ORIGINAL ARTICLE

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

Fuminori ITO[1] , Duc Anh NGUYEN[2], Katsuyuki EGUCHI[3], Ayu TOYOTA[1] and Johan BILLEN[4]

[1]*Faculty of Agriculture, Kagawa University, Miki, Japan,* [2]*Department of Soil Ecology, Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam,* [3]*Systematic Zoology Laboratory, Department of Biological Sciences, Graduate School of Science, Tokyo Metropolitan University, Tokyo, Japan and* [4]*Zoological Institute, University of Leuven, Leuven, Belgium*

Abstract

We collected a queenright colony of the very rare *Myopias conicara* Xu 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* (Forel). However, 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.

Key words: caste difference, Diplopoda, feeding, prey specialization.

INTRODUCTION

The ponerine ant genus *Myopias*, which comprises 39 species, is distributed from India to Australia (Probst *et al*. 2015; antmaps.org 2019; Bolton 2019). 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 *Myopias hollandi* (Forel) (Billen & Ito 2018), as well as fragmental descriptions of the behavior and ecology of this ant genus (Willey & Brown 1983; Probst *et al*. 2015) 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 (Willey & Brown 1983; Billen *et al*. 2013; Probst *et al*. 2015; Billen & Ito 2018). However, detailed 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 that secrete a very wide range of chemicals (Eisner *et al*. 1978; Hopkin & Read 1992). In addition to *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 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 (FI15-29) was collected in Ban Chu (20.20°N, 105.25°E, altitude 200–225 m a.s.l.), Na Hang, Tuyan 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 × 84 × 32 mm). The bottom of the box was covered with plaster of Paris for keeping the humidity high. Inside the box, a smaller polystyrene box (68 × 39 × 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 and Polydesmida) were 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 sodium cacodylate buffer at pH 7.3 with 150 mM saccharose added. After post-fixation in 2% osmium tetroxide in the same buffer and dehydration in a graded acetone series, tissues were embedded in Araldite (Huntsman, The Woodlands, TX). Serial sections with a thickness of 1 μm were made with a Leica (Vienna, Austria) EM UC6 ultramicrotome, stained with methylene blue and thionin and viewed in an Olympus (Hamburg, Germany) 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, 1 dealate queen and
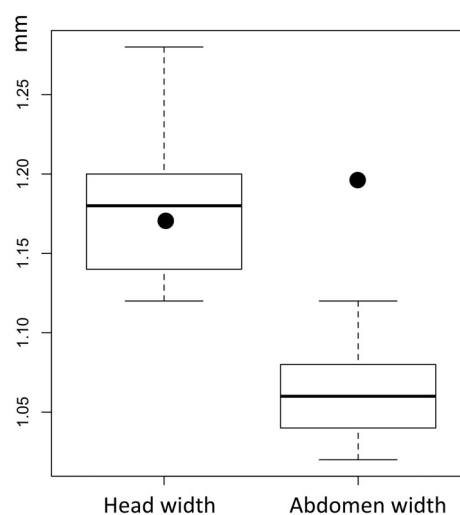

Figure 1 Box plot showing width of head and abdomen (4th abdominal segment) of *Myopias conicara* workers. Black circle, width of queen.

38 larvae. Cocoons and eggs were not present, probably because the reproductive activity of the colony had not yet started 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 s). We did not observe feeding of trophic eggs or larval hemolymph by the queen. Brood care was observed twice: in both cases the queen licked a larva for 5 s and 20 s, respectively. Behavioral interactions between the queen and workers were not frequent:

grooming from workers to the queen was never observed, whereas 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, they sometimes avoided this but usually showed no specific reactions.
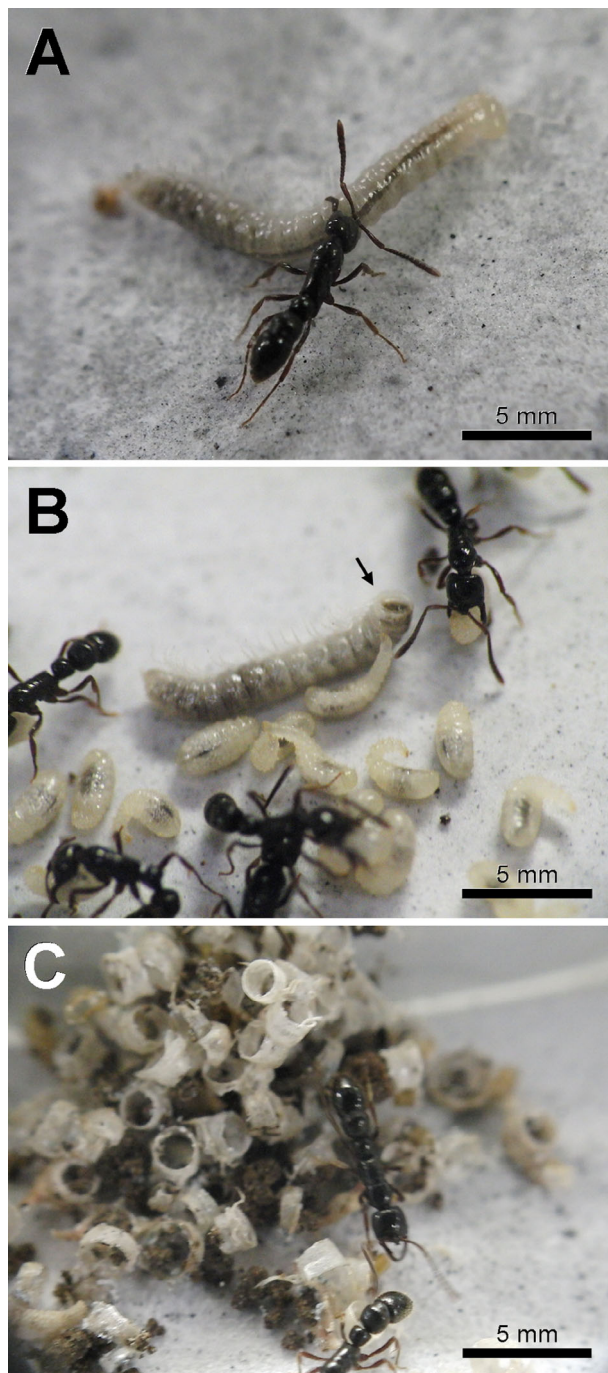
Predation on millipedes

The hunting and feeding behavior on millipedes was observed ten times. As well as 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. The sites of sting insertion 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 1–2 h 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 h.

Figure 2 Hunting and subsequent behavior of *Myopias 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.

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 and 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 of a secretory cell and its accompanying duct cell.
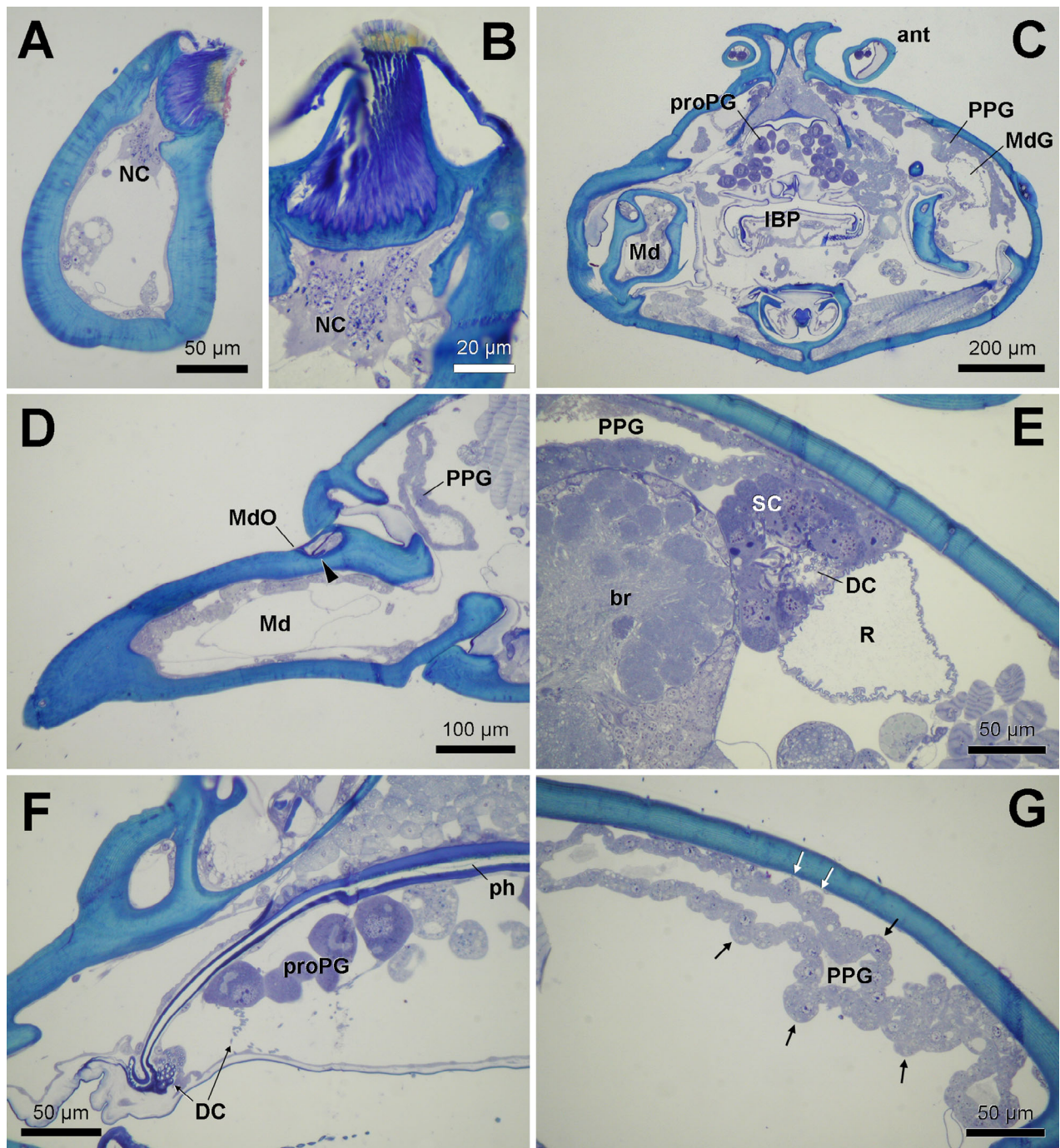
Figure 3 Semithin sections of *Myopias conicara* showing head glands. (A) Cross-section through distal part of mandible, showing sensory field with nerve cells (NC) and modified cuticle. (B) Detail of mandibular sensory field; note yellow colored outer layer of cuticle. (C) Cross-section through head. ant, antenna; IBP, infrabuccal pocket; Md, mandible; MdG, mandibular gland; PPG, postpharyngeal gland; proPG, propharyngeal gland. (D) Longitudinal section through mandible (Md), 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.
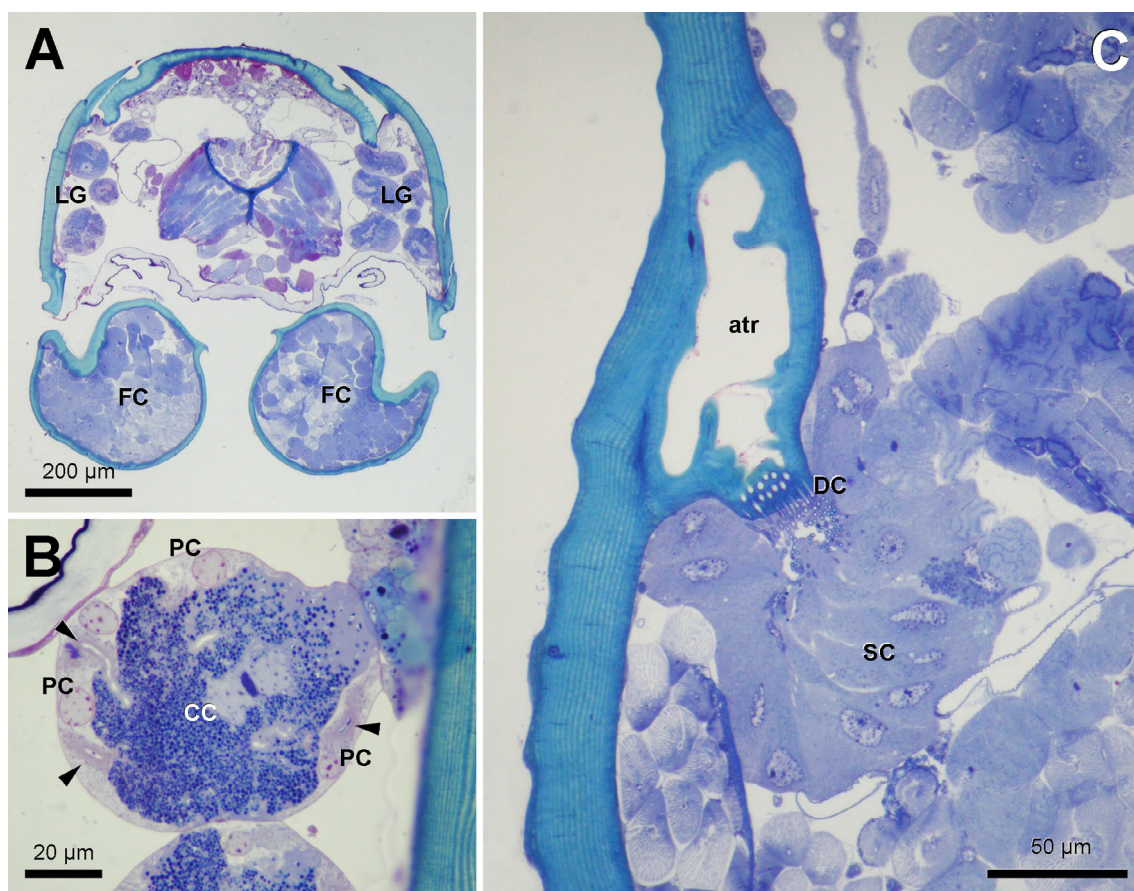
Figure 4 Semithin sections of *Myopias conicara* showing thoracic glands. (A) Cross-section through anterior thorax. FC, foreleg coxae, LG, labial gland. (B) Detail of labial gland acinus with central cell (CC) surrounded by parietal cells (PC), arrowheads indicate winding duct that connects both cell types. (C) Metapleural gland overview showing secretory cells (SC), duct cells (DC) and sclerotized atrium (atr).

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 approximately 25 spherical class-3 cells with a diameter of 31 ± 1 μm ($N = 10$) 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 approximately 50 round secretory cells of class-3 with a diameter of 38 ± 1.3 μm ($N = 10$). 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 four flattened lobes, of which the central
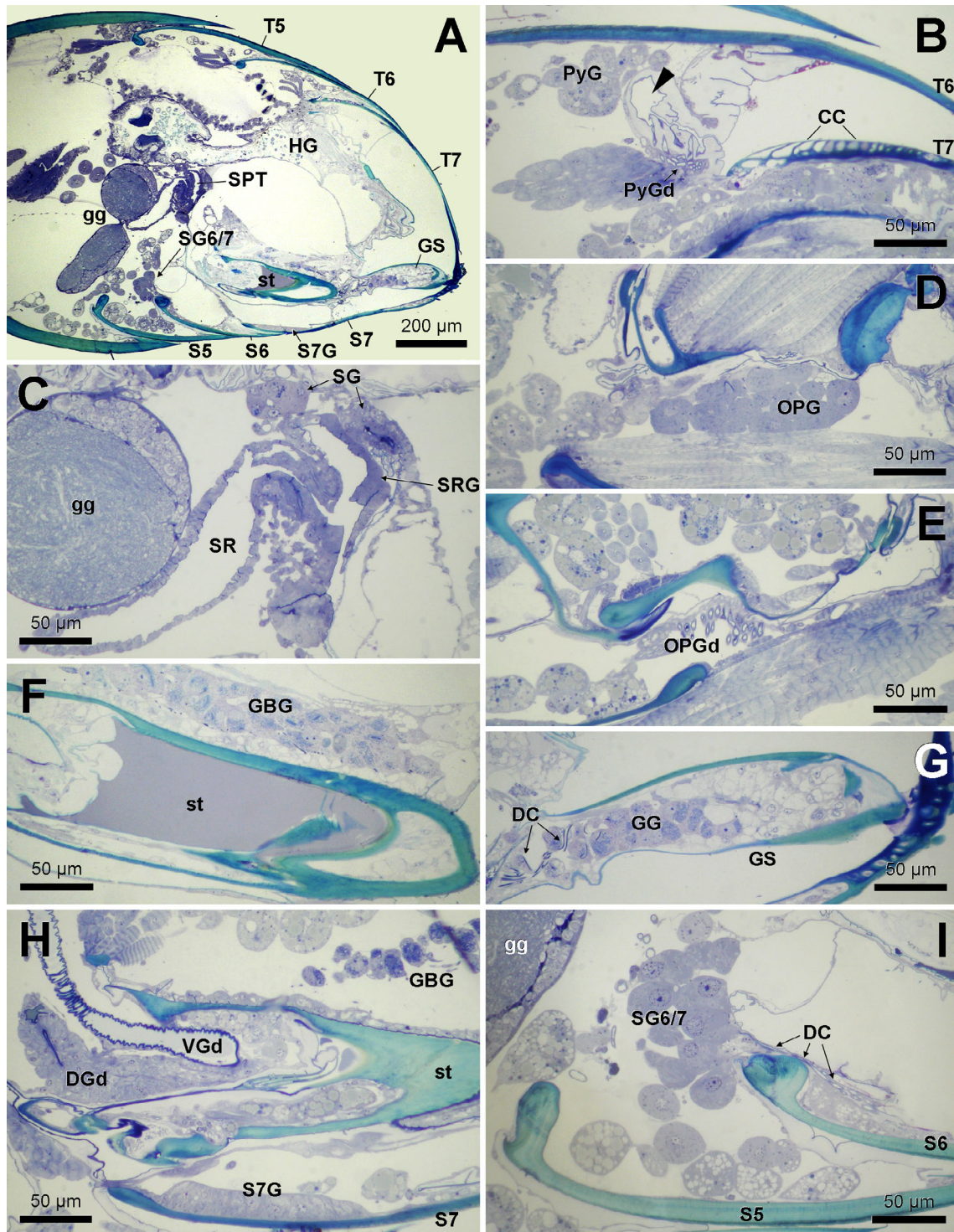
Figure 5 Semithin longitudinal sections of *Myopias conicara* showing abdominal glands. (A) Section through abdomen. gg, ganglion; GS, gonostylus; HG, hindgut; S5-7, sternites 5–7; SG6/7, sternal gland between 6th and 7th sternite; SPT, spermatheca; S7G, epithelial gland of 7th sternite; st, sting; T5–7, 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's 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.

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 50×20 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, approximately 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 approximately 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 two **spermatheca glands** with class-3 secretory cells (Fig. 5C). The epithelial wall of the reservoir is fairly thick (approximately 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 approximately 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, which 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 approximately 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**, which consists of a cluster of approximately 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 venom (dorsally) and Dufour's 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 ± 2.8 μm ($N = 10$) that each reach a length of approximately 1 mm. **Dufour's gland** is a simple tubular gland with a length of approximately 200 μm and a diameter of approximately 25 μm. Its epithelial lining is made up of 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 approximately 30 round class-3 cells with a diameter of 34.4 ± 2.6 μm ($N = 10$). 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 *M. hollandi* (Billen *et al.* 2013) was not found in *M. conicara*.

DISCUSSION

Biology of *Myopias*

Colony size is generally small in *Myopias*: more than 1,000 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 1,000 workers. As in most *Myopias* species, the 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 the 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, such as formicine and dolichoderine ants (Ward 2014), the queens exclusively feed on trophic eggs and/or oral trophallaxis with workers (e.g. *Anoplolepis gracilipes* (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* and *M. emeryi* (Forel) collected in Ulu Gombak, West Malaysia (F. Ito, unpubl. data, 2011). In addition to 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 for this diet diversity could 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 (1992) 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 1 h, 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 for 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 first removed the head of the millipede, and brought larvae that then fed on the inner tissue of the collum. After consuming the tissues of the collum, the exoskeleton was removed, and the feeding sequence was repeated for the following rings.

Exocrine glands

The exocrine repertoire of *M. 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), also a number of small unnoticed glands may occur. However, 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 *et al.* 1979; Jessen & Maschwitz 1983), 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). However, 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 fewer 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.

ACKNOWLEDGMENTS

REFERENCES

antmaps.org (2019) *Myopias* [cited 25 June 2019]. Available from URL: http://antmaps.org/?mode=diversity&genus=Myopias

Bartels PJ (1988) Reproductive caste inhibition by Argentine ant queens: new mechanisms of queen control. *Insectes Sociaux* **35**, 70–81.

Billen J (2009) Occurrence and structural organization of the exocrine glands in the legs of ants. *Arthropod Structure & Development* **38**, 2–15.

Billen J, Al-Khalifa MS (2015) Morphology and ultrastructure of the pro- and postpharyngeal glands in workers of *Brachyponera sennaarensis*. *Sociobiology* **62**, 270–275.

Billen J, Ito F (2018) Novel thoracic glands in the ant *Myopias hollandi*. *Arthropod Structure & Development* **47**, 229–237.

Billen J, Morgan ED (1998) Pheromone communication in social insects: sources and secretions. In: Vander Meer RK, Breed MD, Winston ML, Espelie KE (eds) *Pheromone Communication in Social Insects: Ants, Wasps, Bees, and Termites*, pp 3–33. Westview Press, Boulder, Oxford.

Billen J, Stroobants Z, Wenseleers T, Hashim R, Ito F (2013) Diversity and morphology of abdominal glands in workers of the ant genus *Myopias* (Formicidae, Ponerinae). *Arthropod Structure & Development* **42**, 165–172.

Bolton B (2019) *An Online Catalog of the Ants of the World* [cited 19 Sep 2019]. Available from URL: http://antcat.org

Brandão CRF, Diniz JLM, Tomotake EM (1991) *Thaumatomyrmex* strips millipedes for prey: a novel predatory behaviour in ants, and the first case of sympatry in the genus (Hymenoptera: Formicidae). *Insectes Sociaux* **38**, 335–344.

Brown WL Jr (1992) Two new species of *Gnamptogenys*, and an account of millipede predation by one of them. *Psyche* **99**, 275–289.

Eguchi K, Viet BT, Yamane Sk (2014) Generic synopsis of the Formicidae of Vietnam (Insecta: Hymenoptera), Part II – Cerapachyinae, Aenictinae, Dorylinae, Leptanillinae, Amblyoponinae, Ponerinae, Ectatomminae and Proceratiinae. *Zootaxa* **3860**, 1–46.

Eisner T, Alsop D, Hicks K, Meinwald J (1978) Defensive secretions of millipedes. In: Bettini S (ed.) *Arthropod Venoms (Hand Book of Experimental Pharmacology No. 48)*, pp 41–72. Springer-Verlag, Berlin.

Eisner T, Eisner M, Deyrup M (1996) Millipede defense: Use of detachable bristles to entangle ants. *Proceedings of the National Academy of Sciences of the United States of America* **93**, 10848–10851.

Hölldobler B, Engel H (1978) Tergal and sternal glands in ants. *Psyche* **85**, 285–330.

Hölldobler B, Wilson EO (1983) Queen control in colonies of weaver ants (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* **76**, 235–238.

Hopkin SP, Read HJ (1992) *The Biology of Millipedes*. Oxford University Press, Oxford.

Ito F (1998) Colony composition and specialized predation on millipedes in the enigmatic ponerine ant genus *Probolomyrmex* (Hymenoptera, Formicidae). *Insectes Sociaux* **45**, 79–83.

Jaitrong W, Tasen W, Guénard B (2018) The ant genus *Myopias* Roger, 1861 (Hymenoptera: Formicidae: Ponerinae) in Thailand, with descriptions of three new species. *Zootaxa* **4526**, 151–174.

Jessen K, Maschwitz U (1983) Abdominaldrüsen bei *Pachycondyla tridentata* (Smith): Formicidae, Ponerinae. *Insectes Sociaux* **30**, 123–133.

Jessen K, Maschwitz U, Hahn M (1979) Neue Abdominaldrüsen bei Ameisen. I. Ponerini (Formicidae: Ponerinae). *Zoomorphologie* **94**, 49–66.

Khalife A, Keller R, Billen J *et al.* (2018) Skeletomuscular adaptations of head and legs of *Melissotarsus* ants for tunnelling through living wood. *Frontiers in Zoology* **15**, 30.

Lee CC, Nakao H, Teng SP *et al.* (2017) Worker reproduction of the invasive yellow crazy ant *Anoplolepis gracilipes*. *Frontiers in Zoology* **14**, 24.

Lommelen E, Schoeters E, Billen J (2003) Development of the labial gland of the ponerine ant *Pachycondyla obscuricornis* (Hymenoptera, Formicidae) during the pupal stage. *Arthropod Structure & Development* **32**, 209–217.

Noirot C, Quennedey A (1974) Fine structure of insect epidermal glands. *Annual Review of Entomology* **19**, 61–80.

Peeters C, De Greef S (2015) Predation on large millipedes and self-assembling chains in *Leptogenys* ants from Cambodia. *Insectes Sociaux* **63**, 471–477.

Probst RS, Guénard B, Boudinot BE (2015) Toward understanding the predatory ant genus *Myopias* (Formicidae: Ponerinae), including a key to global species, male-based generic diagnosis, and new species description. *Sociobiology* **62**, 192–212.

Schoeters E, Billen J (1994) The intramandibular gland, a novel exocrine structure in ants (Insecta, Hymenoptera). *Zoomorphology* **114**, 125–131.

Schoeters E, Billen J (1997) The postpharyngeal gland in *Dinoponera* ants (Hymenoptera: Formicidae): unusual morphology and changes during the secretory process. *International Journal of Insect Morphology & Embryology* **25**, 443–447.

Schofield RMS, Nesson MH, Richardson KA (2002) Tooth hardness increases with zinc-content in mandibles of young adult leaf-cutter ants. *Naturwissenschaften* **89**, 579–583.

Ward PS (2014) The phylogeny and evolution of ants. *Annual Review of Ecology, Evolution, and Systematics* **45**, 23–43.

Willey RB, Brown WL Jr (1983) New species of the ant genus *Myopias* (Hymenoptera: Formicidae: Ponerinae). *Psyche* **90**, 249–285.

Xu Z (1998) Two new record genera and three new species of Formicidae (Hymenoptera) from China. *Entomologica Sinica* **5**, 121–127.

Xu Z-H, Liu X (2012) Three new species of the ant genus *Myopias* (Hymenoptera: Formicidae) from China with a key to the known Chinese species. *Sociobiology* **58**, 819–834.