



## Defensive glands in Stylotermitidae (Blattodea, Isoptera)

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## ABSTRACT

The large abundance of termites is partially achieved by their defensive abilities. Stylotermitidae represented by a single extant genus, *Stylotermes*, is a member of a termite group Neoisoptera that encompasses 83% of termite species and 94% of termite genera and is characterized by the presence of the frontal gland. Within Neoisoptera, Stylotermitidae represents a species-poor sister lineage of all other groups. We studied the structure of the frontal, labral and labial glands in soldiers and workers of *Stylotermes faveolus*, and the composition of the frontal gland secretion in *S. faveolus* and *Stylotermes halumicus*. We show that the frontal gland is a small active secretory organ in soldiers and workers. It produces a cocktail of monoterpenes in soldiers, and some of these monoterpenes and unidentified proteins in workers. The labral and labial glands are developed similarly to other termite species and contribute to defensive activities (labral in both castes, labial in soldiers) or to the production of digestive enzymes (labial in workers). Our results support the importance of the frontal gland in the evolution of Neoisoptera. Toxic, irritating and detectable monoterpenes play defensive and pheromonal functions and are likely critical novelties contributing to the ecological success of these termites.

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## 1. Introduction

Termites (Isoptera) are eusocial insects of prime ecological importance, contributing significantly to tropical invertebrate faunas (Bar-on et al., 2018; Tüma et al., 2020). Indeed, termites are

among the main decomposers of dead plant tissues on a global scale and are broadly recognized as key ecosystem engineers (Jouquet et al., 2011; Eggleton, 2011; Bignell, 2016). There are about 3000 described species of termites, out of which about 10% are of economic importance, with many acting as serious invading pests of timber and agriculture (Evans et al., 2013; Krishna et al., 2013). Termites are classified into ten families, i.e., Mastotermitidae, Hodotermopsidae, Archotermopsidae, Hodotermitidae, Stolotermitidae, Kalotermitidae, Stylotermitidae, Rhinotermitidae, Seritermitidae, and Termitidae; the last four of which comprise the crown group Neoisoptera, characterized by the presence of a frontal

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