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# Functional and chemical characterization of mandibles and mandibular glands of *Oecophylla smaragdina* (Fab.) worker ants

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**ABSTRACT**

Ant mandibles and associated mandibular glands are multifunctional mouthparts that play crucial roles in their eusocial life by assisting various functions like food capture, digestion, pheromone secretions, communication and defensive actions. Our study aims to analyze the physio-chemical properties of mandible and mandibular glands of workers of the Weaver ant *Oecophylla smargdina*. GC-MS analysis of mandibular gland contents revealed the presence of chemical components that had various ethological properties in relation to the eusocial life of *O.smaragdina.* SEM imaging provided insights on the topographical features of mandible and mandibular glands of *O. smaragdina*. EDS was used to characterize the presence of metals including manganese and zinc that contribute to the hardness of the mandibular exoskeleton.

**Key words:** Mandible, Mandibular gland, Weaver Ant, Mandibular secretions, Social insects.

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## INTRODUCTION

Ants (Hymenoptera: Formicidae) being one of the well-known eusocial insects, are an example of organisms that depend on pheromonal communications for their survival. They are the largest group of eusocial insects with cooperative signals among colony members for collective resource utilization, defensive actions and further other strategies for the survival of the colony (Chomicki and Renner, 2017). These highly organized colonies may consist of few to many individuals and they vary differentially in their habitat and feeding nature (Gathalkar and Sen, 2018). They exhibit complex morphological polyphenisms and the functioning of the colony is based on the caste system. (Simpson *et al.,* 2011; Londe *et al.,* 2015). The female ants are classified into morphological castes as workers, soldiers, ergatoid queens and queens (Molet *et al.,* 2012). The queen is the only fertile female and stays mostly inside the nest, workers are dimorphic; major workers perform outdoor tasks like foraging and defense whereas minor workers are in indoor tasks like brood maintenance (Anand *et al.,* 2022). Development of the castes depends upon nutrition and the endocrine system. With sufficient amounts of nutritious food, ant larvae could develop into a queen and could turn into a worker or soldier if nutritional deficient food is available. The existence of a reproductive queen in a colony averts the development of other queens in the same colony (Trible and Kronauer, 2021). Ants are symbiotically associated with other ant species, plants, fungi and various microorganisms and hence plays a significant role in the insect ecosystem (Chomicki and Renner, 2017). Basically, ants are active foragers, scavengers and predators that form a ubiquitous component of insect biodiversity. Being predators, they are important biological pest control agents that prey upon a wide range of insects. The foraging habit of various ant species can be beneficial or harmful to

another species (Gathalkar and Sen, 2018). Most foragers are able to quantify, qualify and also measure transportability of food sources, deciding whether or not to recruit accordingly for their colony. These abilities are aided by pheromonal communication. Predatory ants forage either by solitary hunting in case of small prey or by cooperative hunting, forming large raiding groups, which is the much-evolved method (Cerdá and Dejean, 2012).

The mouthparts of ants include a pair of mandibles which could be opened without the assistance of maxillo labial complex (Keller, 2011; Richter *et al.,* 2021). Mandibles are used for various tasks like prey-catching, leaf-cutting, digging, defensive actions, brood care, grooming and communication (Just and Gronenberg, 1999; Zhang *et al.,* 2020; Ferreira *et al.,* 2021). Mandible shapes have been evolved according to prey specialization in predatory ants (Cerdá and Dejean, 2012). The mandible is composed of a basal stem and a distal triangular-shaped blade. The muscles, craniomandibularis internus (0md1) and craniomandibularis externus (0md3) are responsible for the closing and opening of the mandibles respectively (Ozburn, 1935; Richter *et al.,* 2020). A hinge joint connects the shovel-like appendage to the head capsule. A dicondylic proximal articulation with both dorsal and ventral joints are present in the mandible of ants (Ozburn, 1935; Gronenberg *et al.,* 1998). Transition metals exist in the cuticle of several insect species, especially in the mouth parts and the external genitalia as a protective feature (Polidori *et al.,* 2020). The cuticular enrichment of metals improves rigidity of the body structures and prevents its wear and tear (Broomell *et al.,* 2006; Cribb *et al.,* 2008). Apart from numerous abdominal glands present in ants for their reproductive functions, an important exocrine gland associated with their mandibles are present in their head, called the mandibular gland. These are glands with great ethological importance and its chemical constituents are found to be multifunctional in action. Studies have confirmed the presence of certain chemicals present in the mandibular glands of ants to be involved in the interactions with each other and with the other species. The chemical composition of mandibular glands are caste-dependent, as it is in turn associated with their functions (Billen and Al-Khalifa, 2018). The functions of mandibular gland secretions vary from nestmate recognition to antimicrobial defence (Richter *et al.,* 2021). These glands are formed by a cluster of glandular cells and their secretions are released into a reservoir and a duct that opens to the mandalus, a membrane present on the dorsal mandibular base. Ant species with predacious habits and longer mandibles tend to have narrower and more elongated mandalus (Richter *et al.,* 2021). It was found that there is possible involvement of mandibular glands in rescue behavior of certain ant species (Hollis and Nowbahari, 2022). Mandibular glands produce ectosymbiotic secretion with antibiotic properties that diffuse into plants when ants feed or groom the plant. Antibiotic substances released from mandibular glands involve terpenoids and mellein (Offenberg and Damgaard, 2019). Strong antimicrobial activity of mandibular gland reservoir contents was discovered in certain ant species including *O. smaragdina* (Hoenigsberger *et al.,* 2018).

*Oecophylla* is a genus of weaver ants belonging to the subfamily formicinae. There are two main species of *Oecophylla* ants, the African weaver ant (*Oecophylla longinoda*) and the Asian weaver ant (*O. smaragdina*) (Hölldobler and Wilson, 1977; Bolton, 1995; Devarajan, 2016; Kempraj *et al.,* 2022). The weaver ants are believed to have originated in the early Paleogene (ca. 60 Ma) in the Palaearctic region and expanded geographical distribution because of the climatic changes occurred at ca. 43 Ma (Dlussky *et al.,* 2008; Rahman *et al.,* 2021). The Asian Weaver ant, *O. smaragdina* is a dominant arboreal species found in tropical Asia and Northern Australia with evolved predatory behavior and cooperative hunting strategies (Cerdá and Dejean, 2012). The name *O. smaragdina*, is derived from the Greek word oikos, meaning ‘house’ and phyllo, meaning ‘leaf’. They have a unique nesting behaviour wherein they use

hollow nanofibrous silk threads expelled by the final instar larvae to weave leaves of trees or shrubs (Wetterer, 2017). They prefer a polydomous nesting organisation in which more than a hundred nests are distributed over a considerable number of trees in their territory (Wilson and Hölldobler, 1980; Hölldobler, 1983; Sangma and Prasad, 2021). Smaragdina is derived from Latin word smaragdinus meaning emerald, referring to green colored queens of *O.smaragdina* (Wetterer, 2017).The queen is green in colour while the workers are orange-brown (Cole and Jones, 1948; Van Itterbeeck *et al.,* 2014). Being voracious predators, they have been used as biological control agents against insect pests in Asian countries for many centuries. It was found that the direct effects of predation include oviposition deterrence in pest species due to chemical emissions from the ant (Kempraj *et al.,* 2022). The antimicrobial properties of this species have been utilized in the integrated pest management in mango trees (Offenberg and Damgaard, 2019).

This is the first study focuses on the analysis of physicochemical characterization of mandibles and mandibular glands of *O. smaragdina* major workers.

## MATERIALS AND METHODS

### Ant collection

Worker ants of *O. smaragdina* were collected from two colonies located in the campus of Christ (Deemed to be University), Bangalore (12.933233ºN, 77.606673ºE) in Karnataka, India from February 2023 to July 2023. The ants were collected while foraging near their arboreal colonies using forceps and were placed in glass vials having soap solution. The ant was placed dorsally under a simple microscope and the head was dissected using a surgical blade 22. An incision was made at the back of head and the cut was extended till the mouth.

### X-Ray Diffraction analysis

The detached mandibles were fixed in 1 ml of 70% Ethanol and stored at 4°C. Over 60 mandibles were collected and powdered using mortar and pestle. About 0.7 g of the powder was pressed and analysed in Rigaku MiniFlex Powder XRD 600 with Cu- Kα radiation. The sample was scanned within the 2θ range of 10º to 90º at a scan speed of 10°/min.

### SEM (Scanning Electron Microscopy) analysis

Ant heads were dissected to obtain mandible and the associated mandibular gland. The Ant was placed under dissection microscope and head was dorsally cut using dissection scalpel blade. Mandibles and mandibular glands were traced and separated carefully. Transverse and longitudinal sections of mandibles were taken. Samples were preserved in Ethanol (70%). Samples were mounted in SEM viewing stage using carbon adhesive tape, sputter coated with chromium and viewed in Apreo 2 SEM (FEG, Color SEM Technology). The samples were detected by the Trinity Detection System.

### Dissection of mandibular glands

The mandibular glands were dissected using medical grade scapel merged in 0.2 M Phosphate buffer and careful detachment happened under dissection microscope.

### GC-MS analysis of mandibular gland secretions

Ant heads were dissected dorsally to obtain the mandibular glands. The glands obtained from the head were homogenized in chloroform for GC-MS Analysis.

### GC-MS Analysis

It was carried out on GCMS-QP2010SE (SHIMADZU) under the following conditions. Helium was used as carrier gas at a constant flow rate of 1.0 mL/min and an injection volume of 1uL was employed in a split-less mode. Initial oven temperature was maintained at 60º, the injector temperature was 280º and the interface temperature was 290º. Quadrupole mass analyser was used for mass spectral detection in the EI (Electron Ionisation) mode. The compounds present in the sample were identified from the chromatograph by comparing it with standards on the NIST17 mass spectral library.

### Statistical analysis

The data obtained from XRD, GCMS analyses were assessed and graphs were intrigued using Origin 2023b.lnk software

## RESULTS

### X-Ray Diffraction analysis

The XRD analysis confirming the presence of hydroxyapatite as the primary crystalline phase in the powdered ant mandible sample. The detected nanoscale crystallite size and minimal lattice strain designate agreeable hydroxyapatite crystals. The non-appearance of other detectable phases advocates a high degree of purity in the sample. These outcomes subsidize to understanding of the mineral composition and structure of ant mandibles, providing insights into their mechanical properties and potential biomimetic applications (Fig. 1).

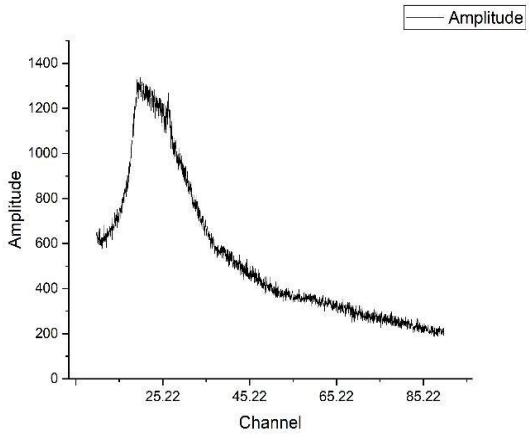


**Figure 1.** XRD analysis of powdered mandibles of *Oecophylla smaragdina*

### SEM Analysis

The topography of mandibular gland and mandible were analyzed by SEM imaging. Images of lateral section and transverse section of mandibles were obtained. Mandibles are elongated, triangular in shape with a masticatory margin on the proximal end and a prominent basal part. The molar region that bears a prominent concavity in the proximal part is associated with grinding of food. The average length and width of the mandible were found to be 435±20µm and 123±20µm


**Figure 2**. SEM Image of longitudinal section of mandible (*Oecophylla smaragdina)*; to-terminal opening, th-trigger hair, mr-molar region, hj-hinge joint.

respectively. The inner margin possessed 6-8 teeth arranged in a row at the distal end of the mandible. The outer lateral margin of the mandible has short thin extensions called trigger hairs (Fig. 2). These hairs act as mechanosensory triggers that likely provide proprioceptive information. The transverse section reveals the three distinguishable layers on the dense cuticle of the mandible, which are the inner basement membrane, middle endocuticle and outer exocuticle. The exocuticle is a highly

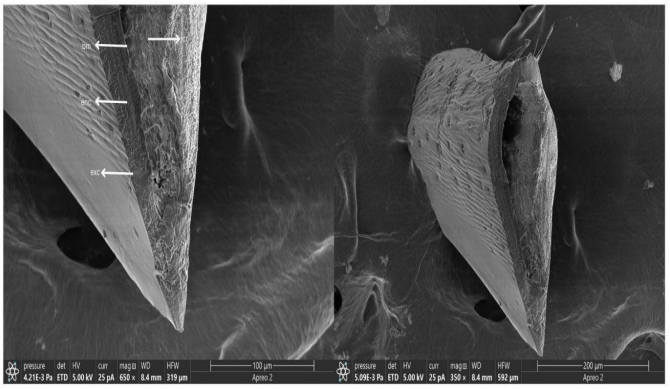


**Figure 3**. SEM Image of transverse section of mandible (*Oecophylla smaragdina)*; bm-basal membrane, enc-endocuticle, exc-exocuticle, cr-core.

sclerotised layer and contributes to the toughness and rigidity of the cuticle, whereas the endocuticle has comparatively a soft and flexible laminated structure (Fig. 3).


**Figure 4**. SEM Image of mandibular gland (*Oecophylla smaragdina)*; mg-mandibular gland, mgd-mandibular gland duct, md-mandible.

The interior cavity of the mandible is the core which opens to the exterior by terminal opening (Fig. 2, 3). And thus, it allows the passage of secretions from the salivary apparatus to outside. The core which is separated from the cuticle by the basement membrane. The mandibular glands are placed laterally inside the cephalic cavity and they open at the inner glands reach the mandible through this duct (Fig. 4). EDX was used to analyse the presence of certain metals like

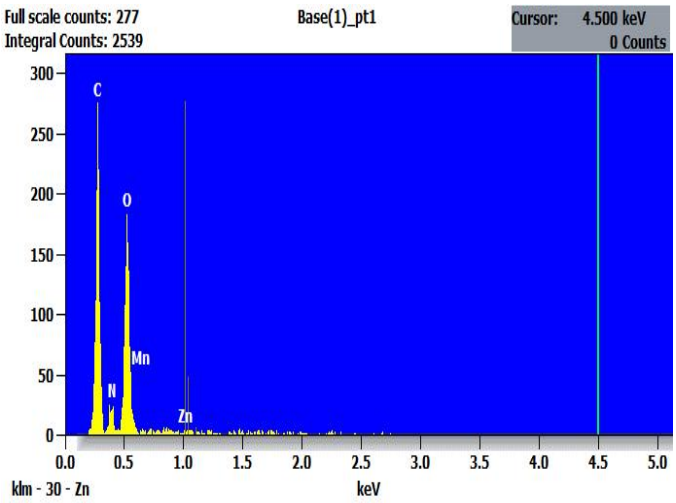


**Figure 5.** EDX analysis of mandible of *Oecophylla smaragdina*

manganese and zinc at various locations of the cutting edges of mandible, which probably contributes to the strengthening of mandible (Fig. 5) margin of mandibles by a narrow duct. The secretions of the glands reach the mandible through this duct (Fig. 4). EDX was used to analyse the presence of certain metals like manganese and zinc at various locations of the cutting edges of mandible, which probably contributes to the strengthening of mandible (Fig. 5)

**GC-MS Analysis**

The GC-MS analysis identified 25 compounds in the mandibular gland of *O. smaragdina*. The compounds and their biological functions were listed in table 1 and the peaks obtained from the analysis were plotted in fig. 6. From the GC-MS result, it is clear that the functional role of mandibular secretions of worker ants in the maintenance of ant colonies. The compounds Dodecane, 1-Eicosanol, Eicosane, 7-hexyl-, Heptacosane, and Phenol, 2,4-bis(1,1-dimethylethyl)-, phosphite present in the mandibular gland of the ant show antibacterial properties. Along with Tetratetracontane, Heptacosane and Phenol, 2,4-bis(1,1-dimethylethyl)-, phosphite provide antioxidant properties to the secretions. 1-Heptadecene is a constituent of the sex hormone, and Dodecyl acrylate acts as a pheromone in insects. 1-Hexacosanol plays a crucial role as a scent marker, which enables the ants to recognize the members of their colony.

**DISCUSSION**

The internal structure of the mandible was elucidated using SEM and the presence of metal zinc and manganese were detected using XRD. The components constituting the mandibular glands were analysed using GC-MS and the functions of each component were reviewed from literature.

The mandible is made of sclerotised cuticular exoskeleton and it is found to have three different layers: exocuticle, endocuticle and basement membrane. Apart from these layers, the inner porous part is the core which serves as passage to the outer environment (Zhang *et al*., 2019). The slightly curved distal extension of the mandible

**Table 1.** GC-MS data analysis of mandibular gland of *Oecophylla smaragdina*

| Compound | Biological Functions | References |
|---|---|---|
| Dodecane | Larviposition pheromone, antibacterial and antifungal properties | Francke and Schulz (1999) |
| 1-Octanol, 2-butyl- | Host plant recognition in whiteflies | Liu *et al*. (2022) |
| Dodecyl acrylate | Pheromone, animal metabolite and antibacterial properties | (Fahem *et al*., 2020) |
| 1-Heptadecene | Male sex hormone | Fockink *et al*., 2013) |
| 1-Eicosanol | Antibacterial activity against *Streptococcus mutans and S. gallinarum.* | Chatterjee *et al*., 2017) |
| 1-Hexacosanol | Acts as scent markers, due to its chemical stability and low volatility it can remain in habitat for a long period, facilitating territorial markings and recognition of individuals of the same species. | Porras *et al*., 2022) |
| Eicosane, 7-hexyl- | Antibacterial properties | Hossain *et al.*, 2013) |
| Bis(2-ethylhexyl) phthalate | Reproductive and developmental toxicity in insect larva. | Planelló *et al*., 2011) |
| Tetratetracontane | Antioxidant and cytoprotective activity | Amudha *et al*., 2018) |
| Heptacosane | Antibacterial and Antioxidant properties | Ibnouf *et al*., 2022) |
| Squalene | An intermediate of cholesterol biosynthesis(cholesterol is not reported to be synthesised in any insects) | Dutton *et al*., 2002) |
| Octacosane, 2-methyl- | Antimicrobial activity | Barretto and Vootla, 2018) |
| Phenol, 2,4-bis(1,1-dimethylethyl)-, phosphite (3:1) | Antioxidant and antibacterial (anti-enterococcal) activity | Tyagi *et al*., 2021) |

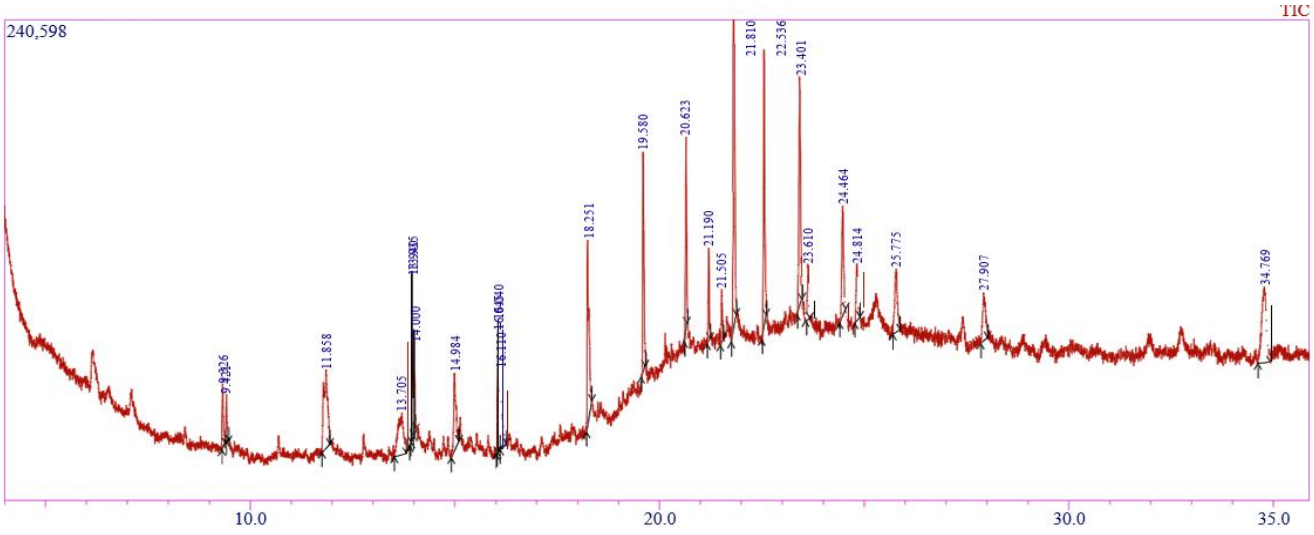


**Figure 6.** GC-MS data analysis of mandibular gland of *Oecophylla smaragdina*

accounts for its cutting and grasping hook-like structure. The molar region and its concavity aids in mastication of food serves as the grinding area (Boublil *et al.,* 2021). The left and right mandibles are slightly asymmetric and their teeth interlock with each other when the mandibles are closed (Boublil *et al.,* 2021). The terminal opening of the mandibular tip is in turn connected to the salivary apparatus which includes the mandibular gland (Kumar and Sahayaraj, 2012). The mandibular glands are known to have small flattened cells with high concentration of F-actin which contributes to its secretory nature (do Amaral and Machado-Santelli, 2008). The secretions are initially released into a reservoir, from which the duct leads the secretions to exterior (Richter *et al.,* 2021). The trigger hairs of the mandible are known to provide sensory information that are necessary to coordinate movements of the mandible (Weihmann *et al*, 2015). The mandibles on each side are hinged to the head capsule by two condyles (dicondylic). The opening and closing of mandibles are aided by a pair of abductor and adductor muscles respectively. Presence of metals; zinc and manganese are known to enhance the hardness of cuticular exoskeleton of the ant mandible (Cribb *et al.,* 2008). After the pre-ecdysial tanning and eclosion, the accumulation of zinc was found to be about 16% of dry mass in the ant Tapinoma sessile. Other heavy metals collected in the mandibular teeth were manganese, calcium and chlorine (Schofield *et al.,* 2003).

One of the main compounds present in the mandibular gland was the Dodecane, an aliphatic compound acting as larviposition pheromone and attracts gravid females to the larva in tsetse fly (*Glossina morsitans*) (Francke and Schulz, 1999). The compound in the leaves of *Silybum marianum*(L) has both antibacterial and antifungal properties (Padma *et al.,* 2019). 1-Octanol, 2-butyl- is used by whiteflies (Bemisia tabaci Gennadius) for host plant recognition (Liu et al., 2022). Dodecyl acrylate could take the role of animal metabolite and pheromone. The compound has antibacterial activities in medicinal plants (Fahem et al., 2020). 1-Heptadecene acts as sex pheromone in male Carrion Beetles (*Oxelytrum discicolle*) (Fockink *et al.,* 2013).

1-Eicosanol has proven to show antibacterial activity against *Streptococcus mutans* and *Streptococcus gallinarum* in the leaves of *Solena amplexicaulis* (Chatterjee *et al.,* 2017). 1-Hexacosanol with chemical stability and low volatility, acts as scent markers and facilitates territorial markings in arthropods (Porras *et al.,* 2022). Eicosane, 7-hexyl- in *Azadirachta indica* has antibacterial properties (Hossain *et al.,* 2013). Bis(2-ethylhexyl) phthalate is an anti-androgenic phthalate and causes reproductive and developmental toxicity in insect larva (Planelló *et al.,* 2011). Antioxidant and cytoprotective activity is exhibited by Tetratetracontane in the leaves of Enhalus acoroides seagrass (Amudha *et al.,* 2018). Heptacosane shows antibacterial and antioxidant properties in actinomycetes (Ibnouf *et al.,* 2022) while Octacosane, 2-methyl- shows antimicrobial activity in Cryptococcus rajasthanensis, a yeast isolated from *Bombyx mori* gut (Barretto and Vootla, 2018). Phenol, 2,4-bis(1,1-dimethylethyl)-, phosphite is an antioxidant and antibacterial (anti-enterococcal) agent in a thermophilic cyanobacterium, *Leptolyngbya* sp (Tyagi *et al.,* 2021). Squalene is an intermediate of cholesterol biosynthesis (Dutton *et al.,* 2002).

Our results revealed the structure of the mandible and identified the chemical compounds present in the mandibular gland of *O. smaragdina*. The transverse section of mandibles of the worker ants revealed three layers primarily of proteins, identified as the basal membrane, endocuticle, exocuticle and the inner core. The metals Zinc and Manganese were detected in the mandibles, enhancing the hardness of the appendage used mainly for food processing and defence. Most of the chemical compounds identified in the mandibular glands are proven to possess antimicrobial properties. The compounds like dodecane and 1-Heptadecene function as hormones, the former being a pheromone and the latter being a sex hormone. Our study provides significant insights into the structural

characteristics of the mandibles and the role of chemical compounds in the mandibular gland of *O. smaragdina* worker ants.

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