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Original Article

A comprehensive review on the documented characteristics of four *Reticulitermes* termites (Rhinotermitidae, Blattodea) of China

Uma revisão abrangente sobre as características documentadas de quatro cupins *Reticulitermes* da China

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Abstract

Termites are known as social insects worldwide. Presently in China 473 species, 44 genera and 4 families of termites have been reported. Of them, 111 *Reticulitermes* species are widely spread in different zones of China. The dispersion flight season of these Chinese *Reticulitermes* species are usually started from February to June, but in some regions different species are distributed, sharing their boundaries and having overlapping flight seasons. These reasons become important sources of hybridization between two different heterospecific populations of termites. It was confirmed that the fertilized eggs and unfertilized eggs of some *Reticulitermes* termites have the capacity of cleavage. While the unfertilized eggs of *R. aculabialis, R. chinensis* and *R. labralis* cleaved normally and the only *R. aculabialis* unfertilized eggs develop in embryos. While, the *R. flaviceps* and *R. chinensis* were observed with their abnormal embryonic development, and not hatching of eggs parthenogenetically. They were reported more threatening to Chinese resources as they propagate with parthenogenesis, hybridization and sexual reproduction. Eggshell and macrophiles of eggs play important roles in species identification and control. Although, they are severe pests and cause a wide range of damages to wooden structures and products in homes, buildings, building materials, trees, crops, and forests in China's Mainland.

Keywords: *Reticulitermes* species, hybridization, embryonic development, parthenogenesis.

Resumo

Os cupins são conhecidos como insetos sociais em todo o mundo. Atualmente na China foram relatadas 473 espécies, 44 gêneros e 4 famílias de cupins. Destas, 111 espécies de *Reticulitermes* estão amplamente distribuídas em diferentes zonas da China. A temporada de voo de dispersão dessas espécies chinesas de *Reticulitermes* geralmente começa de fevereiro a junho, mas em algumas regiões diferentes espécies são distribuídas, compartilhando seus limites e tendo temporadas de voo sobrepostas. Essas razões tornam-se importantes fontes de hibridização entre duas populações heteroespecíficas de cupins. Foi confirmado que os ovos fertilizados e não fertilizados de alguns cupins *Reticulitermes* possuem capacidade de clivagem. Já os ovos não fertilizados de *R. aculabialis*, *R. chinensis* e *R. labralis* clivaram normalmente, e os únicos ovos não fertilizados de *R. aculabialis* se desenvolvem em embriões. *R. flaviceps* e *R. chinensis* foram observados com desenvolvimento embrionário anormal, e não eclosão de ovos por partenogênese. Eles foram relatados como mais ameaçadores para os recursos chineses à medida que se propagam com partenogênese, hibridização e reprodução sexual. Casca de ovo e macrófilos de ovos desempenham papéis importantes na identificação e controle de espécies, embora sejam pragas graves e causem uma ampla gama de danos a estruturas e produtos de madeira em residências, edifícios, materiais de construção, árvores, plantações e florestas na China continental.

Palavras-chave: espécies de *Reticulitermes*, hibridização, desenvolvimento embrionário, partenogênese.

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1. Introduction

Overview of termites as social insects and their damages, evolved from common Cretaceous and Cryptocercus roaches during the Jurassic period (Bourguignon et al., 2015). After their evolution, they adapted the phenomena of metamorphosis, growth and development, polymorphism, trophallaxis, colony defence, hygienic and healthier survival as social insects (Cornette et al., 2013; Chouvenc and Su, 2014; Du et al., 2016, 2017; LeBoeuf et al., 2018; Cremer et al., 2018; Liu et al., 2019). While in termite colony division of labour is categorized by different instar of workers, soldiers and alates that perform activities such as foraging, feeding, sanitation, egg and brood care, reproduction, egg-laying, colony defence against pathogens and diseases individually (Su et al., 2012; Cheng, 2013; Bagnères and Hanus; 2015; Korb, 2016; Yanagihara et al., 2018; Funaro et al., 2018; Otani et al., 2019).

Therefore, termite species have a wide diversity of feeding behaviours, especially they consume cellulose of woods, tree farmings, structural timbers, decompose organic animal matters in different degrees and cause severe losses in the billions of dollars per year due to direct damage and chemical control costs worldwide (Su et al., 2004; Cameron and Whiting, 2007; Ghesini et al., 2011; Lim and Forschler, 2012; Perdereau et al., 2013; Arango et al., 2017; Dutto et al., 2018; Govorushko, 2019; Khan et al., 2019, Khan et al., 2021a). Many gut-associated microorganisms provide essential amino acids to intestines of termite *R. flavipes* (Fisher et al., 2007; Ayayee et al., 2015; Waidele et al., 2016; Arango et al., 2017), decompose cellulose into nutrients through proper metabolic pathway for both of them and also return nitrogen and carbon to the environment as fertilizers. Therefore, this is an important cycle that plays an essential role in the environment (Raychoudhury et al., 2013; Ayayee et al., 2015; Peterson and Scharf, 2016).

A total of 3106 species of termites were reported globally, while 371 of them were counted the most destructive and caused severe damages to human properties (Krishna et al., 2013). The massive economic losses were considered more than 40 billion dollars per year in the world (Rust and Su, 2012; Chouvenc et al., 2015, 2016; Tong et al., 2017). Rawat (2002) estimated the cost of chemical control of termites in the U.S.A is higher than the loss caused by the annual storm. Historically, they are problematic pests that threaten, harm and weak structures of a wide range, including wooden products of human homes, buildings and building materials, clothing, books and sleepers, cotton, poles and cables, more danger to trees, crops and forests in natural and disturbed areas of China (Ab Majid and Ahmad, 2015; Abd-Elkareem and Fouad, 2016; Boscaro et al., 2017; Su et al., 2017; Vesala et al., 2019). From a universal viewpoint, they not only cause minor or significant damage in tropical and subtropical environments but more frequently they can breed, spread, build mounds in the new regions after being invaded resources and also cause severe losses (Li et al., 2010a, 2013b; Jouquet et al., 2016; Paul et al., 2018; Perdereau et al., 2019). They are abundant and responsible for approximately 2 billion RMB annually equivalent to $217 million US (Tonini et al., 2013; Su et al., 2017; Perdereau et al., 2019).

About 150 termite species belonged to 4 families and 28 genera that were reported to damage plants in hilly Southern land (Li et al., 2010a; Paul et al., 2018). They have more active and dynamic breeding activities, which are sped up by their well-developed reproductive abilities (Tonini et al., 2013; Perdereau et al., 2019). The following study was arranged on the *Reticulitermes* termites of China, to know their embryonic development in parthenogenetic and sexual eggs, their related developmental stages, hybridization, and morphology of gonads.

The insect parthenogenesis consists of three mechanisms, first like in honeybee haploid parthenogenesis, the second is the fusion of unfertilized eggs in diploid offspring, including end fusion and nuclear fusion (Verma and Ruttner, 1983). In the third case, parthenogenesis is generally (sporadic parthenogenesis) responsible for the growth of unfertilized eggs directly into embryos such as silkworms (Liu et al., 2015). While, periodic parthenogenesis alternates between parthenogenesis and sexual reproduction in aphids (Dedryver et al., 2013). Additionally, Origin of transmission: males of wasps reproducing two sexual categories of both sexes and parthenogenesis after mating with their sexual females (Ma et al., 2015). Moreover, artificial induction: the warm soup is used to treat silkworms eggs with it, they grow and adapt parthenogenesis for conforming female lines (Long et al., 2015; Rhainds, 2019). Except for finding males, the females produce their offspring with facultative parthenogenesis. It is common in the Isoptera to reproduce with facultative parthenogenesis (Kobayashi and Miyaguni, 2016).

Hybridization is an important corridor for organisms to obtain variation, allowing the gene introgression of an organism to penetrate in the next generation and different populations for their successful adaptation (Harrison and Larson, 2014). Speciation of insects through hybridization is recognized based on chromosomal and isozymal studies in which combination of genes and chromosome sets is due to diploid or polyploid of two species. Recently, reviewed examples in numerous species of insects like planthopper *Muellerianella fairmairei-brevipennis*, grasshopper *Warramaba virgo*; *Otiorrhynchus*, black flies of the genera *Gymnopais* and *Prosimulium* (Bullini and Nascetti, 1990; Taylor and Larson, 2019; Pierce et al., 2014).

This study was arranged with the following aims and objectives.

To know the importance of micropyles and gas exchange through termite eggshell in parthenogenetic, hybrid and sexual eggs.

To know about the damages of the parthenogenetic, sexual and hybrid progeny of *Reticulitermes* species.

To know the comparative reproductive competencies of *Reticulitermes* species.

To know the effect of the hybrid progeny of *Reticulitermes* termites on the local population.

2. Results and Discussion

2.1. Distribution of termites in China

Recently, in China the four most dangerous species, the subterranean termites *Reticulitermes aculabialis*

Tsai et Hwang, *R. chinensis* Snyder (1923), *R. labralis* and *R. flaviceps* Oshima (2011) (Rhinotermitidae, Blattodea) reported that they caused losses in different regions of administrative level and also most widely distributed (Krishna et al., 2013; Li et al., 2010b, 2018). Compared to termites of the Northern part with the South part, the distribution of four termite species is more common in 20 provinces and autonomous regions of China, which mostly cause severe damage to trees, crops, and human constructions. In future, it is more predictable that these termite species more frequently reproduce, expanding and they will damage the North part of China (Gui-Xiang et al., 1994; Mo et al., 2004; Appel et al., 2012).

Termites are generally dispersed in tropical rain forests near the equator, North and South latitudes worldwide (Matsumoto, 1976; Eggleton, 2000; Veera Singham et al., 2017). The distribution of termite species in the Eastern Hemisphere is more than in Northern latitudes. Similarly, in the Eastern Hemisphere, the dispersion is exceeded than in the Western Hemisphere, moreover, the biodiversity of termites in the Northern Hemisphere increased comparative the Southern Hemisphere, and some termite species distributed in the mountains at an elevation of 2000 m (Suiter et al., 2009; Hu et al., 2010; Guo et al., 2013).

In the Northern part of China, the distribution of termites initiates in Gongzhuling of Liaoning province (latitude 43°11’40′′- 44°9’20′′), through Jiexiu of Shanxi (latitude 37° North), Hancheng of Shaanxi (latitude 35.5° North), Gansu Wenxian county (33° North latitude), Westward to Tibet Medog (29.5° North latitude) (Li et al., 2009; Husseneder et al., 2012b; Li et al., 2013b; Tong et al., 2017; Su et al., 2017), which connects a line formed by each point from Northeast to Southwest and termites distributed in the Southeast of the boundary line. Termite species in two provinces such as Yunnan and Hainan distributed, which also have the soil termite genus, that spread up to the parts of China, they cause severe damages than other termite groups (Li et al., 2011a; Hu and Song, 2014; Cao and Jiang, 2014; Soleymaninejadian et al., 2014; Su et al., 2017).

R. flaviceps was collected and identified for the first time from Taipei, Taiwan (Oshima, 1911), and examined as the amplest species based on its abundance, lifestyle and colony size (Li et al., 2011b). Although *R. flaviceps* is distributed in the South part of China especially Fujian, Guangdong, Guangxi, Hunan, Jiangxi, Jiangsu, Zhejiang, Anhui, Hubei, Sichuan, Yunnan, Guizhou and Shaanxi provinces (Krishna et al., 2013; Su et al., 2016). This invasive species crossed the Qinling Mountain range during the last decade, attacked about 100 km North from the Changjiang river basin to Huanghe river basin, and became an urban insect pest in the Northern areas of China (Xing unpublished data).

R. flaviceps is endemic to China and distributed in many tropical, subtropical and temperate regions of China (Veeresh et al., 1990; Mo et al., 2005; Li et al., 2009, 2011a). It is now found the most destructive and notorious subterranean termite pest in *Reticulitermes* throughout China and responsible for structural damage (Li et al., 2011b, 2016c; Rust and Su, 2012; Chouvenc et al., 2015; Veera-Singham et al., 2017; Khan et al., 2019). The subterranean termite *R. chinensis* is an important termite species that is distributed in Beijing, Tianjin, Shaanxi, Shanxi, Huanggang, Chongqing, Changsha and the drainage range of the Yangtse River in China (Wei et al., 2007; Huang et al., 2013). That potential pest damage the trees, wood products of buildings and the xylem of plants (Wu et al., 2019). Another subterranean termite *R. aculabialis* is the main Isopteran species that is a harmful pest to the environment of China. The population distribution of this species was investigated in Xi’an, Shaanxi, Nanjing and Jiangsu (Zhao et al., 2019). *R. aculabialis* is dispersed in 18 provinces and autonomous regions in China (Xing et al., 1998; Kai et al., 2016). According to the Gui-Xiang et al. (1994) and Li et al. (2010a) report, this termite has become a serious pest, causing damage in the Northwest part increasingly and in some zones closed to the South Bank of the Yangtze River. *Reticulitermes* termite populations have been recorded in East Asia, Southern China, Taiwan, Korea and Japan. Hence, these species have diverse ecological requirements (Hochmair and Scheffrahn, 2010, Chouvenc et al., 2015), but they have established populations in many native areas include Northern and Southern parts and expanded in invasive areas due to human transportation, floods and wind (Su, 2013; Corn and Johnson, 2013; Chunco, 2014; Chouvenc et al., 2015; Li et al., 2016c). This observation is currently reviewed in many ecosystems of the world that are responsible for the replacement of this non-native species in native regions of China (Chouvenc et al., 2015; Su et al., 2017; Wu et al., 2020; Fournier and Aron, 2021).

However, the studies of spreading are concerned with interaction and overlap in small localities of the world including the South part of China (Hartke and Baer, 2011; Grace, 2014; Chouvenc et al., 2015; Su et al., 2017). The Formosan subterranean termite (*Coptotermes formosanus*) and the Asian subterranean termite (*C. gestroi*) are the two most destructive structural pests in the world and are responsible for most of the economic loss annually (Messenger et al., 2002; Rust and Su, 2012; Chouvenc et al., 2015; Su et al., 2017).

2.2. Termite morphology

According to external morphology, termites can be classified into first and metamorphic categories from the viewpoint of phylogeny (Eggleton, 2010; Dedeine et al., 2016). There have been no extraordinary variations in their original status and wings, such as the head and thorax (reproductive and workers) species, while they have changes in their external shape of the soldiers like scorpion variability. Such modifications are only found in the soldiers’ thorax and head; those are used as significant sources of classification and identification (Ye et al., 2009; Booth et al., 2012; Perdereau et al., 2013; Perdereau et al., 2019). For example, *R. chinensis* has a sharply pointed lip on the upper lip, and the transparent part of the lip looks like a needle. The *R. flaviceps* has an upper lip narrow like a snail. The alates of *R. flaviceps* have a plate of grey-yellow colour on the anterior side of the thorax. While, the head peak of a soldier is slightly longer, and the forehead is approximately flat.

Termites are divided into two types based on reproductive ability, reproductives (king and queen) and non-reproductives (soldiers and workers). Reproductives are mainly divided based on their forms and sources. Primary reproductives are actual adults in the nest, have visible compound eyes, well-developed wings, and a more pigmented body. They are founders of first nests after dispersion flight and making tandem pairings. In contrast to primary reproductive, the secondary reproductive (workers) from the nest of older individuals. They have the ability of mating and egg-laying after ecdysis and play a significant character in the growth of the colony (Ye et al., 2009; Vidyashree et al., 2018). They are differentiated according to shape, age and divided into various types such as long wing bud types, wing scale types, micro wing bud types and short wing bud types. It can be discriminated into workers and secondary reproductive according to diverse sources. Most of the workers, except the reproduction, are responsible for sustaining the healthy life of the colony and care. The numbers of individuals in the colony of *Reticulitermes* termites are the highest, while the soldiers are only responsible for defence and have no feeding ability (Soleymaninejadian et al., 2014; Lillico-Ouachour et al., 2018; Khan et al., 2021a).

2.3. Classification of termites

According to traditional classification, termites were classified into the order of eusocial insect Isoptera (Donovan et al., 2000). Most of the researchers accept the truth that they are related to Blattodea and even they knew that the termites belong to the net-winged parents. There are arguments about their relationship. Termites are social insects like Hymenoptera while their molecular tree also indicates that their lineages lead to Cryptocercus roaches and assemblage in a monophyletic group.

Taxonomists classified the termite species into 7 families in early 2009. Moreover, the termites were re-identified and divided into 9 families by American scholars Engel, Grimaldi and Krishna after 2009. They are Hodotermitidae, Archatermopsidae, Kalotermitidae, Mastotermitidae, Rhinotermitidae, Serritermitidae, Stolotermitidae, Termiteidae and Stylotermitidae (Krishna et al., 2013). A total of 473 species belonged to 44 genera and 4 families of Isoptera that were divided into the lower and higher termites mainly consisted of seriously destructive agents. Among them, 5 species were found significantly in Southern parts of China (Li et al., 2011a, b; Kuswanto et al., 2015).

2.4. Mating behaviour of termites

Termite adults fly in groups for their reproduction from the parental colony, then they dispersed in different directions distant to the parental colony to build new colonies for egg-laying and hatching more offspring (Hartke and Rosengaus, 2011; Chouvenc et al., 2015; Su et al., 2017). Their dispersion is dependent on the humidity, temperature, pressure and seasons (Krishna, 2013). After dispersion flight, the alates fall off their wings and the males start to follow the females primarily. The kings and queens paired up with each other and form tandem pairings, which is the most important genetic behaviour of termites during building new colonies. The queen leads the king to select the accurate nest site to start the new nest (Matsuura and Nishida, 2001; Raina et al., 2003; Hartke, 2010; Pervez, 2018).

Imagoes mate after the foundation of the initial colony and start egg laying in time about one week (Hu et al., 2010). Similarly, in swarming flights of *R. flaviceps*, thousands of individuals release and fly from matured colonies annually. After the dispersal flight, the alates drop their wings, find females, pair up, and involve in tandem behaviour for mating, eggs laying and hatching after colony set up. While the male initiates tandem behaviour by maintaining contact with the tip of the female's abdomen. The female then leads the way in search of a favourable nesting site, in which both individuals seclude themselves and establish the early colony. It takes up unknown time for maturation and initiates dispersal flights (Xing et al., unpublished data; Li et al., 2011b; Chen et al., 2016).

2.5. Gonads of termites

The termite gonads are positioned in the last segments of the abdomen in females and males. All castes of termite have male and female individuals, but only the fully mature, morphological and physiological functional sexual organs were dissected out from the main reproductive castes such as primary reproductive and secondary reproductive (Su et al., 2015; Brent et al., 2016). The queen reproductive system comprises the genital cavity, accessory gland, spermatheca, oviducts, and branched ovary (Raina et al., 2007) while in king it consists of the accessory gland, ejaculatory duct, seminal vesicle, vas deferens and testis (Laranjo et al., 2018; Vargo, 2019). The ovary is composed of multiple branched oocytes that are arranged in turn inside the ovarian tubes (Husseneder et al., 2012a). The swollen belly of the termite queens is the sign of the matured ovaries, which felled of a large number of eggs in tubes (Aanen, 2018). The female of secondary reproductive in the matured colonies also has notably expanded abdomen as alates due to matured ovaries (Maekawa et al., 2010).

The adult female mate with a male, the sperm are transferred and stored in the spermatheca of the female (Raina et al., 2007; Saran et al., 2007; Husseneder et al., 2012a; Yashiro and Lo, 2019). The sperm is released from the spermatheca, to fertilize the ovum in the genital cavity and then expelled through the gonopore (Raina et al., 2003; Raina et al., 2007). Dispersion flight, site selection and foundation of the colony, tandem pair, mating and fertilization, egg-laying, egg hatching, feeding, and brood care are the life potential processes (Matsuura et al., 2002a; Kusaka and Matsuura, 2018). If the laid eggs are unfertilized (parthenogenetic) in some termites like *R. flaviceps*, they will not be capable to develop usually and hatching offspring (Xing unpublished data; Yashiro and Matsuura, 2014). The mated females reserve sperm in spermatheca with a functional capacity for a long time and use them for fertilization of the ova in the body (Raina et al., 2003; Raina et al., 2007).

2.6. Egg laying of termites

Macrotermes anandalei termite has laid 2949 eggs and the *M. subhyalinus has* 3,600 eggs in 24 hours (Krishna, 2020); while the *G. haviandi* has been laid 8 eggs that were less in number. Similarly, an average record of queens is 25 eggs laying per min, 36,000 eggs daily and 13,140,000 eggs per year (Wako, 2015). Matsuura and Kobayashi (2007) also reported that the termites in the North part of Japan begin egg laying in April with a comparative less in number than the eggs laid in July and in October. Alates of *R. speratus* mostly the female paired up with another female partner cooperatively and started to build a new nest, while a single female can also build and start a colony without mating with male adults (Matsuura et al., 2004). Queens *R. speratus* established colonies by parthenogenesis in the Northern parts of Japan (Matsuura and Nishida, 2001; Li et al., 2016c). Moreover, the queen of *R. speratus* in a mature colony laid a total of 24.7 eggs each day, so the rate of egg production was found greater than 0.3 eggs per day. Hence termite fecundity is also related to the season, temperature and humidity. *R. aculabialis* and *R. flaviceps* female-female (RaFF and RfFF) alates firstly laid eggs 35.12±2.59 and 26.64±3.78 days after colony foundation, and the monthly average number of one colony collected eggs respectively were 18.24±3.18 and 11.53±4.51 in August, 11.16±4.26 and 3.67±1.24 in September. The result suggested that *R. aculabialis* parthenogenetically laid more eggs than *R. flaviceps* in two months. While the *R. flaviceps* laid more eggs in August rather than September. There was no difference in the number of eggs produced parthenogenetically and the eggs sexually in *R. chinensis, R. labralis* and *R. speratus*. There was a significant difference in the number of eggs in the two females without the parthenogenetic ability (Xing unpublished data (Li et al., 2016a).

An interaction of termites and fungi (*Fibulorhizoctonia* sp.) are considered as a mutualistic association between them. However, lower termite *R. chinensis* and *R. labralis* use fungi sclerotia within their egg piles in nests. The fungi sclerotia don't germinate in the egg piles under worker observation; whereas *R. aculabialis* have no such a phenomenon to collect sclerotia in their nests; while *R. okinawanus* has no natural association with the fungi that tended termite balls along with its eggs. To date, it has been found egg-mimicking fungus in four *Reticulitermes* termites (*R. miyatakei, R. amamianus*, *R. kanmonensis* and *R. speratus*) in Japan.

2.7. Termite eggs and embryo development

The insect eggshell is principally made of a high concentration of lipoprotein (Velentzas et al., 2018). The thickness of an insect eggshell is ranged between l-70 µm (Church et al., 2019; Isoe et al., 2019). For example, the thickness of the eggshell of *Apis mellifera* is about 0.35-0.43 mm (Wegener et al., 2009). The micropyles on the external surface of the eggshell were observed, which mostly allow the passage of sperm into the eggs and regulate the exchange of gases during the development of embryos (Yanagimachi et al., 2013; Matsuura, 2017). In insect eggshells, there many micropyles were counted between 1-10 (Pijnacker and Godeke, 1984; Iossa et al., 2016). The termite egg has a significant structure on the surface, such as micropyle, which is the passageway of the air into the egg (Gautam et al., 2014; Bowers et al., 2015). The eggs of different termites have different numbers and shapes of micropyles (Church et al., 2019). The structure and distribution features of micropyles on eggshells can be used for insect identification and classification (Ubero-Pascal and Puig, 2007; Hilker and Meiners, 2011).

The termite eggs are oval cylindrical shaped, and micropyles are situated at one end of the egg. The micropyles of *R. speratus* were found in the funnels shape channels, with an average diameter of 3.23 µm and a total number of 9 egg holes. In the nest, the queen produced eggs asexually in the absence or presence of kings who have no holes in the shell to stop fertilization (Pervez, 2018). The eggs produced through sexual reproduction have holes in eggshells. Moreover, the new queens are more preferred to lay non-porous eggs. Such several micropyles in *R. aculabialis* female-female (RaFF), *R. aculabialis* female-male (RaFM), *R. flaviceps* female-female (RfFF), *R. flaviceps* (RfFM) eggs were 6.31±1.89, 8.18±3.22, 8.15±2.67 and 8.43±3.05 respectively. The number of micropyles in RaFF was significantly more than in RfFF, but there was no significant difference among the other group (Xing unpublished data).

Most of the insect males and females are mating through sexual reproduction, the sperm and egg fused to form a zygote. Furthermore, the zygote is divided commonly through cleavage (Hu and Xu, 2005; Vargo et al., 2012; Rhainds, 2019). At the start of cleavage, the zygote produces a great mass of daughter nuclei, which in turn forms the blastoderms (Kawanishi, 1975; Hu and Xu, 2005). At the beginning of the cleavage, the nucleus is mostly located in the centre of the egg and then migrates to the surface of the yolk (Hinton, 1981; Hu and Xu, 2005). Some species are distributed to the periplasm at 64 subnuclei, while some species reach the periplasm at 1024 nuclei (Perondini et al., 1986). The nucleus of a mature egg on cleavage is divided into two daughter nuclei, this is a type of surface cleavage and complete cleavage, while in most insects it belongs to the surface cleavage (Counce and Ruddle, 1969; Illmensee, 1972; Counce, 1973; Kawamura, 2001).

Complete cleavage occurs in insects with a small amount of yolk, such as the *D. melanogaster*, Hymenoptera (Panfilio, 2008). After the formation of the blastoderm, the cells thicken and become more significant to form an embryonic band (Fernandez-Nicolas and Belles, 2017; Benton et al., 2019). There are three types of insect embryos: long embryos in *Drosophila* (Markova et al., 2019), little embryos in termites (Hu and Xu, 2005) and intermediate embryos in bean weevil (Teixeira et al., 2008). Embryos are mainly classified into invaginate and superficial types depending on where the embryonic primordia occur (Tojo and Machida, 1997, Panfilio, 2008). The invagination type is that the embryo develops in the yolk, while the surface type embryo develops on the peripheral surface of the yolk (Hu and Xu, 2005; Corley and Lavine, 2006). The embryonic band forms different germ layers by invagination and expansion, and the segmentation begins when the germinal layer differentiates (Dearden, 2006; Fang et al., 2014; Korb, 2015). The full front end of the embryo develops into the head region (Korb, 2015). A pair of appendage primordia appear on each part of the embryo and develops into an appendage (Maekawa et al., 2008). Both sides of the embryonic band are sealed at the midline of the back. At this point, the various organ systems inside the insect are fully developed, and the embryo is finally developed (Kishimoto and Ando, 1985; Maekawa et al., 2008; Panfilio, 2008). There are characteristic differences in the development of different types of insect embryos. Termites evolved from the order of the Cryptocercus roaches (Bourguignon et al., 2015; Legendre and Grandcolas, 2018), and the cleavage mode of the sexual reproductive embryos is surface cleavage (Kawanishi, 1975). Embryonic development is divided into six stages: cleavage and blastocyst formation, the formation of the blastoderm, embryonic bands, elongation and segmentation, the formation of a tail bend, rotation, closure, and hatching (Hu and Xu, 2005; Maekawa et al., 2008).

2.8. Parthenogenesis of termites

In sexual reproduction, the eggs of insects are activated by the fusion of the sperm and ovum nuclei after completing meiosis (Maekawa et al., 2008), while the eggs develop in some insect individuals without fertilization through parthenogenesis (Rhainds, 2019). Constant parthenogenetic reproduction was found in a few insect species such as stick insects and bees (Morgan-Richards et al., 2010). In insects, the evolution of parthenogenesis includes viz. self-initiating sources, in some moths, aphids, and stick insects (Wei et al., 2000; Balázs and Burg, 1963; Dedryver et al., 2017) and evolution of hybrid in polyploid animals such as moths, sexual reproduction and parthenogenesis play roles in hybridization (Wei et al., 2000).

Facultative parthenogenesis is very important for the maintenance of sex, evolution and is beneficial in a few aspects of sexual and asexual reproduction (Matsuura and Nishida, 2001; Yashiro and Matsuura, 2014; Stelzer, 2015). For a prosperous colony of termite parthenogenesis play, an essential role in the case of females getting a failure to mate with males (Matsuura and Kobayashi, 2007). If the adult female feels the deficiency of males after dispersion flight, it builds a colony with the cooperation of another female partner and achieves parthenogenesis for continuity of the colony. If a single female builds a nest, it must be responsible for the entire work related to the colony (Matsuura and Nishida, 2001; Matsuura et al., 2002a). The rate of survival of female pairing is closely related to the survival rate of male-female pairing due to cooperation between the coupled females that ensure their normal lives and activities in the colony (Matsuura and Nishida, 2001; Matsuura et al., 2002b). Although twice beneficial adaptations are provided by parthenogenetic reproduction comparative sex reproduction. Both genetic and developmental conditions limit parthenogenesis, and the survival rate of its offspring is usually lower than that of sexual reproduction (Corley et al., 1999).

Currently, few Isopteran species have been found with the ability of parthenogenesis (Matsuura and Nishida, 2001; Matsuura, 2017) and asexual reproduction is also used by some propagative termites (Hayashi et al., 2003). Asexual queen succession (AQS) is an exceptional system of termite parthenogenesis (Matsuura et al., 2009). The AQS system has been recognized already all over the world in the termites such as *R. verginicus* and *R. lucifugus* (Vargo et al., 2012; Luchetti et al., 2013), and two higher termites *Cavitermes tuberosus* and *Embiratermes neotenicus* (Fougeyrollas et al., 2015; Fournier et al., 2016). The process of parthenogenesis in lower termites is considered the "end fusion" (Matsuura et al., 2004; Vargo et al., 2012; Matsuura and Kobayashi, 2010), while in higher termites "central fusion" (Fournier et al., 2016).

R. chinensis with asexual queen succession, produced unfertilized eggs can be but have no phenomenon of egg incubation (Li et al., 2016b). Embryonic development between fertilized and unfertilized eggs in two termite species, *R. chinensis* and *R. aculabialis* for external morphology of eggs, cleavage and embryo were observed by using laser scanning and digital microscope. Both types of egg development were compared in two termite species based on size, width, volume, number of nuclei and cleavage in 24 and 48 hrs that had a significant difference in the FF eggs. In contrast on the 15th day, there are no significant changes occurred in the volume of FF egg, whereas the FM egg significantly increased. The FF eggs died on the 15th-20th day, while the FM eggs were in normal development. Similarly, there was no variance in nuclei number between the fertilized and unfertilized eggs of *R. aculabialis*. While the increase of length, width, volume and nuclei number higher in fertilized than unfertilized eggs 10th to 15th day in *R. aculabialis*. Unfertilized eggs of *R. chinensis* can be cleaved with abnormal development and cannot be hatched in the end. The cleavage features of the unfertilized egg of *R. chinensis* may be an adaptive stage from bisexual reproduction to facultative parthenogenesis in termite reproductive evolution (Tan et al., 2016). *R. aculabialis* have the ability of parthenogenesis while *R. flaviceps* which have no parthenogenesis in both morphological and genetic level (Xing unpublished data). Termite colonies are initiated by a couple of sexual reproducers, sometimes that are replaced by some asexual queens of *Reticulitermes* and *Embiratermes*. Asexual queen succession (*Cavitermes tuberosus*) is also replaced by neotenic daughters, as they were produced by parthenogenesis, which is finally ready to mate with the primary king. Here, to cast light on the evolution of AQS, we investigated another candidate species (Fournier et al., 2016).

2.9. Termite hybridization

Hybridization is a reproductive behavioural phenomenon that commonly occurs between the two species of termites that genetically came from distinct populations (Kuswanto et al., 2015; Chouvenc et al., 2015). They cause genetically interactions of offspring inherited from two parents possibly from different species genetically (Su et al., 2017; Buczkowski and Bertelsmeier, 2017). This variation contains some moderate distinction, accumulates in different ways and is compatible and successful ecologically, overlapped with a new economic influence on the world, some of which are produced by connections between hybrids (Patel et al., 2019).

Heterozygous domains resulting from hybridization have favourable ecological and evolutionary consequences than the parental populations (Roberts et al., 2009; Patel et al., 2019). The resultant progeny from hybridization have dominant effects and promote species dispersion in a wide range in few regions, such an example came from the two invasive fire ant species (*Solenopsis richteri*×*S. invicta*) in the Southern United States where they established a fully hybrid zone now (Gibbons and Simberloff, 2005; Chen et al., 2015) and another one from the subspecies of *A. mellifera* (European honey bee × Africanized honey bee) became trouble for human population in South and North part of America (Schneider et al., 2004; Jensen et al., 2005; Vanengelsdorp and Meixner, 2010).

While the hybridization hinders species formation due to the flow of genes between species with diverse ploidy levels is understood to be improbable, such species are expected to be reproductively isolated from one another due to strong reproductive barriers (Todesco et al., 2016).

Hybridization of organisms enhances the chances of species adaptability and living under severe environmental factors (Pfennig, 2007; Pfennig et al., 2016) and produce variation in offspring that have more advantages over the parents in terms of adaptability, viability, growth potential and stress resistance, especially in the plant kingdom (Mesgaran et al., 2016). Hybridization occurs in various ecological and environmental zones between the nearby population's boundaries that allow the dispersion flight in common period and transmission of the hybrid genome (Harrison and Harrison, 1993; Chunco, 2014). Many crosses occur in regions where territories are closed and intermixed, and these new phenotypes are adapted to the native environment (Chunco, 2014).

There are also gene interactions that occur among the native inhabitants, such as parasites interaction among the herbivorous arthropods (Šimková et al., 2013). There is no standard spatial isolation scale for the measurement of hybridization, but it is dependent on interference from distribution or habitats (Waits et al., 2001; Seifert et al., 2016). Hybridization related to the contacts of parental populations on the boundaries and their population growth may either two native species or invasive species, and the other is a native one, have been recognized in a wide range of organisms (Harbicht et al., 2014; Wielstra et al., 2016). Hybridization increases the chances of adjustments and adaptability of parental populations by differentiation through genes combination and also produces new descendants that are mixed to a level of two ancestral populations but still divergent from the parental population (Abbott et al., 2010; Wielstra et al., 2016).

In organisms, the nature and habits of species are highly restricted and conserved (Chunco, 2014; Matsuura, 2005), and crosses between diverse species often result in reproductive barriers. Reproductive isolation includes pre-zygotic and post-zygotic barriers (Turissini et al., 2018). Pre-zygotic isolation is considered morphology, feeding, breeding season, geography and ecology (Ma et al., 2016). The parents may not become closed for mating and fertilization properly, to produce offspring due to a reasonable gap in a few important parameters (Lowry, 2012).

There are also many ways to segregate post-zygotic barriers, such as gamete isolation, developmental isolation, early death of hybrid embryos, hybrid infertility and poor adaptability and adjustment of hybrids descendants (Palumbi, 1994; Presgraves, 2010). The interactions were found restricted between soldiers and workers from matured colonies, where individuals showed interspecies competence and agonism for the resources access (Du et al., 2016). While the interspecies competition of members from the alates has not yet been examined (Chouvenc et al., 2015).

Hybridization is a characteristic consequence that happened among many species of organisms (Abbott et al., 2013) and also found in a few cross-breeding studies on termites such as *R. lucifugus* and *Z. nevadensis* (Aldrich and Kambhampati, 2009), *N. corniger* (Hartke and Rosengaus, 2011). Chouvenc et al. (2015) observed the *C. formosanus* and *C. gestroi* dispersal flight seasons overlapped of both species for the first time in 2013-2014, their hybridization in the wild at the Southern United States, and the number of offspring was double than the parental species of mating colonies after eighteen months. The vitality and number of offspring were advantageous in interspecific cross-breeding (Chouvenc et al., 2015; Su et al., 2017). These results suggested that the wingless males are heterogeneous, healthy, heavy, and well-known with the environment in *R. chinensis*. They have noticeable advantages in the choice of mate. This principle of mate choice is supportive for termites to evade inbreeding and to continue the genetic change of offspring, which is very significant for the ecological adaptability and expansion of termite colonies (Li et al., 2013a; Farnesi et al., 2015). Whether hybridization was found between two termites viz. *R. flaviceps* and *R. chinensis* under laboratory conditions. The frequencies of acceptance were found significantly higher than that of agonism between interspecies partners. There were no important alterations in occurrences of tandem and mating manners between interspecific and intraspecific partners. However, the allogrooming frequencies of intraspecific partners were importantly lower than interspecific partners. There were no important changes in the time of tandem, mating behaviour, or allogrooming at each time between heterospecific partners and conspecific partners. Additionally, genotypic and morphological analyses exposed that interspecific and intraspecific mating was capable to produce offspring (Wu et al., 2019, Khan et al., 2021a). *R. aculabialis* and *R. flaviceps* can also be hybrid under laboratory experiments (Khan et al., 2021b).

3 Conclusion

Briefly, hybridization and parthenogenesis are the additional reproductive behaviours of termites to achieve more advantages for successful adaptation in a challenging environment. These reproductive advancements of Isoptera have threatened the economy of China. As spreading by sexual reproduction, hybridization and parthenogenesis they can invade new regions and cause more damages to buildings in urban areas, trees and crops. Sufficient importance is needed for effective control and prevention of termite invasion in new areas of economic importance. Hence, a large number of laid eggs, increase embryonic development, survival ship of parthenogenetic and hybridized offspring make them more competent to utilize Chinese resources. This study means to investigate the species, type of reproductive behaviour, egg numbers, micropyle numbers, eggshell, rate of embryonic development, progeny, the season of reproduction, and dispersion flight of *Reticulitermes* termites. They are abundant and responsible for approximately 2 billion RMB annually equivalent to the US $ 217 million.

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