Aggressive Behavior and the Role of Antennal Sensillae in the Termite *Reticulitermes chinensis* (Isoptera: Rhinotermitidae)

by

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ABSTRACT

This study examined aggressive behavior between the colonies in the termite *Reticulitermes chinensis* from China. Strong aggression was observed among workers and soldiers. Intercolonial aggression was strong during the first 0.5 h and then reduced gradually in all the treatments. After cutting the five terminal antennal segments of workers and soldiers, there was still strong intercolonial aggression among workers and soldiers. However, after removal of the ten terminal antennal segments of workers and soldiers, almost no intercolonial aggression happened among workers and soldiers. SEM results of antennae indicated that antennal sensillae mainly occurred on the ten terminal segments including four types of trichode sensilla, both in workers and soldiers of this species. Few antennal sensilla occurred on the basal segments except for a few sensilla chaetica and basiconic capitate peg sensilla. The above findings suggest that antennal sensillae may play a role in nestmate recognition in *R. chinensis*.

Keywords: aggressive behavior, antennal sensilla, *Reticulitermes chinensis*, nestmate recognition.

INTRODUCTION

All social insects need to distinguish nestmates from non-nestmates (Kaib *et al.* 2004). Nestmate recognition ensures integration in a colony and prevents non-colony members from exploiting the colony's resources (Crozier & Pamilo 1996, Yusuf *et al.* 2010). The presence of non-nestmates (intruders) usually induces active aggressive behaviors (Vander Meer & Morel 1998). In the eusocial termites, there is not only interspecific aggression

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but also intercolonial aggression in the same species (Polizzi & Forschler 1998). Intercolonial aggression among subterranean termites is highly variable (Cornelius & Osbrink 2009). In the United States, some colony pairs of *Coptotermes formosanus* showed high levels of aggression, while other colony pairs exhibited almost no aggression (Su & Haverty 1991, Shelton & Grace 1997, Husseneder & Grace 2001, Cornelius & Osbrink 2003). There was strong aggression among colonies of *Odontotermes formosanus* in China (Huang *et al.* 2007). Italian *Reticulitermes lucifugus* populations were moderately aggressive (Uva *et al.* 2004). However, there was no aggression among colonies of *R. santonensis* in France and *R. flavipes* in Massachusetts (Bulmer & Traniello 2002, Dronnet *et al.* 2006).

Intercolonial aggression was correlated with cuticular hydrocarbon profiles in *Macrotermes subhyalinus* (Kaib *et al.* 2004), but there was no correlation between cuticular hydrocarbons and levels of intercolonial aggression in *C. formosanus* (Su & Haverty 1991). However, pairings of workers from different cuticular hydrocarbon phenotypes resulted in immediate aggression in *Reticulitermes* (Haverty *et al.* 1999). Aggressive behavior among colonies of *R. lucifugus* was unrelated to intercolonial geographic distance (Jmhasly & Leuthold 1999, Uva *et al.* 2004). There was a positive correlation between genetic distance and levels of intercolonial agonism in *C. formosanus* (Husseneder *et al.* 2005). In addition, group size, diet, gland secretions, bioassay design and length of time in the laboratory affected intercolonial aggression in termites (Polizzi & Forschler 1998, Florane *et al.* 2004, Zhang *et al.* 2006, Huang *et al.* 2007, Cornelius & Osbrink 2009).

The termite *R. chinensis* (Isoptera: Rhinotermitidae) is widely distributed in China, including Beijing, Tianjin, Shanxi and the Yangtze River drainage basin (Wei *et al.* 2007). This termite species builds its nests in soil and wooden structures (Liu 2003), and is an important pest of forest trees and urban buildings (Li *et al.* 2010). However, knowledge about social behaviors of *R. chinensis* is currently limited, such as foraging behavior, trophallaxis and aggressive behavior. In this study, we combine results derived from aggression tests among colonies, effect of antennal sensillae on intercolonial aggression, and SEM photomicrographs of antennal sensilla to better understand intercolonial aggression in *R. chinensis*.

METHODS AND MATERIALS

Termites

Two colonies of *R. chinensis* were collected from pine stumps in Shizi Hill, Huazhong Agriculture University (30°29' N, 114°21' E), Wuhan city, China at the same time. The two colonies were recorded as Col. A and Col. B respectively. The distances among them were more than 300 meters. One week later, termites were removed from stumps brought into laboratory. Soldiers were used to identify species (Huang *et al.* 2000). Each colony was maintained in separate glass containers with lids. Containers were lined with damp pines slats (1 mm×2 cm×8 cm). Glass containers were kept in a dark laboratory at constant conditions (25±2°C, 85±5% RH). Termites in glass containers were used in the following experiments during three months.

Aggressive Behavior

Each group of 300 workers from one colony were placed in a 15.0 cm diameter glass Petri dish lined with filter paper (15.0 cm) stained with 1.0 g/L solution of Neutral Red in distilled water (Huang *et al.* 2007), and provided with 2 ml of distilled water for moisture. The dishes were then placed in a climate cabinet maintained in complete darkness at 25±2°C and 85±5% RH. The termites were forced to feed on the stained filter paper for 24 h, and then the marked individuals were selected to be used in the study. Simultaneously, healthy workers without staining from the other colony were also selected to be used in this study. 60 workers from Col. A and Col. B were mixed together in a 9.0 cm diameter glass Petri dish with filter paper (9.0 cm diameter) together in ratios of 50:10, 45:15, 30:30, 15:45 and 10:50. The aggressive encounters of workers between Col. A and Col. B were recorded in 5 min intervals at 0, 0.5, 1, 1.5 and 24 h after workers were combined. Then numbers of dead termites were recorded at 24 h. There were 6 replicates for each combination in the experiment on aggression in workers between Col. A and Col. B. There were 3 replicates with marked workers for Col. A and Col. B respectively in each combination. For the experiment of aggression in soldiers between Col. A and Col. B, the abdomens of soldiers were painted by a black marking pen so that the soldiers from different colonies could be distinguished. The soldiers from Col. A and Col. B were placed in a 9.0 cm diameter glass Petri dish with filter paper (9.0 cm diameter) together in ratios of 20:10, 15:10, 10:10, 10:15 and 10:20. The other test processes were the same as described above. For the experiment of aggression between soldiers from Col. A and workers from Col. B, because there were obvious morphological differences between soldiers and workers, the staining process was not needed. The soldiers from Col. A and the workers from Col. B were placed in a 9.0 cm diameter glass Petri dish with filter paper (9.0 cm diameter) together in ratios of 20:10, 15:10, 10:10, 10:15 and 10:20. There were only 3 replicates for each combination in the experiment. The other test processes were the same as the above experiments. Intracolonial aggression in Col. A and Col. B was respectively as control experiment, with the same caste combinations and experimental methods as described above.

Effect of Antennal Sensillae on Aggression

Workers or soldiers in Petri dishes (9.0 cm diameter) were immobilized on the ice, and then the five terminal or ten antennal segments were cut for workers and soldiers under the microscope. The treated workers and soldiers were left at room temperature for 30 min to recover and then used in the following aggression trials between Col. A and Col. B. There were four types of treatments: (1) aggression in workers without the five segments of antennae, (2) aggression in soldiers without the five segments of antennae, (3) aggression in workers without the ten segments of antennae, (4) aggression in soldiers without the ten segments of antennae. The 20 termites from Col. A (10 termites) and Col. B (10 termites) were placed in a 9.0 cm diameter glass Petri dish with filter paper (9.0 cm diameter) together. The numbers of dead termites were recorded at 0.5 h, 1.0 h, 1.5h and 24 h. There were 5 replicates for each treatment. The other test processes were the same as the above experiments.

SEM of Antennal Sensillae

Two samples were observed by scanning electron microscope (SEM), including a worker and a soldier from Col. A. The heads were removed from the bodies and were rinsed in phosphate buffer. Heads were twice dehydrated through a graded ethanol series of 30, 50, 70, 85, 95 and 100% (each for 15 min). The heads were placed in a sample basket which was then put in a sample chamber of a critical point dryer. After covering with a lid, liquid CO2 was injected into the sample chamber up to submerge the sample. The temperature of the sample chamber first increased to 15°C for 10 min and then increased to 35°C which made all the liquid CO2 gasified. After all the CO2 was discharged, the sample could be taken out. The samples were sputter-coated with gold for 5 min. Finally the sample was observed under a JSM-6390LV SEM at 20 kV.

Statistical Analyses

Mortality of termites (%) = Number of dead termites × 100 / Initial number of termites. The 2-tailed paired-samples T Test was used to analyze mortality of termites between the two colonies (SPSS Inc., 1989-2002).

RESULTS

Intercolonial Aggression

When the termites from Col. A and Col. B were placed in the same dish in the five ratios, they showed strong aggression (Fig.1A, Fig.2A and Fig.3B). For example, one used its mandibles to clamp the head, maxilla or abdomen of the other one until it became immobile. For each combination in aggression in workers between Col. A and Col. B, the aggressive encounters were more than 9 in 5 min at 0 h after combining (Fig.1A). When the testing time continued, the aggressive encounters between workers decreased. At 24 h after combining workers from the two colonies, the aggressive encounters between workers from the two colonies were less than 3 (Fig.1B). For each combination in aggression in soldiers between Col. A and Col. B, the aggressive encounters

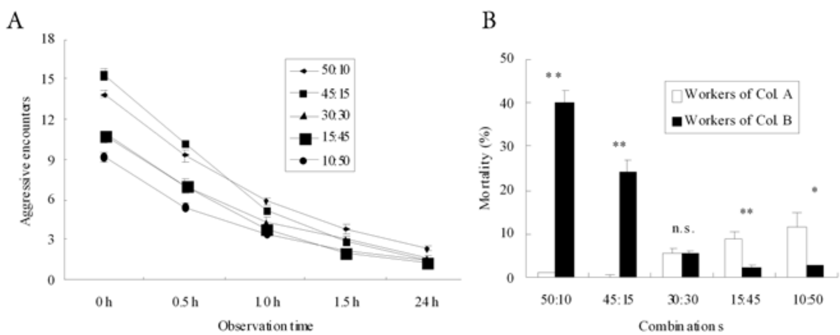

Fig.1. Aggressive behavior in workers between Col. A and Col. B in five combinations; A, aggressive encounters of workers; B, worker mortality at 24 h. **, $p < 0.01$; *, $p < 0.05$; n.s., no significant difference.

were more than 11 in 5 min at 0 h after combining (Fig.2A). Over time, the number of aggressive encounters between workers and soldiers decreased. At 24 h after combining, the aggressive encounters between soldiers from the two colonies were less than 3 (Fig.2A). For each combination in aggression between soldiers from Col. A and workers from Col. B, the aggressive encounters were more than 13 in 5 min at 0 h after combining (Fig.3A). When the testing time continued, the aggressive encounters between soldiers and workers presented the decreasing trend. At 24 h after combining, the aggressive encounters between soldiers from Col. A and workers from Col. B were less than 3 (Fig.3A). There was no intracolonial aggression observed in all the control experiments in Col. A and Col. B.

Worker mortality of Col. A was significantly less than that of Col. B at 24 h when the ratios were 50:10 (t= -16.579, df=5, p=0.001) and 45:15

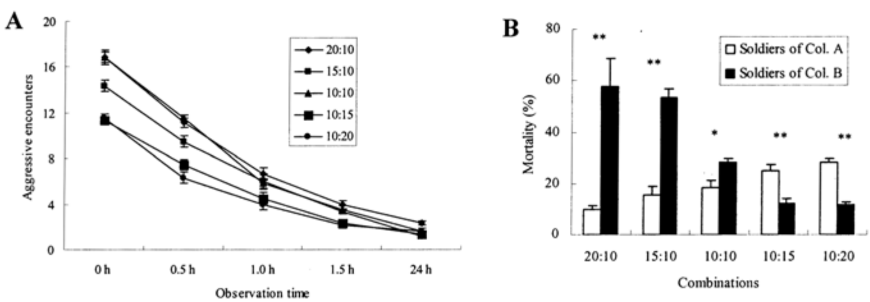

Fig.2. Aggressive behavior in soldiers between Col. A and Col. B in five combinations; A, aggressive encounters of soldiers; B, soldier mortality at 24 h. **, p < 0.01; *, p < 0.05.

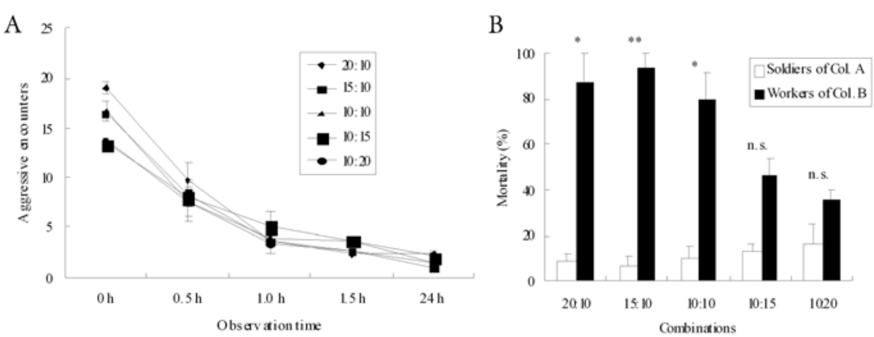

Fig.3. Aggressive behavior between soldiers from Col. A and workers from Col. B in five combinations; A, aggressive encounters of soldiers and workers; B, mortality of soldiers and workers at 24 h. **, p < 0.01; *, p < 0.05; n.s., no significant difference.

(t= -10.07, df=5, p=0.001) (Fig.1B). However, worker mortality of Col. A was significantly higher than that of Col. B at 24 h in 10:50 (t=4.398, df=5, p=0.007) and 15:45 (t=3.045, df=5, p=0.029) (Fig.1B). There was no significant difference in work mortality between Col. A and Col. B at 24 h in 30:30 (t= -0.002, df=5, p=0.999) (Fig.1B). Soldier mortality of Col. A was significantly less than that of Col. B at 24 h when ratios were 20:10 (t= -4.111, df=5, p=0.009), 15:10 (t= -11.087, df=5, p=0.001) and 10:10 (t= -2.739, df=5, p=0.041) (Fig.2B). However, soldier mortality of Col. A was significantly higher than that of Col. B at 24 h in 10:15 (t=8.032, df=5, p=0.001) and 10:20 (t=10.0, df=5, p=0.001) (Fig.2B). Soldier mortality of Col. A was significantly less than worker mortality of Col. B at 24 h when the ratios were 20:10 (t= -6.518, df=2, p=0.023), 15:10 (t= -22.522, df=2, p=0.002) and 10:10 (t= -7.00, df=2, p=0.020) (Fig.3B). However, There was no significant difference between soldier mortality of Col. A and worker mortality of Col. B at 24 h in 10:15 (t= -3.973, df=2, p=0.058) and 10:20 (t= -4.158, df=2, p=0.053) (Fig.3B).

Effect of Antennal Sensillae on Aggression

After five terminal segments of the two antennae of workers were cut, strong aggression still occurred in workers between Col. A and Col. B. The aggressive encounters were 20 in 5 min at 0 h after combining (Fig.4A). When the testing time continued, the aggressive encounters between workers presented the decreasing trend. At 24 h after combining, the aggressive encounters between workers from the two colonies were 3 (Fig.4A). There

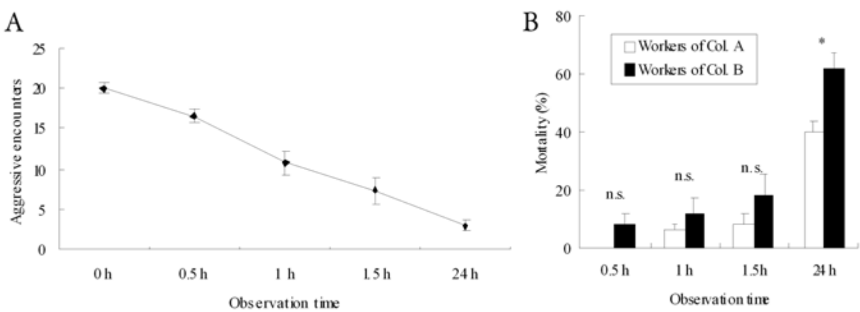

Fig.4. Aggressive behavior in workers without the five segments of antennae between Col. A and Col. B when the combination was 10:10; A, aggressive encounters of workers; B, worker mortality. *, $p < 0.05$; n.s., no significant difference.

was no significant difference between worker mortality of Col. A and worker mortality of Col. B at 0.5 h (t= -2.138, df=4, p=0.099), 1 h (t= -2.449, df=4, p=0.07) and 1.5 h (t= -2.236, df=4, p=0.089) (Fig.4B). However, worker mortality of Col. A was significantly less than that of Col. B at 24 h (t= -3.773, df=4, p=0.02) (Fig.4B).

After cutting five terminal segments of the two antennae of soldiers, there was strong aggression in soldiers between Col. A and Col. B. The aggressive encounters were 21.8 in 5 min at 0 h after combining (Fig.5A). When the testing time continued, the aggressive encounters between soldiers presented the decreasing trend. At 24 h after combining, the aggressive encounters between soldiers from the two colonies were 2.6 (Fig.5A). Soldier mortality of Col. A was significantly less than that of Col. B at 0.5 h (t= -4.00, df=4, p=0.016), 1.0 h (t= -3.207, df=4, p=0.033), 1.5 h (t= -5.715, df=4, p=0.005), 24 h (t= -3.207, df=4, p=0.033) (Fig.5B). However, after cutting

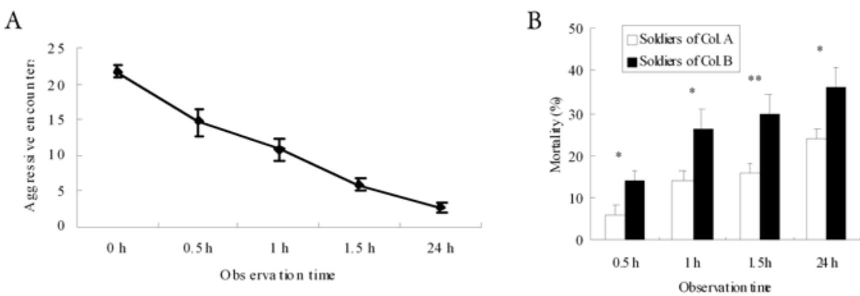

Fig.5. Aggressive behavior in soldiers without the five segments of antennae between Col. A and Col. B when the combination was 10:10; A, aggressive encounters of soldiers; B, soldier mortality. **, p < 0.01; *, p < 0.05.

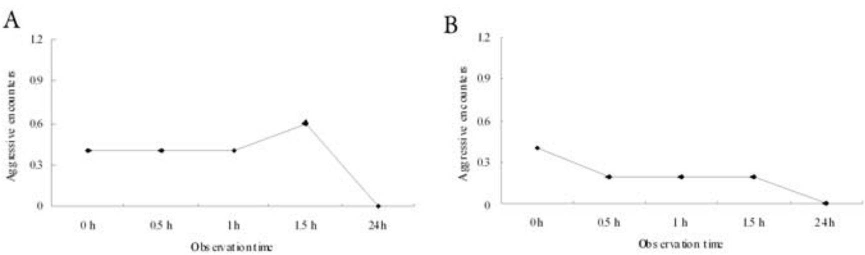

Fig.6. Aggressive behavior in workers and soldiers without the ten segments of antennae between Col. A and Col. B when the combination was 10:10; A, aggressive encounters of workers; B, aggressive encounters of soldiers.

ten terminal segments of the two antennae of workers, there was almost no aggression in workers between Col. A and Col. B (Fig.6A). Similarly, almost no aggression happened in soldiers without ten terminal segments between Col. A and Col. B (Fig.6B).

SEM Observation of Antennal Sensilla

Antennal sensillae of both workers and soldiers of *R. chinensis* occurred mainly on the ten terminal segments of antennae (Fig.7A; Fig.8A), which included four types of trichodea sensilla (TS) (Fig.7B, D; Fig.8B, D). There were few antennal sensillae on the basal segments of antennae of both workers and soldiers of *R. chinensis* (Fig.7C; Fig.8C), exception for a few sensilla chaetica (SCh) and basiconic capitate peg sensilla (BCPS) (Fig.7E, F; Fig.8E, F).

DISCUSSION

In this study, we observed strong intercolonial aggression in the termite *R. chinensis*. For the five combinations, all the aggressive encounters were almost more than 9 in 5 min at 0 h after termites from the two colonies were combined, but those dropped to less than 3 in 5min at 24 h. There are two

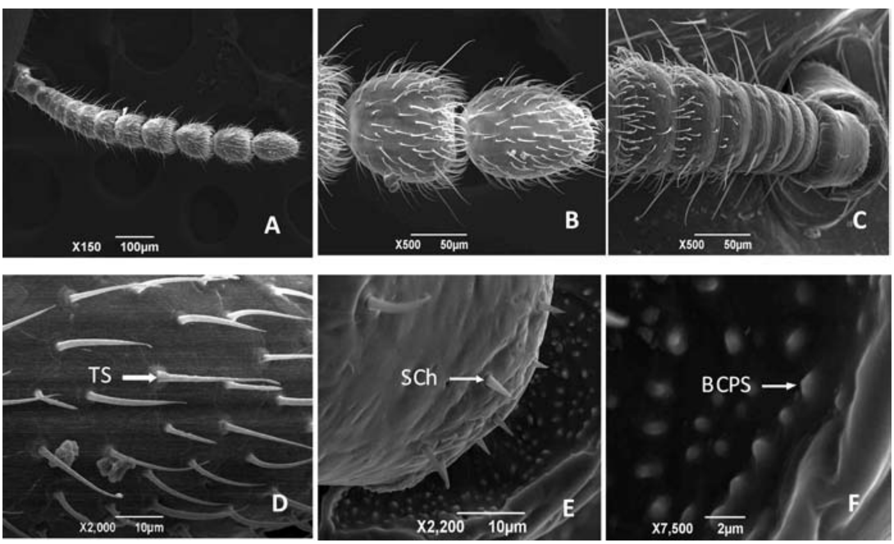

Fig.7. SEM photomicrographs of antennal sensillae of *R. chinensis* worker; A, entire antenna; B, terminal segments of antenna; C, basal segments of antenna; D, trichodea sensilla (TS); E, sensilla chaetica (SCh); F, basiconic capitate peg sensilla (BCPS).

potential explanations for this reducing trend: 1)some of the termites were already dead or injured due to their strong aggression, 2) remaining individuals were calm because of large amounts of energy consumption (Huang *et al*. 2007).

The worker mortality of Col. A was significantly less than that of Col. B at 24 h when the combinations were 50:10 and 45:15 (Col. A : Col. B), and the worker mortality of Col. A was significantly higher than that of Col. B at 24 h in 10:50 and 15:45 (Col. A : Col. B). These results indicated that there was positive correlation between group size and levels of intercolonial aggression in workers of *R. chinensis*, unlike the aggressive behavior in workers between *R. flavipes* and *R. virginicus* (Polizzi & Forschler 1998). The soldier mortality of Col. A was significantly less than that of Col. B at 24 h when the combinations were 20:10 and 15:10 (Col. A : Col. B), and the soldier mortality of Col. A was significantly higher than that of Col. B at 24 h in 10:15 and 10:20 (Col. A : Col. B). These results also suggested that the advantage of individual numbers could produce an agonistic advantage in soldiers of *R. chinensis* (Huang *et al* 2007). Furthermore, the soldier mortality of Col. A was significantly less than worker mortality of Col. B at 24 h when the combinations were 10:10 (Col. A : Col. B), and there was no significant

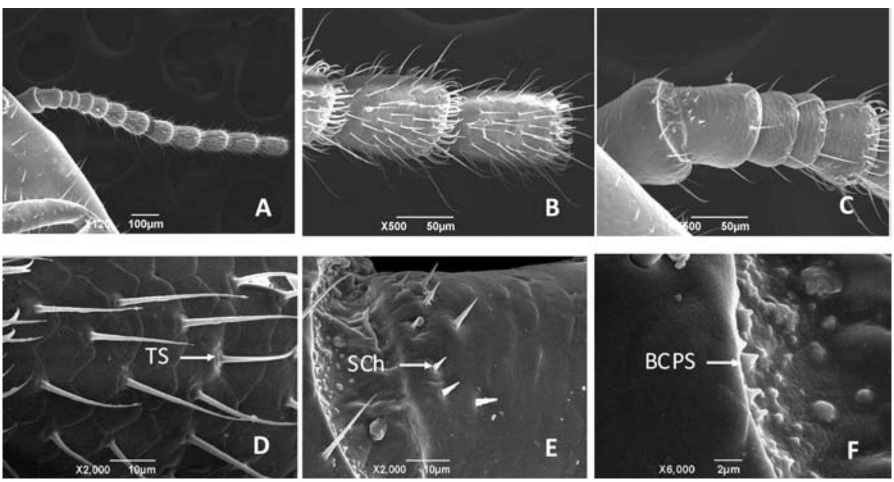

Fig.8. SEM photomicrographs of antennal sensillae of *R. chinensis* soldier; A, entire antenna; B, terminal segments of antenna; C, basal segments of antenna; D, trichodea sensilla (TS); E, sensilla chaetica (SCh); F, basiconic capitate peg sensilla (BCPS).

difference between soldier mortality of Col. A and worker mortality of Col. B at 24 h in 10:15and 10:20 (Col. A : Col. B). These results indicated that the soldier caste were more aggressive than the worker caste in *R. chinensis* (Binder 1988), which is possibly correlated with soldiers' strong mandibles and frontal gland secretions (He *et al*. 2006; Zhang *et al*. 2006).

After cutting five terminal segments of the two antennae of workers and soldiers, there was still strong aggression among workers and soldiers from Col. A and Col. B. However, after cutting ten terminal segments of the two antennae of workers and soldiers, almost no aggression happened among workers and soldiers between the two colonies. These results indicate that chemosensory sensilla with function of nestmate recognition mainly located in the ten terminal segments of antennae in *R. chinensis* (He 2006). As shown by scanning electron microscopy, antennal sensillae of both workers and soldiers of *R. chinensis* occurred mainly on ten terminal segments of antennae, including four types of trichodea sensilla, but there were few antennal sensilla on the basal segments of antennae of both workers and soldiers, except for a few sensilla chaetica and basiconic capitate peg sensilla (Tarumingkeng *et al*. 1976; Li *et al*. 2009). These findings suggest that antennal sensillae might be responsible for nestmate recognition in *R. chinensis* (Ozaki *et al*. 2005).

The above findings suggest that antennal sensillae may play a role in nestmate recognition in *R. chinensis*. However, the other factors involved in aggression in termites should also be studied for *R. chinensis*, such as diet, geographic distance, genetic distance, bioassay design and length of time in the laboratory (Cornelius & Osbrink 2009). Currently, very little is known about molecular mechanisms of aggressive behavior in termites (Dierick & Greenspan 2006; Alaux *et al.* 2009), so identification of genes affecting aggression in *R. chinensis* should also be initiated.

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