Colony composition, queen behavior, specialized predation on millipedes, and exocrine glands in the ponerine ant *Myopias conicara* Xu, 1998 (Hymenoptera: Formicidae)

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Abstract

We could collect a queenright colony of the very rare *Myopias conicara* in Vietnam (1 dealate queen, 41 workers and 38 larvae). Both the queen and workers fed on xystodesmid millipedes. After paralyzing a millipede, its head was first removed by the workers, and then the larvae were put on the opening of the collum (anteriormost ring of the trunk). After the inner tissue of the collum was consumed, the exoskeleton of the collum was discarded. The feeding sequence was then repeated on the following rings of the trunk, until the entire prey was consumed. The ring-shaped exoskeletons of the prey were deposited next to the nest entrance. The exocrine system of the workers (excluding the legs) contains 15 glands of which the structural features are similar to these of other ponerine ants. The presence of an oblong plate gland is interesting, as this gland had only been found previously in *Myopias hollandi*. On the other hand, none of the novel thoracic glands that were recently described in *M. hollandi* occur in *M. conicara*, which illustrates the variation within the genus *Myopias*. A unique characteristic of the class-3 glands of *Myopias* ants is the gradual widening of the ducts, which has never been found in other insects, although the functional significance remains unknown.

Keywords: caste difference, Diplopoda, feeding, prey specialization,

Introduction

The ponerine ant genus *Myopias*, that comprises 39 species, is distributed from India to Australia (antmaps.org 2019; Bolton 2019; Probst *et al.* 2015). The highest diversity is found

from the Oriental tropics to New Guinea (antmaps.org 2019). So far, detailed studies of the abdominal glands of some species (Billen *et al.* 2013) and of several novel thoracic glands of *M. hollandi* (Forel) (Billen & Ito 2018), as well as fragmental descriptions of the behavior and ecology of this ant genus (Probst *et al.* 2015; Willey & Brown 1983) have already been published. These reports indicate that these ants are characterized by several novel glands, that colony size is generally small, and that some species specialize on millipedes as prey (Billen *et al.* 2013; Billen & Ito 2018; Probst *et al.* 2015; Willey & Brown 1983). However, rigid information on colony composition and hunting strategy on millipedes have not been reported so far.

Specialization on millipedes is peculiar in ants, because of their strong defense system (Hopkin & Read 1992). Polyxenida have many setae and special caudal tufts that are used against predators (Eisner *et al.* 1996). Polyxenida predation by ants is known only in two genera, *Probolomyrmex* and *Thaumatomyrmex* (Brandão *et al.* 1991; Ito 1998). Other millipede orders including Glomerida, Spirobolida, Spirostreptida, Julida, Callipodida, Platydesmida, Polyzoniida, and Polydesmida have defensive glands which secrete a very wide range of chemicals (Eisner *et al.* 1978, Hopkin & Read 1992). Beside *Myopias*, predation on millipedes with strong chemical defense has been reported for a few species of *Leptogenys*, *Plectroctena* and *Gnamptogenys* only (Brown 1992; Peeters & De Greef 2015).

Myopias conicara Xu was described from southern Yunnan, China (Xu 1998). As this species is very rare (Xu & Liu 2012), information on its natural history therefore has not been reported to date. We collected one colony of *M. conicara* from northern Vietnam. In spite of intensive collection of ants in Vietnam (Eguchi *et al.* 2014), this is the first record of *Myopias* from this country. Although we had only one colony available for our study, we here report on its colony composition, caste difference, predation of millipedes, and the exocrine gland system.

Materials and methods

Our colony (F115-29) was collected in Ban Chu (20.20 N, 105.25E, alt. 200–225 m), Na Hang, Tuyen Quang, northern Vietnam, on 11 March 2015. All colony members were collected using an aspirator. Immediately after collection, the colony composition was recorded. The colony was kept in the laboratory in a polystyrene box (148 x 84 x 32 mm). The bottom of the box was covered with Plaster of Paris for keeping the humidity high. Inside the box, a small polystyrene box (68 x 39 x 15 mm) with an entrance hole served as a nest chamber. The bottom layer of the chamber was also covered with Plaster of Paris. As prey we offered several

arthropods including mealworms and millipedes. The hunting and subsequent behavior against millipedes (nymphs of *Xystodesmus* sp., Xystodesmidae, Polydesmida) was observed 10 times. The behavior of the queen was recorded for 440 min. After the behavioral observations, the queen and 10 workers were dissected to check their reproductive condition (mating status and ovary development).

The head, the anterior as well as posterior part of the thorax, and the abdomen of workers were fixed in cold 2% glutaraldehyde in a 50 mM Na-cacodylate buffer at pH 7.3 with 150 mM saccharose added. After postfixation in 2% osmium tetroxide in the same buffer and dehydration in a graded acetone series, tissues were embedded in Araldite. Serial sections with a thickness of 1 μ m were made with a Leica EM UC6 ultramicrotome, stained with methylene blue and thionin and viewed in an Olympus BX-51 microscope. Longitudinal images in this paper are always shown with the anterior side at the left.

Results

Colony composition

The colony of *Myopias conicara* nested under a stone in evergreen forest on limestone karst. Colony size was small with only 41 workers, one dealate queen and 38 larvae. Cocoons and eggs were not present, probably because the reproductive activity of the colony had not started yet in March (early spring in northern Vietnam). Workers were monomorphic, and caste differences between queen and workers were small (Fig. 1). The head width of the queen (1.16 mm) was smaller than the mean head width of workers (1.19 ± 0.05 mm, $N = 25$), however, the abdomen width of the queen (1.26 mm) was remarkably larger than that of workers (1.06 ± 0.03 mm, $N = 25$). The queen had three ocelli, and has a fully segmented flight thorax with tegulae, indicating she had wings previously. Both the queen and the workers ($n = 10$) had six (3-3) ovarioles and a spermatheca. The spermatheca of the queen contained sperm whereas the worker spermatheca was empty and small; the existence of a spermatheca in the worker was hardly recognized under a binocular microscope, but it was later confirmed by semithin sections of the abdomen with light microscopy ($N = 2$).

Queen behavior

The queen usually stayed near the brood inside the nest chamber. She directly fed on millipedes inside the nest chamber. During 440 min of observation, feeding of prey by the queen was noticed 14 times (35 min. 53 sec.). We never observed feeding of trophic eggs nor larval

hemolymph feeding by the queen. Brood care was observed twice: in both cases the queen licked a larva just 5 and 20 seconds, respectively. Behavioral interactions between the queen and workers were not frequent: grooming from workers to the queen was never observed while allogrooming among workers was observed 10 times during 440 min. The queen often walked inside the nest chamber. During wandering, she often showed antennation towards workers. When the workers received such antennation from the queen, workers sometimes avoided this but they usually showed no specific reactions.

Predation on millipedes

The hunting and feeding behavior on millipedes was observed ten times. Beside millipedes, the ants fed on mealworms, however, they never accepted termites or cockroaches. When a worker met a millipede in the foraging arena, the worker immediately grasped a leg or the body of the millipede (Fig. 2A), and stung it ventrally. Points of insertion of the sting varied. If there were nestmate workers near the prey, these workers also joined in attacking. The paralyzed prey was retrieved to the nest chamber immediately, by pulling the appendages. Inside the nest chamber, workers first licked the prey. After one to two hours of licking, they started dividing the prey. Workers inserted their mandibles in an intersegment between the head and collum (anteriormost ring of the trunk), and removed the head from the collum (Fig. 2B). Workers then brought a few larvae to the cut prey. Heads of larvae were inserted into the opening of the collum. Workers and the dealate queen also fed on the cut prey together with the larvae. After the inner tissue of the collum was consumed, the exoskeleton of the collum was removed by workers. The removed ring-shaped exoskeletons were deposited outside the nest entrance (Fig. 2C). Again, a few larvae together with the queen and workers consumed the soft tissues inside the next ring of the trunk. This behavioral sequence was repeated until complete consumption of the prey. For consuming one millipede (ca. 20 mm length), the ants spent more than 12 hours.

Exocrine glands

The glandular repertoire of *Myopias conicara* includes the standard exocrine structures as well as some glands that have only been found in the genus *Myopias* so far. We here describe the various glands in the head (Fig. 3), thorax (Fig. 4) and abdomen (Fig. 5). The classification of insect exocrine glands follows the pioneer paper by Noirot & Quennedey (1974), that distinguishes class-1 glands with an epithelial arrangement of the secretory cells,

and class-3 glands, that are formed by bicellular units, each unit made up by a secretory cell and its accompanying duct cell.

Exocrine glands in the head

Although not forming part of the exocrine system, serial sections revealed the existence of two sensory structures in each mandible. These are situated on the upper inner side, the first near the distal tip, the second near the middle of the elongated mandible. Each of the four sensory structures consists of nerve cells underneath a conspicuous fibrillar modification of the cuticle (Fig. 3A,B). At their cupola-shaped tip, the sensory structures are covered by yellow-staining material (Fig. 3A,B).

The major exocrine glands in the head are the mandibular, propharyngeal and postpharyngeal glands (Fig. 3C). The interior of the mandibles contains some fat cells, but intramandibular gland cells were not found (Fig. 3D). The opening of the paired **mandibular gland** appears as a slit on the upper proximal part of each mandible, with the mandibular gland duct appearing as an anchor-shaped structure (Fig. 3D). The secretory part of the mandibular gland at each side is formed by approx. 25 spherical class-3 cells with a diameter of $31 \pm 1 \mu\text{m}$ ($N = 10$), that are clustered as a cap on top of the mandibular gland reservoir. The reservoir appears as a thin-walled wrinkled sac with a diameter of 70-80 μm , into which the duct cells open at the distal side (Fig. 3E). The ducts have a diameter of 0.5 μm when they leave the secretory cells, and gradually reach 1.5 μm where they open into the reservoir. The **propharyngeal gland** consists of a left and a right cluster with each approx. 50 round secretory cells of class-3 with a diameter of $38 \pm 1.3 \mu\text{m}$ ($N = 10$). Long slender ducts connect the secretory cells at each side with a small lateral chamber at each side of the pharynx, in which they open as a sieve-plate. The diameter of the ducts measures 0.5 μm near the secretory cell and increases to 2 μm towards their opening site (Fig. 3F). The **postpharyngeal gland** is formed by 4 flattened lobes of which the central cuticle-covered lumen is lined by a class-1 epithelium of 10-15 μm thickness. The epithelium is characterized by bulbous basal protrusions (Fig. 3G).

Exocrine glands in the thorax

The **labial (= salivary) gland** in the prothorax is formed by spherical acini with a diameter of 80-100 μm . Each acinus is formed by a large central cell that is filled with abundant dark secretory granules and smaller parietal cells surrounding it, with spiraling ducts between both cell types (Fig. 4A,B). The paired **metapleural gland** in the metathorax at each side

consists of a cluster of elongated secretory cells of 50 x 20 µm. The class-3 cells are connected with duct cells that open in the ventral part of a heavily sclerotized atrium through a sieve plate area (Fig. 4C). On cross sections through the clustered ducts, approx. 90 ducts per side could be seen, which is therefore also indicative for the number of secretory cells per side. The ducts' internal diameter is 0.5 µm when they leave the secretory cell, and gradually increases up to 3 µm when they open into the atrium. None of the novel thoracic glands that have been recently described in *Myopias hollandi* (Billen & Ito 2018) have been found in *M. conicara*.

Exocrine glands in the abdomen

The abdominal glands of *M. conicara* include the common structures as the pygidial, venom and Dufour's glands, but also other exocrine structures are found (Fig. 5A). The paired **pygidial gland** at each side is made up of approx. 25 round class-3 secretory cells with a diameter of 37.0 ± 2.8 µm (N = 5), that are connected through duct cells with the invaginated reservoir between the 6th and 7th abdominal tergite. Duct diameter gradually increases from near the secretory cell towards the opening into the reservoir. The anterior portion of the 7th tergite shows conspicuous cuticular cups (Fig. 5B), in which secretion can be temporarily stored. The spermatheca contains a large reservoir and 2 **spermatheca glands** with class-3 secretory cells (Fig. 5C). The epithelial wall of the reservoir is fairly thick with a thickness around 10 µm, and can therefore be considered as a class-1 **epithelial spermatheca reservoir gland**. Several exocrine structures are associated with the sting apparatus: at each side, the oblong plate is connected with an **oblong plate gland**, that is formed by approx. 30 spherical class-3 secretory cells (Fig. 5D) with a diameter of 28.6 ± 2.4 µm (N = 10). The duct cells have a very narrow diameter of less than 0.5 µm near their junction with the secretory cell, that widens to 2-3 µm near their opening site in the membrane that connects the oblong plate and the ventral sting chamber (Fig. 5E). Dorsally to the sting we found an elongate cluster of approx. 30 rounded class-3 secretory cells with a diameter of 21.9 ± 1.3 µm (N = 10), that form part of the **gonostyli base gland** (Fig. 5F). The ducts of these cells run anteriorly to open at the base of the gonostyli (= sting sheaths in Hölldobler & Engel 1978), at a site where also posteriorly running ducts open. The latter form part of the **gonostyli gland**, that consists of a cluster of approx. 20 round class-3 secretory cells with a diameter of 20.6 ± 1.9 µm (N = 10) that occur inside the proximal part of each gonostylus (Fig. 5G). The ducts of the venom (dorsally) and Dufour glands (ventrally) are the only glands to open directly through the sting (Fig. 5H). The secretory part of the **venom gland** consists of two slender secretory filaments with a diameter

of $43.2 \pm 2.8 \mu\text{m}$ ($N = 10$) that each reach a length around 1 mm. **Dufour's gland** is a simple tubular gland with a length around 200 μm and a diameter around 25 μm . Its epithelial lining is made up by squamous class-1 cells with a thickness of 2-4 μm . The epithelium of the anterior part of the 7th abdominal sternite is differentiated into an unpaired **sternal epithelial gland**, with secretory cells reaching a thickness of 15 μm (Fig. 5A,H). An unpaired **sternal gland** with ducts opening through the intersegmental membrane between the 6th and 7th sternite is formed by a cluster of approx. 30 round class-3 cells with a diameter of $34.4 \pm 2.6 \mu\text{m}$ ($N = 10$). The internal diameter of the ducts gradually widens (Fig. 5I) from 0.5 μm near their junction with the secretory cells to 2 μm at their opening site through the intersegmental membrane. A sting shaft gland, that was recently found in workers of *Myopias hollandi* (Billen *et al.* 2013) was not found in *M. conicara*.

Discussion

Biology of *Myopias*

Colony size is generally small in *Myopias*: more than 1000 workers/colony have not been recorded (reviewed in Probst *et al.* 2015). Recently Jaitrong *et al.* (2018) mentioned that *M. bidense* (Emery) makes bigger colonies with up to a thousand workers. As in most *Myopias* species, colony size of *M. conicara* in northern Vietnam is small with 41 workers. Queen-worker dimorphism is not pronounced in *M. conicara*. This is also the case for *Myopias* ants of which both queens and workers have been studied so far (Willey & Brown 1983; Jaitrong *et al.* 2018).

The behavioral specialization of queen seems not much developed in *M. conicara*. The queen fed on millipede prey directly with workers and larvae. Although queen feeding of ponerine ants has been reported for a limited number of species, direct feeding on prey animals is apparently the ancestral condition. In advanced species as formicine and dolichoderine ants (Ward 2014), the queens exclusively feed on trophic eggs and/or oral trophallaxis with workers (e.g., *Anoplolepis gracillipes* (F. Smith), Lee *et al.* 2017; *Oecophylla longinoda* Latreille, Hölldobler & Wilson 1983; *Linepithema humile* (Mayr), Bartels 1988). Although we observed only one queen, the queen rarely received allogrooming, which is frequently shown among workers. The reason is unknown, however, this is a notable behavioral characteristic.

Predation on millipedes in *Myopias julivola* Willey & Brown and *M. concava* Willey & Brown was suggested by Willey and Brown (1983), based on field observations, where the empty rings of dead millipedes were found in the nest chamber, and/or fresh millipede corpses were found near the larvae. In this study, we confirmed specialized predation on millipedes in

M. conicara under laboratory conditions. A very similar behavior of hunting and feeding on millipedes is also observed for *M. hollandi* (Forel) and *M. emeryi* (Forel) collected in Ulu Gombak, West Malaysia (Ito, unpublished). Beside these species, *M. delta* Willey & Brown seems to be an ant predator specializing on Myrmicinae, and *M. tenuis* (Emery) feeds on entomobryid collembola (Willey & Brown, 1983). Although the number of species in this genus is small (39 species), considerable variation of feeding habit occurs. One of the reasons of this diet diversity may be the remarkable size variation among species, ranging from 0.45 mm in head width of the collembola feeder *M. tenuis* to 2.6 mm in *M. gigas* Willey & Brown (Willey & Brown, 1983).

Brown (1993) described specialized predation on millipedes by the ectatommine ant *Gnamptogenys ingeborgae* Brown. Their hunting and prey dragging behavior against *Oxydes* millipedes is well stereotyped: after stinging the millipede, the worker stayed near the prey for 10 min to one hour, probably because defensive chemicals emitted by the millipede are still effective. After that, according to Brown's description (G = *Gnamptogenys*, O = *Oxydes*), "G went to O head first and reached over the upraised mandibles of the immobile millipede to seize it with her own jaws by the "throat," that is, the ventral region of O just caudad of O's mouthparts, somewhat as in Fig. 6, but without the under-curling of the ant's gastral apex. With a heave from this position, the ant threw the body of the millipede over her own body and, facing the same way while maintaining her grip in the millipede's postgnathal region, moved off to the nest with the carcass over her back and trailing to the floor behind". Such behavioral sequence was never found in our observation for *Myopias conicara*. One of the reasons of the behavioral difference between our *Myopias* and *G. ingeborgae* is that we offered only millipede nymphs. Strong chemical defense is only found in adult millipedes (Hopkin & Read 1992). In contrast, feeding behavior is very similar in both genera. In both, workers firstly removed the head of the millipede, and brought larvae that then fed on the inner tissue of the collum. After consuming the tissue of the collum, the exoskeleton was removed, and the feeding sequence was repeated for the following rings.

Exocrine glands

The exocrine repertoire of *Myopias conicara* workers revealed a total of at least 15 glands, although the real number will be considerably higher, as our study did not include the legs (in which a variety of 20 glands may exist: Billen 2009), while also a number of small unnoticed glands may occur. On the other hand, we did not find any intramandibular gland,

which is an exocrine structure that is found in a wide variety of ant species (Schoeters & Billen 1994).

The general anatomical features of the glands are similar to these of other ponerine ants (Jessen & Maschwitz 1983; Jessen et al. 1979), such as the occurrence of basal protrusions of the postpharyngeal gland epithelium (Schoeters & Billen 1997; Billen & Al-Khalifa 2015), the acinar type of the labial gland (Lommelen *et al.* 2003) and the well-developed gonostyli base gland and gonostyli gland. These gonostylar glands (= sting sheath glands in Hölldobler & Engel 1978) show the peculiarity in *M. conicara* that the ducts of both glands open near to each other through the membrane that connects the gonostylar base with the sting chamber, but that the secretory cells of the gonostyli glands are located inside the gonostyli (with hence posteriorly running ducts) while the secretory cells of the gonostyli base gland are located outside the gonostyli (and hence with anteriorly running ducts). The presence of a well-developed oblong plate gland is noteworthy, as this gland so far has only been found in two other *Myopias* species (Billen et al. 2013). On the other hand, four novel thoracic glands that have recently been described in *Myopias hollandi*, were not found in *M. conicara*. This illustrates the variation that exists within the genus *Myopias*, as was already reported for the occurrence of a number of abdominal glands, with *M. emeryi* having considerably less glands than *M. maligna* (now *M. hollandi*) and *Myopias* sp.1 (Billen et al. 2013). A peculiar characteristic of the majority of class-3 glands of *M. conicara* is the gradual widening of their duct diameter from 0.5 µm near their junction with the secretory cells to 1.5 - 3 µm at their opening site. This is remarkable because all exocrine glands of class-3 have ducts with a uniform and standard diameter between 0.5 and 1 µm (Noirot & Quennedey 1974; Billen & Morgan 1998), irrespective of the size of the insect. The only exception to the best of our knowledge is found in class-3 glands of *Myopias* ants (Billen et al. 2013; Billen & Ito 2018). The functional significance of this feature remains unknown, but provides another illustration of the peculiar interest of *Myopias* ants for the study of insect exocrine glands.

Apart from the exocrine system, we noticed the presence of two hitherto unknown sensory fields along the upper inner margin of each mandible. The yellow-staining material on top of the cupola-shaped sensory field probably represents zinc reinforcements (Schofield *et al.* 2002; Khalife *et al.* 2018). With the limited material available, we unfortunately could not perform scanning or transmission electron microscopy to give a more detailed description.

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Figure legends

Fig. 1. Box plot showing width of head and abdomen (IVth abdominal segment) of workers. Black circle: width of queen.

Fig. 2. Hunting and subsequent behavior of *M. conicara*. **A:** Attacking millipede nymph. **B:** After head of millipede has been removed (arrow), larvae were transported to the prey. **C:** Accumulation of ring-shaped exoskeletons at the entrance of nest chamber.

Fig. 3. Semithin sections showing head glands. **A.** Cross section through distal part of mandible, showing sensory field with nerve cells (NC) and modified cuticle. **B.** Detail of mandibular sensory field; note yellow coloured outer layer of cuticle. **C.** Cross section through head (ant: antenna; IBP: infrabuccal pocket; Md: mandible; MdG: mandibular gland; PPG: postpharyngeal gland; proPG: propharyngeal gland). **D.** Longitudinal section through mandible, showing mandibular gland opening (MdO) through anchor-shaped apparatus (arrowhead). **E.** General view of mandibular gland with secretory cells (SC), duct cells (DC) and reservoir (R). br: brain. **F.** Cross section through anterior region of pharynx (ph) at site where duct cells of propharyngeal gland open into pharyngeal atrium (DC). **G.** View of postpharyngeal gland, arrows indicate bulbous ventral protrusions of glandular epithelium.

Fig. 4. Semithin sections showing thoracic glands. **A.** Cross section through anterior thorax. FC: foreleg coxae, LG: labial gland. **B.** Detail of labial gland acinus with central cell (CC) surrounded by parietal cells (PC), arrowheads indicate winding duct that connects both cell types. **C.** Metapleural gland overview showing secretory cells (SC), duct cells (DC) and sclerotized atrium (atr).

Fig. 5. Semithin longitudinal sections showing abdominal glands. **A.** Section through abdomen. gg: ganglion; GS: gonostylus; HG: hindgut; S5-7: sternites 5-7; SG6/7: sternal gland between 6th and 7th sternite; SPT: spermatheca; S7G: epithelial gland of 7th sternite; st: sting; T5-7: tergites 5-7. **B.** Overview of pygidial gland (PyG). CC: cuticular cups; PyGd: pygidial gland ducts. Arrowhead indicates invaginated membrane between 6th and 7th tergite. **C.** Spermatheca with spermatheca glands (SG), spermatheca reservoir (SR) and spermatheca gland reservoir (SRG). **D.** Detail of secretory cells of oblong plate gland (OPG). **E.** Ducts cells of oblong plate gland (OPGd). **F.** Sting (st) and gonostyli base gland (GBG). **G.** Section through gonostylus showing secretory cells of gonostyli gland (GG) and its duct cells (DC). **H.** Sting base with opening of Dufour gland duct (DGd) and venom gland duct (VGd). Note epithelial gland of 7th sternite (S7G) and oblong plate gland (OPG). **I.** Detail of sternal gland between 6th and 7th sternites (SG6/7), with duct cells (DC) opening through intersegmental membrane.