



Bamboo sap ejection from the nests of *Tetraoponera binghami* (Hymenoptera: Formicidae: Pseudomyrmecinae) and the role of flood control in arboreal ants

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Abstract

Some tree-dwelling ants that live in plant cavities are known to use flood defences to prevent flooding of their nests by rain or seawater. Here, we report for the first time on a flood-defence technique used by the South-East Asian ant *Tetraoponera binghami* to prevent flooding of its nest by bamboo sap. *Tetraoponera binghami* workers bite entry holes into the walls of bamboo culm shoots of *Dendrocalamus*, *Gigantochloa*, and *Cephalostachyum* in order to nest in their cavities. As sap oozes from the damaged vascular bundles into the newly created entry holes, the internode cavities are at risk of flooding. To prevent this, *T. binghami* workers remain in the tubular entrance holes and expel the intruding sap from the nest with rapid pumping movements of their gaster. Meanwhile, they are immersed in the bamboo sap, and their bodies are partially enveloped in a layer of air held in place by hydrofuge hairs. We discuss how the unique sap ejection behaviour of *T. binghami* works and review other flood control methods used by arboreal ants. We propose that sophisticated flood control methods have evolved only in arboreal ants that nest in cavities in living plants that can hold water and have a nest entrance hole of the right size. Other factors, such as the amount of water run-off, the characteristics of the nest substrate, and the evolutionary history of the ants also influence the occurrence of flood control behaviour.

Key words: Bamboo-internode nest, nest flooding, flood defence, abdominal pumping, hydrofuge hairs.

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Introduction

Terrestrial ants have developed a variety of methods to prevent nest flooding. For example, they build nests on elevated sites, design them to facilitate the drainage of seepage water, and when nests are flooded, they seal the entrances, form floating rafts, or migrate to dry areas. Ants can also survive submerged for some time, either in nest tunnels with trapped air or in direct contact with water (reviewed in HÖLLDOBLER & WILSON 1990, NIELSEN 2011).

Some arboreal species that live in plant cavities have developed other ways to prevent their nests from being flooded by rainwater: (1) *Cataulacus muticus* is known to reduce the inflow of water into its nest by blocking the entrance hole with its head (MASCHWITZ & al. 2000), (2) *C. muticus* drinks excess rainwater and defecates outside the nest (MASCHWITZ & MOOG 2000), (3) *Camponotus* sp. workers drain artificially flooded nests by carrying

water droplets adhering to their bodies out of the nest (FEDERLE & al. 1998), and (4) *Tetraoponera binghami* and several *Cladomyrma* species ingest excess rainwater and regurgitate it outside the nest (KLEIN & al. 1993, MOOG & al. 1997). A special case is the Australian *Colobopsis anderseni* (synonym *Camponotus anderseni*, see WARD & al. 2016), which lives in the thin branches of the mangrove tree *Sonneratia alba*. Its nests, located in the lower parts of the trees, are flooded at high tide. To prevent seawater from entering the nest cavity during flooding, a soldier or the queen blocks the entrance hole with her head (NIELSEN 2000, 2011).

In the present study, we report on a newly observed technique for preventing flooding by plant sap in the arboreal ant *Tetraoponera binghami*. This species nests exclusively in the hollows of living bamboo culms and

is distributed from Nepal to the Malay Peninsula. Other *Tetraponera* species are found in the tropical Old World and Australia. They inhabit cavities in dead twigs and branches, some are facultative colonisers of living plants, and a few species live in symbiosis with myrmecophytes (WARD 2001, DJIÉTO-LORDON & al. 2005, DEJEAN & al. 2008).

Colonies of *Tetraponera binghami* are monogynous and can number several thousand individuals, nesting in numerous bamboo internodes of several adjacent culms (BUSCHINGER & al. 1994, KLEIN & al. 1994). The colony feeds on the honeydew of the phloem-sucking mealy bug *Kermicus wroughtoni* (Pseudococcidae), which is brought into the internode cavity nests by colony-founding queens (KLEIN & al. 1992). Workers are timid and rarely leave their nest in order to defecate, to scavenge plant material, faeces, or dead arthropods, or to visit other nest cavities in the same colony (KLEIN & al. 1994). Because workers extract phloem sap from their host plants via the mealybugs and do not protect their plant from herbivores or other plants, they have been considered as parasites of their host plants (DOROW & MASCHWITZ 1990, SCHELLERICH-KAADEN & al. 1997, MASCHWITZ & al. 2000).

Here, we describe how *Tetraponera binghami* workers bite new entry holes in culm shoots (= young shoots that have grown to several meters in height), expel the bamboo sap that oozes out of the newly created holes, and discuss the function of this behaviour. We also review the flood-defence behaviour known from other arboreal ants and discuss the factors responsible for its evolution.

Materials and methods

The first observations of *Tetraponera binghami* biting holes in culm shoots and removing sap from nest entrances were made by DK during the Malaysian Nature Society's Belum Expedition in 1993 (Temengor Forest Reserve, Hulu Perak, Peninsular Malaysia, 5° 19' 58" N, 101° 22' 03" E) and later at the Ulu Gombak Field Studies Centre, University of Malaya, near Kuala Lumpur (3° 19' 33" N, 101° 45' 17" E) in 1993 and 1994. Subsequent observations, including experiments with submerged ants, were conducted in northern Thailand, Pangmapha District, Mae Hong Son Province (19° 30' 57" N, 98° 15' 15" E) in 2008 and 2014. Observations were made between August and January in peninsular Malaysia and between September and March in northern Thailand. The rainy season was between August and November in peninsular Malaysia and between June and October in northern Thailand. The first bamboo shoots started to grow in August (peninsular Malaysia) and June (northern Thailand).

The length of the culm shoots and internodes colonised by *Tetraponera binghami* was measured with a tape measure, and the diameter, wall thickness, and size of the entrance holes were measured with callipers. Thin wooden sticks were inserted into the holes made by *T. binghami* to measure their depth. A Zeiss[®] (Oberkochen, Germany) prism head lens F (8 ×) was used to observe the sap-expelling ants on the stem surface and a rigid endoscope to

observe them inside the internode cavity. The endoscope was 23 cm long, 8 mm in diameter and the viewing directions were 0° and 90°. It was equipped with a light source powered by a portable rechargeable battery. For insertion of the endoscope tube, artificial holes (diameter: 9 mm) were drilled in the internode nests perpendicular to the entrance hole. The observation holes were closed with plastic plugs when not in use. To assess their suitability as entry holes for *T. binghami*, artificial holes were drilled in the intact internodes of mature bamboo culms near the *T. binghami* nests. The holes were 2 mm and 5 mm in diameter and remained open throughout.

To determine the exact allocation of the air layer observed in sap-expelling ants, 10 *Tetraponera binghami* were held by the mesosoma with forceps and immersed in water under an Olympus SZH stereomicroscope. Hydrofuge hairs occurring on the body surface of *T. binghami* specimens were examined by using a Hitachi CamScan CS24 scanning electron microscope (SEM). For SEM examination, specimens stored in 70% ethanol were dehydrated in a graded series of ethanol solutions and then transferred to hexamethyldisilazane (= HMDS; NATION 1983). The HMDS containing the samples was then allowed to evaporate under a fume hood. Dried samples were mounted on stubs, coated with palladium gold, and examined by SEM. The species was identified using the key to the species of the Oriental and Australian *Tetraponera* species (WARD 2001).

Results

Habitat and creation of nest entry holes

Tetraponera binghami workers lived in culm shoots and mature bamboo culms of *Gigantochloa latifolia* and *Gigantochloa scortechinii* in peninsular Malaysia, and *Dendrocalamus strictus* and *Cephalostachyum pergracile* in northern Thailand. Culm shoots of *G. scortechinii* newly colonised by *T. binghami* were 3.20 - 7.00 m tall (n = 6), whereas mature culms were about 20 m tall (n = 20). Internodes occupied by *T. binghami* were about 30 cm long, 8 - 10 cm in diameter, and the thickness of the internode walls was about 1.2 cm (n = 20).

Individuals of *Tetraponera binghami* were able to make holes in the walls of immature bamboo culms by themselves (Fig. 1A, B). Up to 17 workers gathered around the hole and took turns to penetrate the bamboo wall (Fig. 1A). As a worker ant bit off pieces of the bamboo wall, it rotated around the hole. The bites were thrown to the ground every 3 - 4 minutes. Sometimes, the chewing worker ant would crawl backwards out of the unfinished hole and clean its head. Holes were made during the day (n ≥ 20). On two days, boring was observed once an hour between 8.00 and 21.00 h, but the ants were only active between 10.45 and 17.25 h. Entry holes were completed after 5 - 6 days (n = 3), that is, the ants advanced towards the internode cavity at a rate of about 2 - 3 mm per day. Workers were less numerous and active on rainy days.

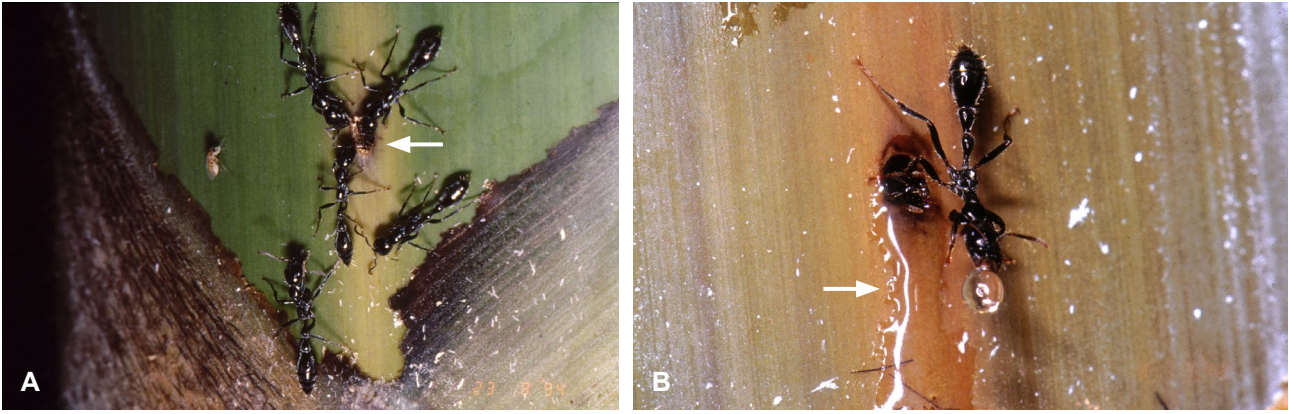


Fig. 1: *Tetraponera binghami* workers biting a nest entry hole and expelling bamboo sap. A: Worker ants (length about 9 - 10 mm) biting a nest entry hole in a bamboo shoot culm of *Gigantochloa scortechinii* in Peninsular Malaysia. The arrow points to the newly made hole. B: A worker ant ejects bamboo sap from a nest entrance hole at night. The head protrudes from the hole and a trickle of sap flows down the surface of the bamboo (arrow). A fellow worker ant stands on the surface of the bamboo next to the entrance hole and helps to remove the expelled bamboo sap by ingesting it and regurgitating the sap droplets onto the ground.

Tetraponera binghami entry holes were made in the lower, already elongated internodes of shoots. The holes were located approximately in the middle of the internode, usually within the triangular area formed by the overlapping culm sheaths (Fig. 2, left). There was only one entry hole per internode. The outer opening of the entrance hole was round to slightly oval and 1.6 to 1.8 mm in diameter ($n = 5$). The size of the inner opening of the entrance hole was larger than the outer opening and bell-shaped (Fig. 2, middle and right).

On one occasion, *Tetraponera binghami* workers started to bore a hole in a mature bamboo culm of *Gigantochloa scortechinii*. The ants were forced to find a new nest as their culm had been felled and their internode nests damaged. With no shoots available in Peninsular Malaysia in early June, the ants began chewing a hole in a nearby mature bamboo culm (branches and leaves already present) that was about a year old. After eleven consecutive days, the hole-boring ants had reached a depth of 5 mm (wall thickness about 10 mm). On the twelfth day, the site was abandoned, probably because the ants had found a more accessible internode. The workers making the hole in the mature bamboo culm were active day and night (last observation at 1:30 h), unlike the workers penetrating immature culms, who were only active during the day.

Occasionally, *Tetraponera binghami* took over entrance holes newly made by the beetle larvae of *Lasiochila goryi* (Chrysomelidae; $n = 4$). These entrance holes were oval, about 1 - 2 mm high and 1 mm wide, and occurred at the same place on the internodium as the holes made by *T. binghami* (see SCHILLHAMMER & KOVAC 2023). *Tetraponera binghami* workers slightly widened the entrance of *L. goryi* and enlarged the internal opening of the tube. Small holes made by Crambidae moth larvae (diameter about 3 mm; referred to as Tortricidae in KLEIN & al. 1992) and small artificial holes (diameter 2 mm; present study) were also accepted as entry holes. Internodes with larger

openings, such as the round exit holes of the longhorn beetle *Abryna regispetri* (diameter about 1 cm; KOVAC & YONG 1992) or large artificial holes (diameter 5 mm, present study), were not colonised by *T. binghami*.

Flooding effect on internode nests

Culm shoots felled in Malaysia and Thailand showed hundreds of internodes colonised by *Tetraponera binghami* that were dry, always clean, and contained only mealybugs and brood. However, some *T. binghami* internodes also contained water. In twelve culm shoots cut during the dry season (February and March) in northern Thailand, three internodes contained 60, 70, and 100 ml of water as well as some *T. binghami* brood and mealybugs. In two other cases, the amount of water was greater (285 and 490 ml) and there were only a few *T. binghami* workers, some mealybugs on the upper internode septum, but no brood. In the same culms, internodes penetrated by *Lasiochila* contained up to 310 ml of water ($n = 18$, average 136 ml, two internodes were dry), and internodes penetrated by Crambidae larvae contained up to 900 ml of water ($n = 22$, average 479 ml).

Tetraponera binghami internodes continuously observed with the endoscope over several months in Peninsular Malaysia (see SCHILLHAMMER & KOVAC 2023) always contained large amounts of liquid as bamboo sap seeped from the endoscope hole into the internode cavity, despite being sealed with a plastic plug. In such water-filled internodes, the number of *Tetraponera* workers remained low (up to 17), there were only a few coccids attached to the upper internode septum, and brood was usually absent. In at least one internode, there were dead *T. binghami* lying in the water. Occasionally, mealybug crawlers or brood could be seen floating on the surface of the water and the workers would try to pull them ashore. The workers made no effort to remove liquid from such internode cavities. Internodes filled with water were abandoned by *Tetraponera* after a while.

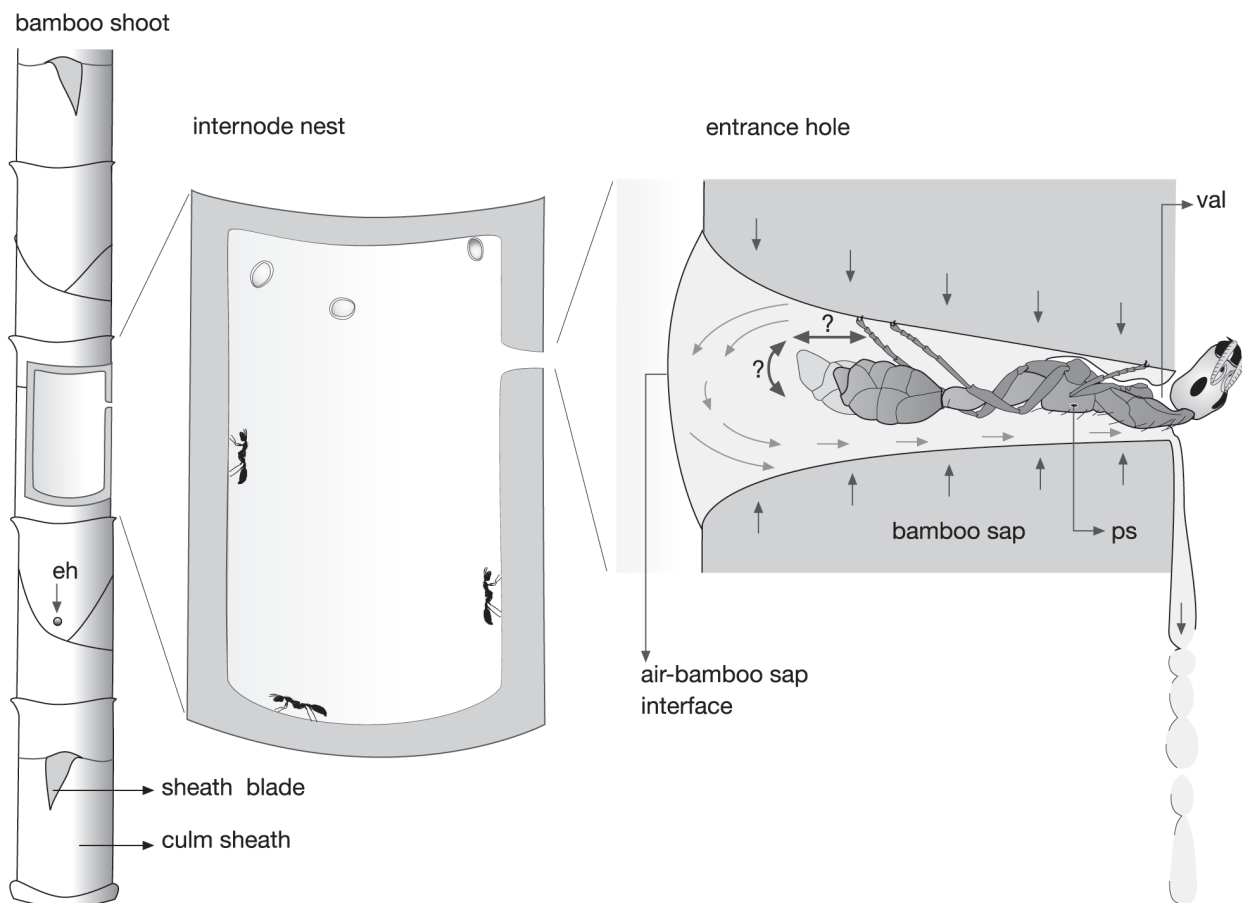


Fig. 2: Schematic illustration of a culm shoot internode newly colonised by *Tetraponera binghami* and the hypothesised mode of the bamboo sap ejection. Left: Bamboo culm shoot with a newly made nest entrance hole of *T. binghami*. The hole is located between the overlapping internode sheaths. Middle: Enlarged internode nest with *T. binghami* workers and a few mealybugs attached to the bamboo wall; brood, which normally lies at the bottom of the internode, is not yet present. Right: Enlarged freshly made entry hole. The thin arrows show the influx of bamboo sap from the bamboo wall into the entry hole. The sap is expelled by the worker ant stuck in the hole. The two double arrows symbolise the hypothetical movements of the ant's gaster during the pumping process (a contraction / expansion movement and lateral movements as indicated in the drawing). Note the air layer on the ventral side of the head and mesosoma held in place by hydrofuge hairs. eh: entrance hole, ps: propodeal spiracle, val: ventral air layer.

Bamboo sap ejection and hydrofuge hairs

The bamboo sap ejection behaviour of *Tetraponera binghami* was observed during nocturnal monitoring of newly pierced culm shoots. The pumping worker ants were occasionally replaced by conspecifics waiting at the inner opening of the entrance tube. Individuals ejecting bamboo sap remained in the sap-filled entry holes, usually positioned upside down, with their heads protruding from the holes (Fig. 2, right). Their mandibles were sometimes open and their antennae were usually folded. Bamboo sap, consisting of xylem (water) and phloem (sap), emerged from the holes at night and trickled down along the surface of the bamboo trunk (Figs. 1B, 2, right). The sap was thin and clear and probably consisted mainly of water. Sometimes, the bamboo sap contained tiny particles of bamboo from the damaged tissue.

Using the prism lens, an alternating increase and decrease in the flow of liquid below the outer opening of

the entrance hole could be observed at intervals of about 1.25 per second (6 observations in different culm shoots). The rhythmic change in water volume was indicated by the changing reflections on the water surface. When the inner opening of the entrance hole was observed with the endoscope, distinct pulsating movements of the gaster were visible. There were 1.25 beats per second (100 beats over a period of 80 seconds), and each beat of the gaster pushed bamboo sap out of the hole. Occasionally, gas bubbles would appear at the tip of the gaster, increasing in size with each pumping motion and eventually disintegrating. The exact nature of the gaster movement was not visible through the endoscope because the view of the rear part of the ant was obscured by the air-bamboo sap interface located between the inner opening of the entrance hole and the internode cavity (Fig. 2, right).

Worker ants immersed in bamboo sap had a layer of air on the ventral side of their heads that was partially visible

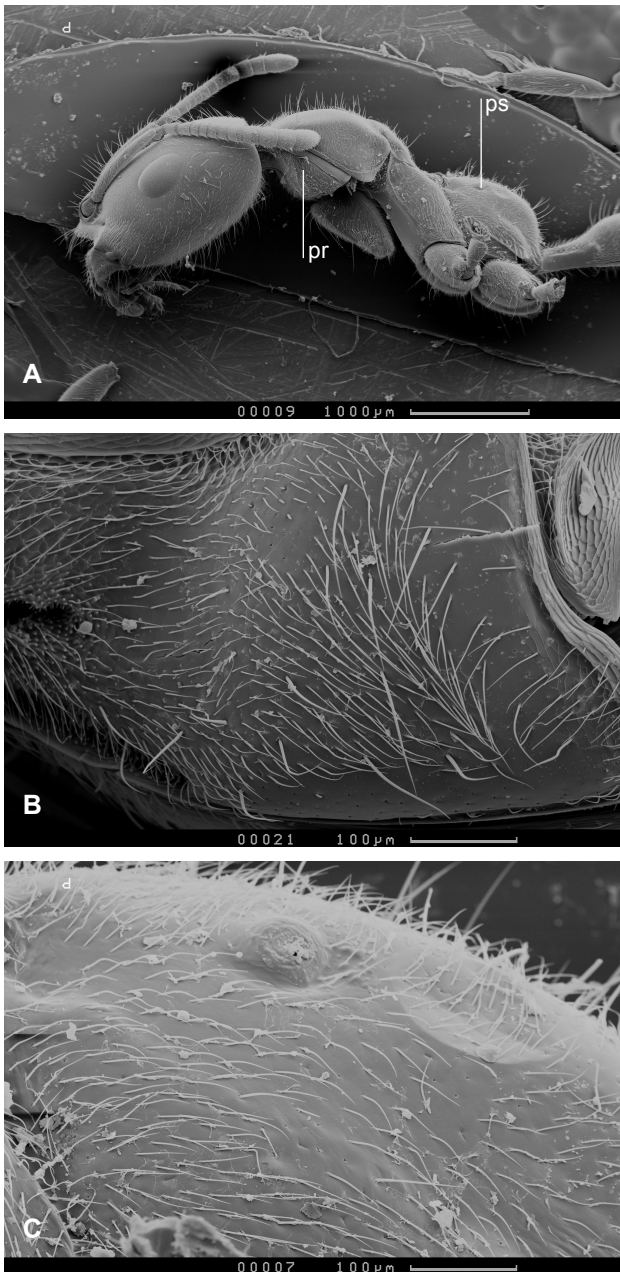


Fig. 3: Hydrofuge hairs located on the body surface of *Tetraponera binghami* from northern Thailand (scanning electron microscope photographs). A: Overview of the anterior part of *T. binghami* (head, mesosoma, and part of petiole); legs removed. B: Hydrofuge hairs on propleuron. In submerged specimens, these hairs were covered by a layer of air. C: Less dense hairs surrounding the propodeal spiracle. In submerged specimens, this part of the body surface was not covered by a layer of air. pr: propleuron, ps: propodeal spiracle.

when viewed from the outside. The air layer was connected to the atmospheric air and extended caudally along the ant body (Fig. 2, right). To determine the exact location and extent of the air layer, 10 *Tetraponera binghami* workers were held by the mesosoma with forceps and submerged in water under a stereomicroscope. In the submerged specimens, a permanent layer of air was trapped on the

ventral side of the head and mesosoma up to the base of the hind legs (Fig. 2, right). Worker ants held by a pair of tweezers and submerged in water began to make pumping movements after a while, that is, they alternately shortened and lengthened their gaster. Occasionally, gas bubbles appeared at the tip of the gaster.

The hydrofuge hairs present on the ant body varied in size and distribution (Fig. 3A - C). Hairs supporting the air layer were located on the ventral head, propleuron, coxae, and along the ventral edges of the katepisternum and propodeum. The hairs were about 50 - 100 μm long, and their density was about $3 - 6 \times 10^5$ per cm^2 (Fig. 3B). Other areas of the body surface were not covered by an air layer, or the air layer disappeared after a short time. In these areas, the hairs were absent, short or very long, and less dense (Fig. 3C). The body surface between the coxae was smooth but still covered by the air layer held in place by the hydrofuge hairs of the coxae. The metanotal and propodeal spiracles located on the dorsal part of the mesosoma and the remaining abdominal spiracles were not covered by an air layer.

Apart from the pumping motion, *Tetraponera binghami* workers also used other methods to remove bamboo sap. Sometimes, they would repeatedly crawl into the entrance hole from the surface of the bamboo and then crawl backwards, using their bodies to push the bamboo sap towards the outer surface of the bamboo stem. In addition, worker ants were regularly seen standing next to the outer opening of the entrance hole, removing bamboo sap which was expelled from the entrance by swallowing it and then dropping the regurgitated sap onto the ground (Fig. 1B).

Discussion

Biting entry holes and bamboo sap leakage

Tetraponera binghami is the only Oriental ant known to be able to make holes in bamboo walls. The only other ant capable of penetrating bamboo is the South American *Camponotus mirabilis* (DAVIDSON & al. 2006). Both species use culm shoots to gain access to the internode cavities. *Tetraponera binghami* also attempted to enter a mature, lignified bamboo culm on one occasion. However, the entry hole was not completed and the progress of the bore was much slower than that of the culm shoots. This suggests that stems of shoots are preferred because they are softer and easier to penetrate than stems of the mature bamboo.

It is likely that the degree of softness of an internode also influenced the location of the entry hole. A culm shoot internode was always softer at the base than at the top, making the base more suitable for penetration. However, the soft basal walls were protected by the hard culm sheaths, which *Tetraponera binghami* could not penetrate. Holes were therefore often made in the triangular area between the overlapping sheaths (Fig. 2, left), which was the lowest and softest part of the internode not protected by the sheaths. *Tetraponera binghami* also accepted freshly made entry holes made by other insects,

as well as artificial holes, provided they were less than 3 mm in diameter. Internodes with larger holes were not colonised, probably because they could not be effectively defended against predators and water influx.

At night, when the root pressure of the culm shoots was high, bamboo sap leaked from the damaged vascular bundles in the freshly made holes. The sap stopped flowing after about four nights, due to wound reactions of the culm shoot. In wounded bamboo, plugs form to close the sieve tubes after three days and then additional wall layers are formed (LIESE 1998). Although *Tetraponera binghami* was active during both day and night, the culm shoots were only penetrated during daylight hours. This may have been because the strong sap flow during the night interfered with the boring process. The single mature culm was also penetrated at night, perhaps because the sap flow from the mature culm was weak, or because the colony was in urgent need of a new nest as the old nest had been damaged and the colony was at risk from predators.

Sap ejection behaviour

As the nest entrance hole filled up with sap, a liquid-air interface formed at both openings of the entrance tube until the pressure increased. Bamboo sap then leaked into the internode cavity because the inner opening was bell-shaped and larger than the outer one (Fig. 2, right). To drain the sap before this happened, the worker ant broke through the outer film of water with its head and redirected the sap outwards with rhythmic movements of its gaster (Fig. 2, right). The exact nature of the movement could not be seen through the endoscope, but experimentally immersed workers performed pumping movements, that is, they contracted and extended their gasters. Occasionally, air bubbles appeared at the tip of the gaster, presumably from the compressed tracheae. Ants observed in the field also showed bubbles at the tip of the gaster. It is therefore possible that the worker ants that were observed in the field were performing essentially the same pumping movements as the experimentally submerged ants. Our hypothesis is that the contracted gaster, perhaps combined with an up and down or lateral movement, pushed the bamboo sap towards the outer opening of the entrance hole along the bottom of the hole as the upper part of the hole was blocked by the ant's body (Fig. 2, right).

Due to the small size of the entrance hole and the small volume of sap involved, adhesion and cohesion were important factors in the flow characteristics of the sap. The expelled sap formed a tiny stream on the surface of the bamboo, surrounded by a film of water (Figs. 1B, 2, right). This film appeared to be static, except that it widened and narrowed with each beat of the gaster during pumping. Inside the water film, the liquid did not flow down by gravity, but was pushed down by the ant against the resistance of the water column. To assist the pumping ant, other ants standing at the external entrance opening removed the sap by sucking it up and then regurgitating it onto the ground (Fig. 1B). Experiments with submerged ants indicate that the stigmata on the dorsal part of the mesosoma, petiole,

postpetiole, and gaster were not covered by the air layer during pumping. This suggests that the air layer did not act as an air reservoir or a physical gill.

Judging from the variety of methods used by *Tetraponera binghami* to avoid flooding, such as pumping out bamboo sap, pushing liquid out of the entrance holes, ingesting water and regurgitating it outside the nest, it is clear that keeping the internode cavities dry is essential for *T. binghami*. The main reason for this is probably that the brood would drown in the flooded internodes lying unprotected at the bottom of the internode cavity. The same applies to mealybugs from the lower part of the internode cavity or their walking crawler stages when they fall to the water surface.

When a fresh nest entrance hole is made, the brood is not yet present. Nevertheless, the sap is expelled immediately because a large amount of liquid would make the internode unsuitable for nesting. This can be seen from the fact that *Tetraponera binghami* abandons internodes with large amounts of water, probably because it is not profitable to drain them. As *T. binghami* is known to drain rainwater from its nest at a rate of about 1 ml per hour (KLEIN & al. 1993), it would take, for example, almost two weeks for workers to expel 300 ml of water from the internode cavity. Another reason for protecting occupied internodes from flooding may be the difficulty in obtaining replacement internodes. Internodes with older, suitably sized holes are already filled with water and debris, whereas new, intact, immature internodes are only available during the growing season and will take days to penetrate.

Factors influencing the occurrence of flood control behaviour in arboreal ants

An important factor influencing whether arboreal ants exhibit flooding behaviour is the way they nest. Most arboreal ants probably live in cavities in dead or living plants (reviewed by BLÜTHGEN & FELDHAAR 2009, PRIEST 2018, PRIEST & al. 2021). Species living in soft substrates such as decaying wood can excavate their own cavities, whereas in living, hard wood, ants are usually dependent on cavities made by wood-boring insects and other animals. Cavity entrances made by wood-boring insects are often widened or narrowed to suit the size of the ant (PRIEST & al. 2021). A number of arboreal ants are able to build free-hanging silk or carton nests in sheltered places under leaves, on tree trunks and branches, between roots of epiphytes or in tree holes (WEISSFLOG 2001). Migratory herdsmen ants are a special case. They live in temporary bivouac nests built with their bodies (MASCHWITZ & HÄNEL 1985, DILL & al. 2002). Only ants living in plant hollows are known to exhibit flood control behaviour. This is probably because nests in plant cavities can retain rainwater. Silk, carton, or bivouac nests, however, drain quickly when water enters.

Among the arboreal ants that live in plant cavities, some species show flood control behaviour, while others do not. For example, *Echinopla* sp., a formicine species living in dead twigs, could not be experimentally induced to drain water (A. Reichardt, pers. comm., in MOOG & al.

1997). The same is true for *Cataulacus catuvolicus*, which colonises small dead twigs, and *Cataulacus horridus*, which inhabits dead logs (MASCHWITZ & MOOG 2000). Thus, ants nesting in dead wood appear to relocate their nests in response to flooding rather than develop flood control methods (MASCHWITZ & MOOG 2000). This may be because water drains more easily in dead wood than in living wood, dead branches may have larger or more openings that cannot be effectively protected from water intrusion, and relocation to a new nest is frequent because dead twigs and branches are a relatively short-lived and easily disturbed habitat.

Ants living in the hollows of myrmecophyte plants show a variable response to flooding. *Crematogaster* spp. living in thin stems of *Macaranga* did not respond to artificial flooding, whereas several species of *Cladomyrma* living in *Saraca* trees or other myrmecophyte trees and vines ingested rainwater and regurgitated it outside the nest (MOOG & al. 1997). As *Crematogaster* spp. have small entrance holes, it is possible that their nests were not flooded because the surface tension was sufficient to prevent rainwater from entering. This was also found for small *Tapinoma*, *Crematogaster*, *Monomorium*, and *Tetraponera* nesting in *Sonneratia* branches (reviewed by NIELSEN 2011). In addition, nests in thin *Macaranga* stems, often in the apical parts of the plant, are unlikely to be exposed to large amounts of rainwater run-off. In contrast, *Cladomyrma* species have entrances that are large enough to allow flooding, and they often live in larger and longer, more or less upright stems and large branches of trees and vines, which are likely to be sometimes exposed to significant amounts of canopy run-off.

Some ants that live on myrmecophytes may not show flood control behaviour because of special plant structures that myrmecophytes provide to make it easier for the ants to colonise the plant. For example, some myrmecophyte plants produce prostomata, which are thin zones in the walls where ants chew new entry holes. Prostomata reduce the risk of nest cavities being flooded with plant sap because they lack vascular bundles or latex vessels (FEDERLE & al. 2001). Nests of ants living in domatia (hollow structures produced by the plants that serve as shelters for the ant colonies) that are set back from the plant stem may also have a low risk of flooding because the nests are not exposed to large amounts of water run-off.

Two ant species living in large bamboo stems, *Tetraponera binghami* and *Cataulacus muticus* (KLEIN & al. 1993, MASCHWITZ & MOOG 2000, this study), were found to have the most elaborate and diverse flood control methods. This is probably due to the unique structure of their habitat as the large, cylindrical cavities are particularly susceptible to flooding and water accumulation. The internode cavities easily fill with water as large amounts of rainwater run off the canopy along the very long bamboo stems. More than 20 litres of rainwater have been measured at the base of a single *Gigantochloa scortechinii* bamboo stem during a single rain event (D. Kovac, unpubl.). Due to the smooth surface of the bamboo, the entrance holes are exposed to

the run-off water, especially if they are on the inside of the curved bamboo stem. Even cavities with small entrance holes fill with water as they seem to absorb rainwater by capillary forces. In culm shoots, the main source of liquid is probably bamboo sap, whereas in mature culms it is rainwater.

Two other ant species that are restricted to large bamboo cavities in Southeast Asia, *Polyrhachis arachne* and *Polyrhachis schellerichae* (DOROW & MASCHWITZ 1990, SCHELLERICH-KAADEN & al. 1997), did not show any elaborate methods to control flooding. *Polyrhachis schellerichae* seemed to block the entrance holes with its head during rainfall (SCHELLERICH-KAADEN & al. 1997), but this was probably not very effective. Nest openings were sometimes large (up to 15 mm long) and irregularly shaped, making them difficult to seal against water ingress. Experiments (SCHELLERICH-KAADEN & al. 1997) failed to induce any other flood-defence behaviour. No flood-defence behaviour was observed in *Polyrhachis arachne*, nor would it be expected. This species inhabits living and dead internodes with often very large openings that cannot be protected from water ingress.

Polyrhachis arachne and *Polyrhachis schellerichae* are able to survive in bamboo internodes, although they do not exhibit flood protection behaviour. This is because they are able to attach their brood above the water surface with larval silk. The brood is therefore not threatened by flooding. The water level can only rise to the lowest hole, which is usually located in the lower part of the internode. The same is true for the many Southeast Asian generalists such as *Pheidole*, *Crematogaster*, or *Camponotus* species, which nest in dead or living water-filled bamboo internodes as well as in other habitats (SCHELLERICH-KAADEN 2001; D. Kovac, unpubl.). The South American bamboo ant *Camponotus mirabilis* raises its brood on carton shelves above the water surface (DAVIDSON & al. 2006).

Tetraponera binghami, however, is not adapted to build a nest above the water surface. This is probably because its ancestors, like most *Tetraponera*, lived in small cavities in dead branches and therefore did not build nests. To use the cavities of living bamboo culms, they had to develop sophisticated flood control techniques, including the expulsion of bamboo sap.

In summary, only arboreal ants that nest in the hollows of living plants that can hold water and have a small entrance hole show flood control behaviour. Species that live in nests with large holes that cannot be protected from intruding water, or with very small holes, where the surface tension is sufficient to prevent water from entering, do not show flood control behaviour. Other factors, such as the amount of water run-off, the characteristics of the nest substrate, and the evolutionary history of the ants also influence the occurrence of flood-defence behaviour. It is likely that other ant species living in plant cavities with the above characteristics have also developed methods to prevent water from entering their nests.

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