



RESEARCH ARTICLE - WASPS

Description of the Intramandibular Gland II in *Polybia emaciata* Lucas, 1879 (Hymenoptera: Vespidae)

C CELY¹, AP ARÉVALO², J BILLEN³, CE SARMIENTO²

1 - Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, USA

2 - Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia

3 - Zoological Institute, Katholieke Universiteit Leuven, Leuven, Belgium

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Corresponding author

Carlos E. Sarmiento

Laboratorio de Sistemática y Biología

Comparada de Insectos

Instituto de Ciencias Naturales

Universidad Nacional de Colombia

A. A. 7495 - Bogotá, Colombia.

E-Mail: cesarmientom@unal.edu.co

Abstract

The intramandibular gland II in *Polybia emaciata* Lucas is described. This species is among the few that uses mud for nest construction, and their nests persist for a long time following abandonment. The intramandibular gland II has been found in single representatives of the genera *Mischocyttarus*, *Apoica* and *Leipomeles*, and this record is the second for the genus *Polybia*. Despite expectations derived from the nest characteristics of the species, gland dimensions such as cell diameter were well within the range observed for other species, with the cell number even comparatively small. Gland function remains to be investigated.

Introduction

Exocrine glands have a major role in insect social life, because these glands regulate communication, social structuring, and nest construction of colonies, among other behaviors (Billen & Morgan, 1998). The characterization of exocrine glands has been an important research area dated back to the 17th century (Heselhaus, 1922; Billen & Wilson, 2008). However, the discovery of new glands is ongoing with new reports published on a regular basis, particularly for social wasps for which studies are less frequent (Samacá et al., 2013; da Silva et al., 2015; Penagos-Arévalo et al., 2015).

Polybia emaciata Lucas, 1879 is a medium-sized wasp (head width 2.18 mm, wing length 10 mm), with a color pattern that is primarily dark yellow with black or brown markings on several parts of the body. The wasp is a

swarm-founding species found extensively from Mexico to Brazil, from sea level up to 1500 m.a.s.l., and is very common in farmlands. The colonies range from 100 to 500 individuals and include several queens (Richards, 1978; Strassman et al., 1992). A notorious characteristic of this species, shared only with four other congeneric species of the Polistinae, is the use of mud for the nest; these nests persist for a long time even after being abandoned (Rau, 1933; Skutch, 1971; O'Donnell & Jeanne, 2007). This persistence may be attributed to the mud-saliva mixture used in nest construction (Schremmer, 1984). Given the results of Schremmer (1984) on nest composition and characteristics, which require extensive chewing and processing behaviors from the wasps, we agreed with the proposed role of the head glands in determining the characteristics of the nest materials for this species. In addition to the salivary glands, palpal and mandibular glands also occur and may have a function



associated with nest construction material characteristics; however, these structures have not been investigated.

Inside the mandibles of Neotropical social wasps, three glands have been identified, the intramandibular gland I, the intramandibular gland II, and the ectal mandibular gland (Penagos-Arévalo et al., 2015). The intramandibular gland I is a class 1 gland, whereas the other two are class 3 glands. Class 1 glands are a lining of epithelial cells on the internal surface of the body wall, and class 3 glands are bicellular units consisting of a large secretory cell and a duct cell (Noirot & Quennedey, 1974). Previous authors have identified the intramandibular gland II in other hymenopterans (Nedel, 1960; Costa Leonardo, 1978; Schoeters & Billen 1994). Cely-Ortiz observed this gland in *Polybia emaciata* in his unpublished undergraduate work (2011). However, in vespids, Penagos-Arévalo et al., (2015) provide the formal record of this gland. These authors recorded the gland in four of 33 species studied, and although *P. emaciata* was included in their extensive study, they did not report the intramandibular gland II in this species. Here, we describe the intramandibular gland II for *Polybia emaciata*.

Materials and Methods

For our results to be more comparable with previous publications (Penagos-Arévalo et al., 2015) and because foragers are the caste involved in nest construction, foragers of *Polybia emaciata* were net-collected from Sylvania, a farmland municipality in Cundinamarca, Colombia (4°24'19.7"N, 74°22'30.9"W, 1475 m.a.s.l.). Wasps were delicately handled with soft forceps. Head section preparation followed standard protocols as described by Billen (1998), Samacá et al. (2013) and Penagos-Arévalo et al. (2015). Forager heads were sectioned after the posterior part of the vertex was removed and were immediately submerged in 2% glutaraldehyde in Na-cacodylate buffer for approximately 12 h at 4°C. The heads were then transferred to fresh buffer. Tissues were then dehydrated in a graded acetone series and embedded in Araldite. Serial sections of 2 µm in thickness were obtained with a Leica EM-UC6 ultramicrotome (Leica microsystems, Vienna, Austria), followed by staining with methylene blue and thionin. A Zeiss Jenaval optical microscope (Carl Zeiss, Jena, Germany) was used for morphological analysis and a Canon D90 digital camera for photography (Canon, Japan).

We described cell shape, cell distribution, and duct presence of the gland cells following Herzner et al. (2007) and Samacá et al. (2013). Gland description included the following: location, cell type according to the classification provided by Noirot and Quennedey (1974), maximum dorsoventral or anteroposterior extension, and cell diameter (Britto et al., 2004; Billen, 2009; Penagos-Arévalo et al., 2015).

Results

As described by Penagos-Arévalo et al. (2015) for other species, the intramandibular gland II is a class 3 exocrine organ

located inside the mandibles at the mesal and ectal sides close to the denticles. In *P. emaciata*, secretory cell clusters were formed by approximately 28 round-shaped well-defined cells, with an average diameter of 22.3 µm. The nuclear membrane was not clearly defined but between 4 and 5 nucleoli were observed per cell. Ducts with an internal diameter of 0.5µm directed to the mesal part of the mandible exoskeleton were observed, although we did not find skeletal pores (Fig 1).

Discussion

Contrary to our expectations, given the nature of the material used for nest construction and the potential role of head glands in processing this material, the gland characteristics observed in *P. emaciata* fit well within those observed for the other four species in which the gland has been observed: *Mischocyttarus angulatus* Richards, 1978; *Apoica gelida* Van der Vecht, 1973; *Leipomeles spilogastra* (Cameron, 1912); and *Polybia liliacea* (Fabricius, 1804).

The gland cell diameter of *P. emaciata*, 22.3 µm, was within the range of 10-70 µm for the other four species, as described by Penagos-Arévalo et al. (2015). The diameter was most similar to that observed for the distant species *Mischocyttarus angulatus* (25 µm) and most different from that of the more closely related species *Polybia liliacea* (70 µm). The number of glandular cells was much lower than the range of 50-150 cells observed in the other species, including in the congeneric *P. liliacea* (60) (Penagos-Arévalo et al., 2015). We did not observe any pattern for the number of cells and the species *Mischocyttarus angulatus* and *Apoica gelida*, show the extreme variations in cell number (50 and 150 cells, respectively). The low number of cells might be a consequence of the age stage at which wasps were captured. Task partitioning is well known in vespids (Jeanne, 1991), and several studies demonstrate a relationship between gland size and task frequency (Downing, 1991; García & Noll, 2013); however, studies have also debated this correlation (Britto et al., 2004). We collected foragers of *P. emaciata*, and therefore, the gland was possibly not active in individuals at this stage. A planned sampling strategy is required to determine the relation in *P. emaciata*.

The hypopharyngeal and clypeal glands of *P. emaciata* are not particularly different in gland cell diameter and cell number from other polistines of similar size or from congeneric species (Penagos-Arévalo et al., 2015). For example, the cell number for the hypopharyngeal gland of *P. emaciata* is within the range observed in other species of similar head-widths, such as *Brachygastra augusti* (de Saussure, 1854), *Angiopolybia pallens* (Lepelletier, 1836) and *Polybia occidentalis* (Olivier, 1791). For this gland in *P. emaciata*, the number of cells was also within the range of the number for seven other *Polybia* species.

The taxonomic distribution of this gland is somewhat challenging, because the gland has been found in only four phylogenetically dispersed genera, including *Mischocyttarus*,

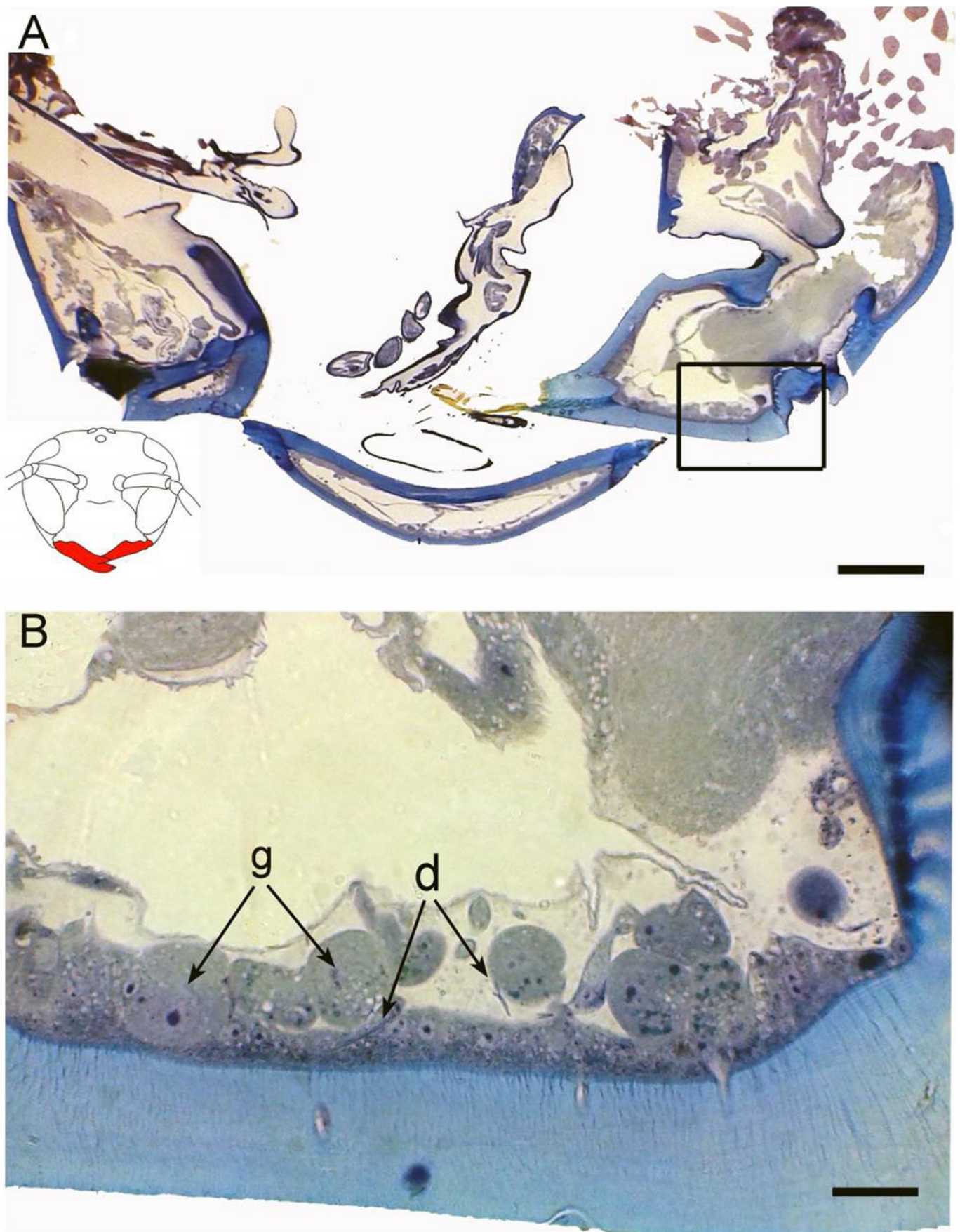


Fig 1 A-B. Intramandibular gland II in forager of *Polybia emaciata* Lucas. A. General cross-sectional view of the mandibles; the inset indicates the location of gland cells at the base of the mandible. B. Close-up view of framed part in A, showing gland cells (g) and ducts (d). Scale bars: A=50 μ m, B=20 μ m.

Apoica, *Leipomeles* and *Polybia* itself; additionally, congeneric species of *Mischocyttarus* and *Apoica* that have been carefully studied previously do not present this organ (Penagos-Arévalo et al., 2015). Within the genus *Polybia*, we observe a similar situation, because the gland was reported for *Polybia liliacea* (F. 1804) by Penagos-Arévalo et al. (2015), but not for six other species studied.

In all species of Neotropical Polistinae studied, glands are found such as the hypopharyngeal gland, the periocular gland, and the intramandibular gland I (Penagos-Arévalo et al., 2015); however, either a reversal of a gland or a scattered occurrence in the Polistinae has been previously reported. For example, following a more precise definition of Richards' gland, this gland apparently evolved in the Epiponini but two reversals occurred (Samacá et al., 2013). In the study by Penagos-Arévalo et al. (2015) conducted with 33 species of Neotropical Polistinae, the periocular gland, the posterobasal gland, the ocellar gland I, the ocellar gland II, and the subantennal gland were reported in only a few taxa or absent in some species. Clarifying the factors responsible for this lability in gland occurrence should be an interesting area of research that requires detailed information.

Schremmer (1984) conducted an interesting study on the nests of *P. emaciata*, and the results strongly indicate that organic compounds provided by the workers are the agents responsible for the physical characteristics of the structure. He hypothesized that the salivary glands could provide these molecules. Although we did not directly study the salivary gland, our results and the comparative data provided by Penagos-Arévalo et al. (2015) for all the other head glands provide indirect support to that hypothesis, because none of the morphometric characteristics observed in these organs are significantly different from other species. A specific study on this organ will help to confirm this hypothesis.

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