

Nest structure of the bark-digging ant *Rhopalomastix* (Formicidae, Myrmicinae) and notes on its mutualistic associations with diaspidids in a Thai mango plantation

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ABSTRACT. *Rhopalomastix* is a bark digger ant that nests in the bark of living trees. The ants share a mutualistic relationship with diaspidids (armoured scale insects), housing them in their nest tunnels in the bark of a tree. Two colonies of *Rhopalomastix sp.* were sampled from two cultivars of mango trees in a mango plantation in Thailand. The architecture of the nest was mapped out and the respective resident diaspidid partners collected. *Rhopalomastix* built two different types of tunnels, one chewed through the live wood while the other was created by covering fissures in the bark with a frass roof. Tunnels were constructed at different depths and were inter-connected to form a complex network. Ant brood and diaspidids were not evenly distributed, with most found in deeper and wider chewed tunnels. A new species of pupillarial diaspidid, *Ligaspsis sp.* was found in both colonies - this is the second report of a pupillarial diaspidid being associated with *Rhopalomastix*. We discuss the trophic relationship between ants and their diaspidid partners, and the potential impact this association has on host fruit trees.

Keywords Fruit, ant-plant, *Ligaspsis*, pupillarial

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INTRODUCTION

Rhopalomastix is an arboreal myrmicine ant that nests in the bark of trees throughout tropical Asia (Wang et al. 2018). A total of five species of *Rhopalomastix* have been identified from Thailand (Wang et al. 2021). Armoured scale insects (Di-

aspididae) have been found to be living within its dug tunnels, with five different genera found living with four different species of ants in Singapore (Yong et al. 2019). The diaspidids and ants form a mutualism, where ants provide diaspidids shelter and protection from predation while the diaspidids provide the ants with food. Glands for

shield secretions remain functional in diaspidids living in ant nests, providing wax and proteins as food for the ants. The exuviae of developing diaspidids were also found to be missing in ant associated diaspidids and could have been eaten by the ants (Peeters et. al 2017, Yong et. al 2019). In some cases, the flesh of the diaspidid has also been suggested to be harvested by the ants as food (Fisher & Robertson 1999, Ben-Dov 2010; Schneider et al. 2013, Yong et. al 2019).

Like its sister genus *Melissotarsus*, *Rhopalomastix* possess large opener and closer muscles in its head that allows it to chew live wood in the bark of living trees to build its nest (Khalife et. al 2018). This is different from ant-myrmecophyte associations, whereby the myrmecophyte host possess special structures such as hollow stems for ants to nest in (Fiala et. al 1989, 1994; Janzen 1966, 1969). Owing to the bark-digging nature of *Rhopalomastix*, they can construct a complex network of tunnels and chambers in the cork cambium layer (Yong et. al 2019) to house their brood and diaspidid partners. Ants like *Camponotus* (Tschinkel 2005), *Acromyrmex* (Verza et. al 2020) and *Formica* (Mikheyev and Tschinkel 2004) have been documented to con-

struct a complex maze of tunnels underground, with chambers and tunnels for different purposes. While the distribution and composition of tunnels and chambers within these subterranean nests are well-documented, little is known about the nest architecture of ants living in live bark. Hence, the ability of *Rhopalomastix* to chew tunnels in wood of a living tree provides a rare opportunity to study ant nest architecture in a different substrate, and also provides a more intimate look at the ant's association with diaspidids.

Out of the 12 colonies previously studied in Singapore (Yong et. al 2019), almost half were found in fruit trees like durian (*Durio zibethinus*) and mango (*Mangifera sp.*). Hence, a mango plantation in Thailand was chosen as a suitable site to gain a better understanding of the potential implications of such a relationship on fruit trees. In this study, we map out the nest structure of two *Rhopalomastix* nests in mango trees from the plantation, illustrating the distribution of tunnels, ant brood and diaspidids within a typical nest. The mutualistic relationship between the ants and its pupillarial diaspidid partner, *Ligaspsis sp.* is described, and the impact of this relationship on fruit trees is discussed.



Fig. 1. – Branch from the Khieo Sawoei mango tree. Vertical frass lines observed along the branch. Image by Gordon Yong.

MATERIALS AND METHODS

Study area and organisms

Two colonies of *Rhopalomastix* were sampled from a private mango plantation (~17.5 ha) in Cha-Om, Khaeng Khoi district, Saraburi province, Thailand from 6 to 11 December 2018. Each colony was found inhabiting a different mango tree (*Mangifera sp.*) belonging to two different cultivars – ‘Falan’ and ‘Khieo Sawoei’. The two varieties of mangoes were identified by the owner of the plantation, Dr Pitchaya Pothinuch. Both mango trees had a maximum height of 15 metres and both were observed to be fruiting healthily. We sampled the bark of trunks from the roots at the base of the trunk to branches up to 4 m above ground. The leaves and external surface of the branches of each tree were also checked for presence of diaspidids. One branch was cut from each tree and brought back to the laboratory for further observations. The branch from Falan was 42 cm in length, and had an average diameter of 21 cm. The branch from Khieo Sawoei was 27 cm in length with an average diameter of 12 cm (Fig. 1).

In the laboratory, small sections on each branch were isolated. The inner layer of bark of these isolated sections was carefully shaved off to expose the spatial distribution of the ant tunnels, brood and diaspidids. Drawings of the nest architecture were made. Behavioural observations were also conducted after exposing the ant tunnels.

Identification of ants and diaspidids

Rhopalomastix ants were identified to be from the *Rhopalomastix rothneyi* species group (Wheeler 1929) using taxonomic keys from Wang et al. (2018). Voucher specimens were deposited in the Lee Kong Chian Natural History Museum, Singapore. The diaspidids were identified by Danièle Matile-Ferrero to be a new species belonging to the genus *Ligaspis* (Matile-Ferrero in prep.). Diaspidid vouchers were deposited in the Muséum National d’Histoire Naturelle, Paris.

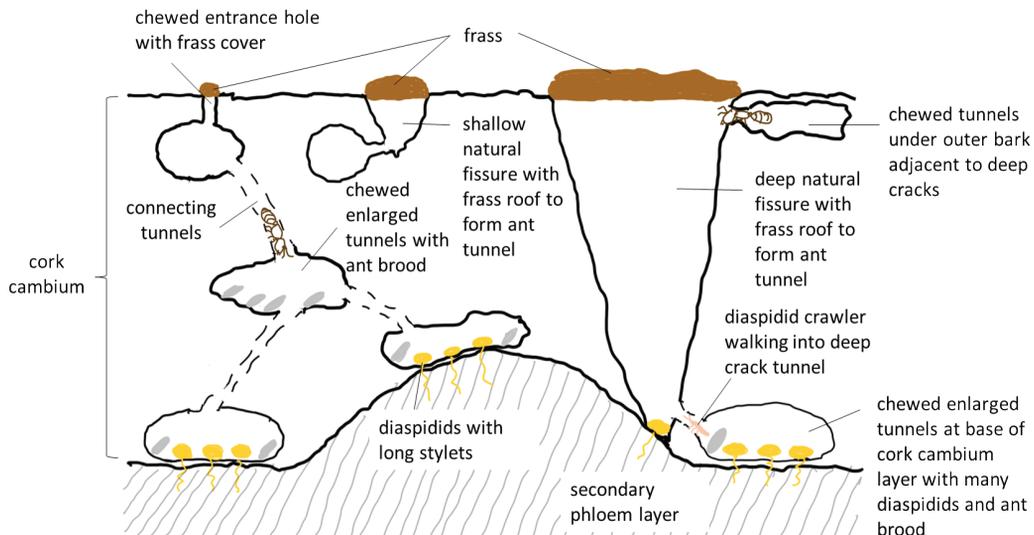


Fig. 2. – Illustration of the nest architecture of *Rhopalomastix* in mango bark. Thickness of cork cambium layer is uneven. Two types of tunnels are built, one chewed in cork cambium, the other being bark fissures covered by frass roofs. Tunnels are interconnected, with most diaspidids found in deepest tunnels closest to secondary phloem layer. Entrance hole covered by frass.



Fig. 3. – Frass covering vertical fissures in the bark of the main trunk of Falan mango tree. Image by Christian Peeters.

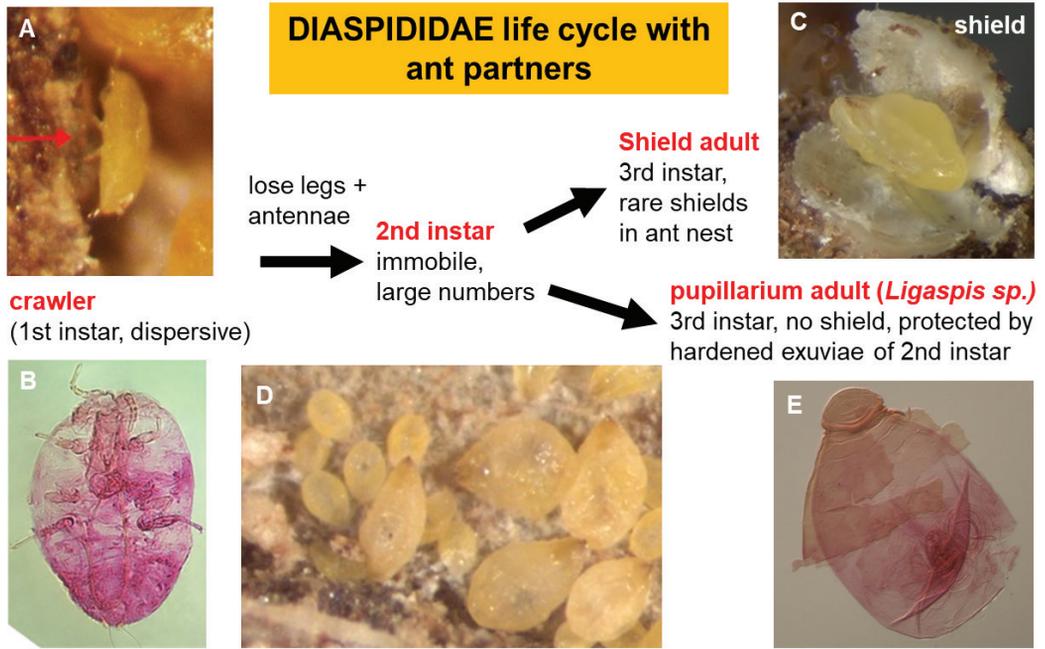


Fig. 4. – (A & B) Diaspidids start their life as a mobile crawler that are able to disperse by walking to new areas within the nest. They then settle down and stop moving, in the process losing their legs and antennae as they develop into the second instar. (C) In free-living diaspidids outside the ant nest, these second instar are often protected by shields. (D) However, in the ant nest, the diaspidids develop into naked third instar adults with only very few adults developing shields in the process. (E) Pupillarial diaspidids like *Ligaspsis* do not develop shields in the free-living form or in ant nests, growing within the pupillarium of the second instar adult instead.

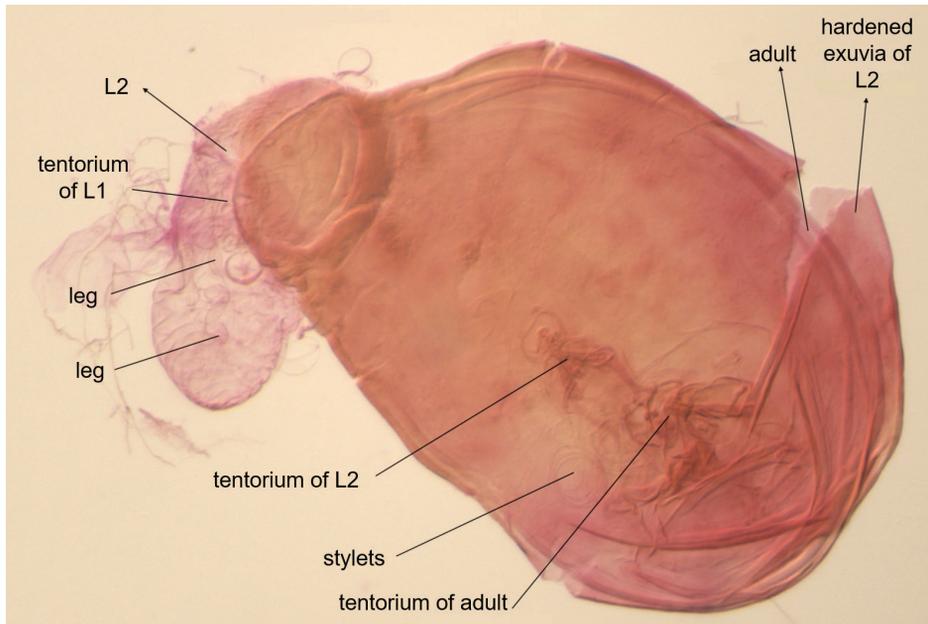


Fig. 5. – Mounted *Ligaspsis sp.* Unlike most Diaspididae, ‘pupillarial’ adult females develop and lay eggs within the enlarged and hardened exuvia of the second instar (L2). A crawler (L1) had just emerged from the adult female (L2). Unlike the adult female (L2) the crawler has legs and is able to walk, allowing it to disperse. The tentorium of both crawler and adult are visible. The long, coiled stylets of the adult is visible. Image by Christian Peeters.



Fig. 6. – Aggregation of freshly moulted second instar *Ligaspis* sp inside a tunnel of the *Rhopalomastix rothneyi* species group from the Khieo Sawoei branch. Circle shows a single long stylet of a diaspidid that had pierced into the secondary phloem layer. Image by Christian Peeters.

RESULTS

Rhopalomastix nest structure

Ant tunnels were found in the cork cambium layer of the inner bark in both cultivars. Two different types of ant tunnels were observed. The first type were tunnels chewed by the ants in the cork cambium layer where no fissures in the bark were observed. The second type were tunnels found along fissures of the bark. These tunnels were formed by the covering of these fissures with frass to form a roof (Fig. 2). This frass roof gives rise to the distinctive lines of frass observed on the outermost surface of bark for both cultivars. The lines of frass mostly ran parallel to the branch (Fig. 1) or trunk (Fig. 3).

In the Khieo Sawoei (KSW) branch, narrow lines of frass covered fine fissures to form narrow and shallow tunnels. No ant broods were found in these narrower and shallower tunnels.

Ant broods were instead found in bigger and deeper chewed tunnels in sections of bark adjacent to these frass lines (Fig. 2). In the Falan branch, deep fissures covered by frass were observed running parallel to the branch. Some ant brood were found in these fissures while most were found in chewed tunnels adjacent to these frass lines (Fig. 2). In both branches, tunnels were observed to be chewed at different depths in the cork cambium but not extending into the secondary phloem layer. Narrow tunnels linked sections of the nest at different depths (Fig. 2).

The extent of ant tunnels started at the base of the KSW tree just above the soil. Ant tunnels were observed on the main trunk of the Falan tree 4 m above the ground. Tunnels were not found in the bark of the roots of both cultivars. Moss was observed growing over parts of both branches. Tunnels were found in the cork cambium layer under the moss mat. Some frass was

found mixed with the mat of moss for both cultivars. An entrance hole connecting the external environment to the tunnels in the cork cambium layer was observed in the moss area of the Falan branch. The entrance was covered by a small aggregate of frass that was attached by some silk on one end to the bark surface. The aggregate could be easily moved to expose the entrance but stayed firmly attached to the bark surface without dropping off.

Association with diaspidids

No diaspidids were found on the leaves and external surface of the branches of either tree. Diaspidids were found living inside the tunnels of both branches. Diaspidids start life as mobile crawlers that are able to disperse by walking to new areas within the nest. They then settle down and stop moving, in the process losing their legs and antennae as they develop into the second instar. In free-living diaspidids outside the ant nest, these second instars are often protected by shields which they produce (Foldi 1990). However, diaspidids living in ant nests develop into third instar adults with only very few adults developing shields in the process (Yong et. al 2019). Some genera of diaspidids do not develop shields even in free-living species (Fig. 4); these species show pupillarial development, where the adult female is entirely enclosed within enlarged and sclerotised exuvia cast by the second instar (Takagi 2002).

Diaspidids found in the tunnels of both Falan and Khieo Sawoei (KSW) colonies were determined to be of the genus *Ligaspiis* (Aspidiotinae, tribe Parlatoriini) which exhibits pupillarial development. Takagi (2002) recorded two species of *Ligaspiis* from Luzon, the Philippines. Both species were found living on different nut trees (*Semecarpus cuneiformis*). However, the association with *Rhopalomastix* was not recorded in that study. In our study, we found many second instar females and adult females. Sixteen slide-mounted adult females revealed 10 crawlers within the pupillarial exuvia (Fig. 5). In the Falan branch, three crawlers were observed to walk into and subsequently along a tunnel formed from frass covering a deep crack in the outer bark. The crawlers entered the deep crack from connecting chewed tunnels in adjacent sections of bark (Fig. 2).

Diaspidid stylets were observed to be over 2 mm long and penetrated the cork cambium into the secondary phloem layer (Fig. 2 and Fig. 6). Diaspidids were present throughout all the tunnels but were more commonly found at the base of deeper tunnels just above the secondary phloem layer. In the KSW branch, aggregations of diaspidids were not found in the shallow and narrow tunnels formed from fissures in the bark. Diaspidids were only found in the deeper chewed tunnels in adjacent regions. In the Falan branch, only a small number of diaspidids were found in tunnels formed from deep fissures, while a larger number were found in the chewed tunnels in regions adjacent to these fissures.

Ant behaviour

In the Khieo Sawoei (KSW) colony, we observed “tidying” behaviour when the tunnels were exposed in a fragment of bark. Several second instar diaspidids in the exposed regions of the nest were completely pulled out from their fixed positions by the ants, exposing their long stylets in the process. Ants struggled in the process of removal, taking roughly one minute to remove each diaspidid from their fixed spot. The ants then ‘packaged’ the diaspidids together using orally-spewed silk strands and the whole package was thrown over the edge of the fragment. Both forelegs of *Rhopalomastix* were observed to be used during silk spinning. The legs moved in a circular motion under their mandibles, drawing out silk strands from silk glands in the head (Billen & Peeters 2020).

DISCUSSION

Our study sheds light on the internal nest structure of enigmatic bark-digging *Rhopalomastix* ants and their mutualistic associations with diaspidid partners. We confirmed that *Rhopalomastix* lives together with diaspidids in a nest constructed in the bark of living trees (Yong et. al 2019). In our sample of two nests, we observed two different types of tunnels. The first are chewed tunnels in the cork cambium layer which are subsequently used as nest chambers to store ant brood and diaspidid partners. These tunnels were found entirely within the cork cambium layer and are hence did not have frass roofs and were not exposed to the external environment.

A second type of tunnel constructed by *Rhopalomastix* ants are made using frass roofs to cover and enclose exposed fissures in the bark. These fissures can form naturally when bark layers tear under pressure from the radial expansion of new tissues beneath. These fissure tunnels may also have been created as a result of the chewing of tunnels under the bark which weakens the bark layer, causing it to tear more easily when the tree grows. Bark fissures are used by many other arthropods as a space to traverse between the canopy and the soil (MacFarlane & Luo 2009). *Rhopalomastix* may use these enclosed fissures for a similar purpose, as tunnels to connect to other parts of the nest (Fig. 2). The use of fissures in the bark also reduces the need for the ants to create new tunnels by chewing more healthy wood, which has elastic fibres that are hard to break down (Aicher and Stapf 2016). This is important as nest construction is an energy intensive affair, requiring up to 20% of a colony's energy in soil dwelling ants (Mikheyev and Tschinkel 2004). The energy requirement is likely to be even higher in the case of *Rhopalomastix* due to the need to use its large opener and closer muscles in its head (Khalife et. al 2018) to chew through live wood during nest construction. Hence, incorporating these fissures in the bark in the nest architecture may allow the ant colony to optimise energy usage to chew tunnels in other areas of the bark.

Tunnels made using these fissures were also found to house few diaspidids or ant brood. This could be due to the fragility of the frass roof, which is made up of chewed bark mixed with silk (Yong et. al 2019). These roofs can be removed with little effort compared to the stronger and more durable cork cambium layer. *Pheidole sp.*, *Crematogaster sewardi* and *Tetramorium sp.* ants were observed to quickly grab ant brood when the tunnels were exposed in the field (Yong et. al 2019). This makes it highly risky for precious ant brood to be housed under the more fragile frass roofs. Hence, these fissure tunnels could primarily serve the function as connection passageways between neighbouring patches of dug tunnels in the larger bark cork cambium matrix.

Rhopalomastix digs extensively into the cork cambium layer of the bark, creating a complex network of tunnels (Yong et. al 2019).

Dug tunnels and fissure tunnels were found to be connected, with dug tunnels connecting to deep fissures at different depths. Dug tunnels of different depths were also found to be interconnected through vertical tunnels (Fig. 2) giving rise to a complex network of vertical and horizontal tunnels within the cork cambium layer. This is similar to subterranean ant nest architecture, where many chambers of different depths are connected to each other and the surface via tunnels (Moreira et al. 2004).

The depth of tunnels was associated with different contents found within them. Diaspidids were absent in shallow tunnels that were further away from the secondary phloem layer. Aggregations of diaspidids were instead found in deeper tunnels closer to the secondary phloem layer. While diaspidids never move once their stylets are inserted into the plant tissue, individuals at the mobile crawler stage were observed to walk within the tunnels (Fig. 2). This suggests that the crawlers can choose the tunnels to insert their stylets and may prefer deeper tunnels closer to the secondary phloem layer. Hence, the tunnels dug by *Rhopalomastix* may bring diaspidids closer to the parenchyma tissues in the secondary phloem, providing them with greater accessibility to their food source for easier feeding. This adds to other benefits provided by the ants in this mutualism that was previously studied, namely protection from weather and predation (Yong et. al 2019).

A good understanding of diaspidid biology is needed to assess the benefits of the mutualism between ants and armoured scale insects. This is the second record of *Rhopalomastix* association with a pupillarial diaspidid, the first being with *Fiorinia* in Singapore (Yong et. al 2019). Pupillarial diaspidids have smaller wax-secreting ducts and glands as they do not produce typical waxy cover for protection (Takagi 2002; Suh 2012). Instead, adult females develop inside hardened exuvia of the second instar, also known as a 'pupillarium'. New crawlers develop and eventually emerge from this pupillarium (Fig. 5). This kind of development means lower food availability to ants in terms of wax and protein secretions, unlike other non-pupillarial diaspidids which can feed on these secretions for food. Hence, the only trophic benefit to ants would be through predation on pupillarial diaspidids.

While we did not directly observe ants feeding on second instars, the presence of large numbers of pupillarial adults in the nest suggests that the ants feed on second instar diaspidids, sparing the pupillarial adults as progenitors. Hence, we expect that *Rhopalomastix* ants can obtain trophic benefits from the wax secretions, exuviae and flesh of second instar depending on the type of diaspidid partner found in its nest.

The “tidying” behaviour observed also shows that ants are able to pull diaspidids out of their fixed positions. This would allow ants to transport removed diaspidids to tunnels containing ant brood for feeding. This would also allow ants to remove any damaged or unwanted diaspidids from the nest. This “culling” action was also observed in *Melissotarsus* (Schneider et al. 2013) and is fatal to the diaspidid adults, as their stylets cannot be reinserted and are no longer embedded in the secondary phloem layer, depriving them access to parenchymal tissues for food. This behaviour suggest that ants have the ability to actively choose and “farm” their diaspidid partners by removing undesirable individuals from their nest while keeping others for food.

Successful ant-scale-insect mutualisms have been presumed to impact tree health (Handler et al. 2007). *Melissotarsus* was suggested to have a negative impact on commercial fruit trees in South Africa due to its highly populous colonies (Mony et al. 2002). The bark of this mango tree was thickened (up to 10 cm) and riddled with tunnels of ants like a sponge as a result (Mony et al. 2002). This was not the case for mango trees inhabited by *Rhopalomastix* observed in this study. The bark of inhabited mango trees varied in thickness. While chewed tunnels were extensive in some patches of the tree, there were large sections of the tree that were without any ants or tunnels. Furthermore, it was noted that the mango trees with *Rhopalomastix* in the plantation showed little signs of stress and were able to grow to maturity, producing fruits in the process. However, our sample size of two trees can only provide limited qualitative evidence on the impact of this mutualism on mango trees. Future studies must look at a greater geographical range and sample size to better assess the potential economic implications of such mutualisms on fruit plantations.

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