of the abdomen and moved forward to the thorax (3–5 s per contraction). Molting termites usually remained in one place during the peristaltic contractions, with all legs firmly grasping the substrate. The contractions occurred in a relatively high frequency at the beginning (≈10 per min) and their frequency decreased when the termite approached the dorsal breach (≈6 per min). When nestmates were present, they occasionally groomed the individual undergoing peristalsis and the contractions lasted ≈15 min. Finally, a split appeared dorsally (dorsal breach) in the first abdominal segment and metathorax (Fig. 3A).

Expansion of the Dorsal Breach (Phase 2). The dorsal breach continued to expand toward the tip of the abdomen and the exuvium at the dorsal thoracic segments moved laterally. The exuvium then formed a "V" as the breach expanded (Fig. 3B). With sufficient dorsal expansion of the dorsal breach, the termite laid on its side and an exuvial sac formed at the tip of the abdomen. Nestmates, if present, occasionally groomed the molting individual.

Separation of the Head Capsule and Legs Exuviae (Phase 3). While the termite started pulling its legs out of the exuvium, the old cuticle of the head capsule stretched to the antennal sulcus. During the leg-pulling period, two long white strings of old trachea were pulled out of the spiracular openings in the thorax. Toward the end of leg-pulling, the termite began to extricate its antennae from the old cuticle (Fig. 3C). By the time that antennae were completely separated from the exuvium, the mandibles and maxillary palps were also separated from the old cuticle. Each molting termite remained in the jack-knife posture (Su and Scheffrahn 1993) until the end of this phase.

Separation of the Tracheal Exuvium (Phase 4). After the antennae were pulled out of the exuvium, the termite stretched its body straight from the jack-knife posture but remained motionless on its side. Nestmates, if present, helped the molting individual by providing grooming and by pulling off the remaining structures of the exuvium still attached to the termite, mainly the long longitudinal tracheal trunks that were extricated from the spiracular openings of the mesothorax (Fig. 3D). Once the old exuvium was completely removed from the newly molted termite, it took less than an hour for the termite to regain mobility.

Role of Nestmates in the Molting Process. For both groups, with or without nestmates, 14 of 15 individuals successfully completed ecdysis. Termites with nestmates completed Phase 1 and Phase 4 faster than isolated individuals ($P < 0.05$), whereas time taken to finish Phase 2 and Phase 3 was similar for both groups ($P > 0.05$) (Fig. 4). On average, it took 33.17 ± 2.94 min (mean ± SE) for a termite with nestmates to complete all four phases, whereas it took 69.62 ± 5.13 min for isolated termites ($P < 0.05$).

Histological Description of the Termite Molting Process. *Intermolt (Control).* Cuticles of termites in the intermolt period were relatively smooth and flagellates and spirochetes were present in the termite hindgut (Fig. 5A and B). There was no separation of the cuticular lining of the tracheal system during this period. Muscles were attached to the cuticle, and epidermal cells underneath cuticles were not easily observed.

Premolting or Fasting. Termites voided their hind gut during premolting, thus no gut fauna was observed from termites sampled in their late fasting period, and the old hindgut intima began to separate (Fig. 5C). The exoskeleton cuticle texture during this period was still smooth and not visibly different from termites in intermolt. The cuticular lining of the trachea was still properly attached to the cuticle of the tracheal system.

Pre-ecdysis and Ecdysis. At the beginning of the pre-ecdysis, some of the muscles began to detach from the old cuticle and in these areas, a new cuticle started to form on top of the layer of epidermal cells. Muscle remained attached together with the help of an internal membrane, and muscle extensions going through this membrane connected to the epidermal cells (Fig. 5D). The old cuticle of the exoskeleton started detaching from the epidermal cells and later during the pre-ecdysis, most of the old cuticular structures appeared thinner (apolysis). The newly synthesized cuticle first appeared as a soft membrane on top of the epidermis and two layers of cuticle were ob-

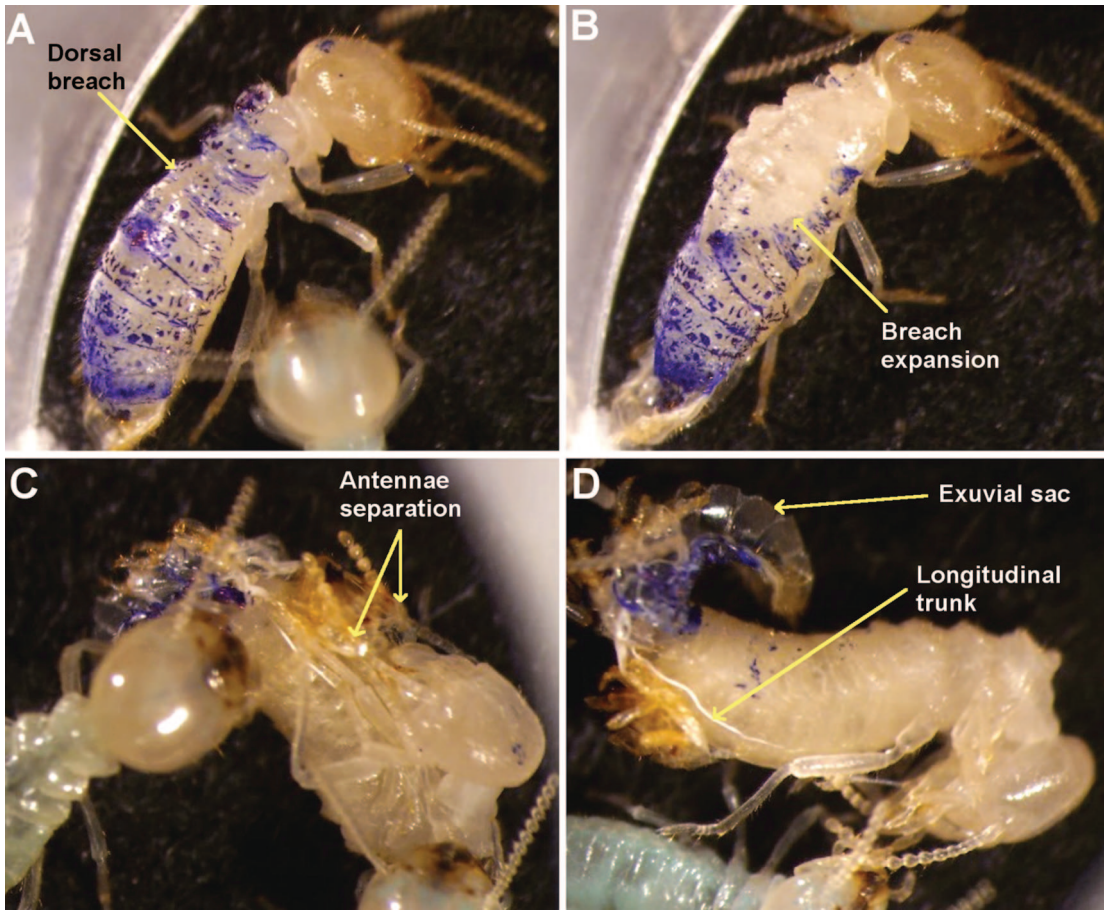

Fig. 3. The ecdysis in *Coptotermes formosanus* was separated into four distinct phases. (A) Phase 1: from the abdominal peristalsis to the appearance of the dorsal breach. (B) Phase 2: expansion of the breach and initiation of leg-pulling. (C) Phase 3: legs and antennae were extricated from the exuvium. (D) Phase 4: the longitudinal tracheal trunks were extracted from the spiracle openings. (Online figure in color.)

served on most of the surface of the individuals. The new cuticle thickened quickly and displayed heavily wrinkled features (Fig. 5E). Before ecdysis, the old cuticular linings of the tracheae were detached (Fig. 5F) and were voided during the ecdysis. The cuticular intima of the foregut was also subjected to the separation of the old cuticle with the production of a new cuticle underneath.

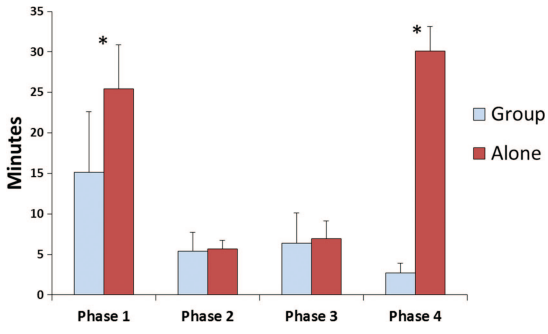

Fig. 4. Time required for termites to complete each phase (see Fig. 3) of the ecdysis. *Significant difference between treatments (Student *t*-test; $\alpha = 0.05$). (Online figure in color.)

Newly Molted. The new cuticle appeared heavily wrinkled just after ecdysis, but the texture appeared not brittle, contrary to the one from the old cuticle during pre-ecdysis. Protozoans were not observed in newly molted individuals, and no old cuticular linings were observed in the tracheal system. Later on, as the termite initiated its new intermolt phase, the cuticle became smooth by expanding, which allowed for more hemocoel volume than the previous intermolt.

Discussion

Pre-ecdysis in termites was defined by the appearance of a mottled head capsule, which differed from the definition given by Nation (2008), who described that pre-ecdysis began with dorsoventral contractions in other insects. We adopted the pre-ecdysis definition

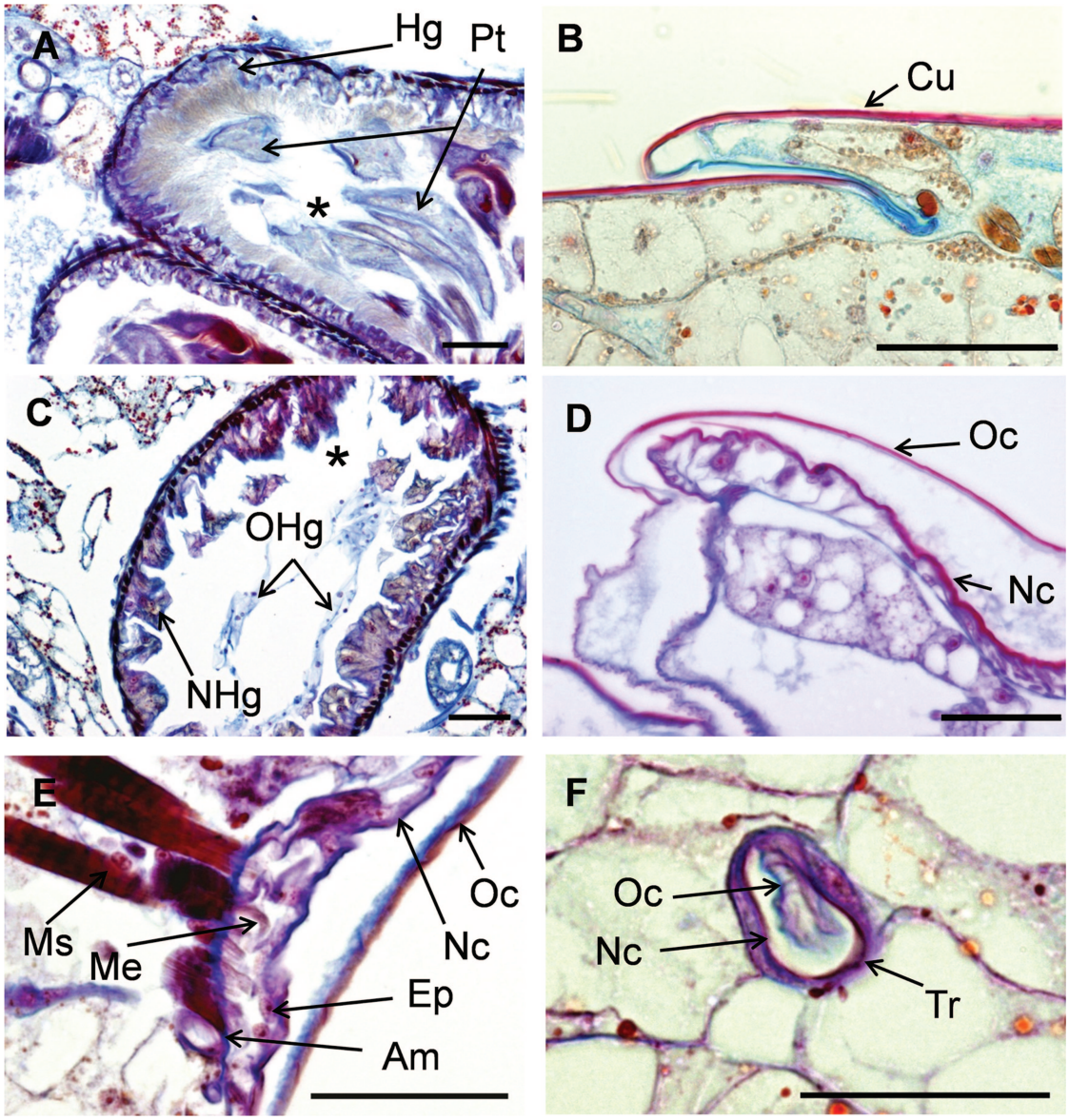

Fig. 5. Histological observation of ecdysis in *C. formosanus*. (A) Termite in its intermolt with protozoan in the hindgut. (B) Termite in its intermolt with smooth cuticle on the abdominal segments. (C) Fasting termite without protozoan in the hindgut. (D) Termite in pre-ecdysis with a wrinkled new cuticle on the abdominal segments. (E) Muscle attachment during pre-ecdysis. (F) Old cuticular lining of the trachea in a termite during pre-ecdysis. *Am* = attachment membrane, *Ep* = epidermal cell, *Hg* = hindgut, *Cu* = intermolt cuticle, *Me* = muscle extension, *Ms* = muscles, *Nc* = new cuticle, NHg = new hindgut intima, *Oc* = old cuticle, OHg = old hindgut intima, *Pt* = protozoan, *Tr* = trachea, * = gut lumen. (Online figure in color.)

from Raina et al. (2008), as precise beginning of dorsoventral contraction was difficult to determine in termites. The mottled head capsule feature was an easy characteristic to observe and corresponds approximately to the initiation of the pre-ecdysis.

The molting process in other insects is usually described as the succession of the apolysis, the secretion of the novel cuticle, and, finally, the ecdysis (Wigglesworth 1973). The apolysis is the separation of the epidermis from the old cuticle with the creation of the exuvial space, which is filled with molting fluid. The secretion of the new cuticle by the epidermal cells occurs at the same time that the old endocuticle is digested by chitinases and proteases. The ecdysis is a process that allows the insect to shed its old cuticle. Compared with other hemimetabolous insects (Wigglesworth 1973, Nation 2008), the digestion of the endocuticle applied to termites in our study. From

our histological observation of molting termites with a visible exuvial space, the old cuticle was relatively thin and the staining showed that there was no endocuticle binding to the old cuticle, which was consistent with other insects (Nation 2008). The digestion of the old cuticle results in reabsorption of valuable nutrients, minimizing the loss of resources during the process. The dorsal breach in termites at the initiation of the ecdysis was different from some larval stages of holometabolous insects, where the ecdysial line starts at the head capsule (Hinton 1963). Instead, it was similar to other hemimetabolous insects, where the presence of the legs imposes a constraint for a dorsal exuvial breach at the thoracic and the abdominal level (Nation 2008).

Contractions during the abdominal peristalsis may have two effects on the molting process. First, the peristalsis from the distal to proximal portion of the abdomen may increase the pressure at the thoracic level and stimulates the occurrence of the dorsal breach. Second, the contraction helped the two layers (old and new) of the abdominal cuticle to slide against each other, possibly to help the two layers to properly separate during the dorsal breach, allowing the termite to shed the old cuticle layer. This behavioral observation indicated that before the initiation of the ecdysis process, most of the muscles of the abdomen have completed the detachment from the old cuticle and reattachment to the newly formed cuticle, therefore facilitating the peristaltic movement to occur properly. Moreover, at the beginning of ecdysis, the molting termite maintained its standing posture before it laid sideways to extricate its legs (Phase 2), suggesting that the muscles in the legs also finished their reattachment. In the histological preparations, we observed that despite a muscle detachment from the old cuticle during the pre-ecdysis, the muscles maintained a connection to the epidermal cells through a membrane, which helped the muscle reattachment at the proper place to the newly formed cuticle just before the ecdysis.

In most of our histological sections of termites in pre-ecdysis, the distance between the two cuticle layers was beyond 20 μm, and sometimes the old cuticle was missing, which was an artifact, as the fixation and sectioning techniques stretched the distance between the new and the old cuticle. This shows that the old cuticle was already loose and detached from the body. Our observation of the presence of the new cuticle underneath the old one during pre-ecdysis confirmed what was found by Bourguignon et al. (2012) that when pseudergates of *Psammotermes hybostoma* Desneux approached nymphal molt, their new cuticles were completely formed underneath the old one.

During the pre-ecdysis and ecdysis period, the newly formed cuticle was dense and heavily wrinkled, whereas the old cuticle lost most of its density and appeared thin and brittle. The changes in thickness and hardness of the old cuticle may provide enough flexibility for the detachment. In comparison, the newly formed cuticle must allow for more volume of the hemocoel and, therefore, will result in more total body surface. Because the new cuticle was trapped within the old cuticle during the pre-ecdysis, there was no room for full expansion. Therefore, the new cuticle, although still soft, folded on itself, creating this wrinkled pattern, and when the exuvium was completely removed, it took at least 3 h for the cuticle to fully expand and complete its hardening. In addition, in termites in the pre-ecdysis phase, the old cuticle from the tracheal system was totally detached from the newly formed cuticle, which explained why the old tracheal lining cuticle could be pulled out during ecdysis. Wigglesworth (1973), who studied the molting process of *Rhodnius prolixus* Stal, reported that the old cuticle of the tracheae existed inside the newly formed tracheal system, and before the ecdysis, the two layers of cuticle were completely separated. Our findings confirmed this process in termites. The lining of the foregut and the hindgut was also replaced during the molting process. Exuviae from molted individuals were observed, but no hindgut lining was found, probably because of the extremely thin nature of the cuticular intima and the possibility that the old hindgut intima was previously shed with the voiding of the gut fauna.

As a social insect, termites benefit from the presence of nestmates during ecdysis in comparison with solitary insects. However, contrary to the assumption by Raina et al. (2008) that termites cannot molt without the help of nestmates, our results showed that isolated termite can still successfully complete ecdysis, but molting termites associated with nestmates took less time than isolated termites to complete ecdysis. In particular, the time between the beginning of the peristalsis and the formation of the dorsal breach (Phase 1) was reduced, and we suggest that mechanical stimuli such as grooming by the nestmates may have helped initiate ecdysis. Also, longitudinal tracheal trunks needed to be extricated from the thorax (Phase 4) and the presence of nestmates facilitated this process. The presence of nestmates throughout the molting process appears beneficial to the individuals. Indeed, because mature colonies of subterranean termites can reach millions of individuals (Su et al. 1993) and because at any given time $\approx$1% of all individuals are engaged in their molting process (in laboratory conditions, as observed by Raina et al. 2008), a large number of molting individuals directly depend on their nestmates for hygienic behaviors (Chouvenc and Su 2010). In addition, because molting individuals are not found at foraging sites (Raina et al. 2008), we suggest that such individuals are mainly located into a less accessible part of the colony, presumably in the carton nest. This would reduce their risk of predation, and would optimize the ratio of active workers at foraging sites.

Finally, our study provided a description of the structural changes through histological observations during ecdysis in *C. formosanus.* This description will serve as a basis to compare the cuticular alterations during ecdysis when individuals are exposed to CSIs. Therefore, our future work will describe the physical alteration of the molting process because of CSIs at the

histological level, which will provide novel information on the mode of action of such compounds in termites, which may allow for improvements of bating technologies.

Acknowledgments

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