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REVIEW

Glandular Secretions of Ants (Hymenoptera: Formicidae): A Review on Extraction, Chemical Characterization and Antibiotic Potential

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Abstract

Ants live under ideal microclimatic conditions for the development of microorganisms. As mechanisms to ensure the health of the colony and as a defense strategy, these insects developed exocrine glands that work in the production of antibiotics (chemical defense) and in the immune defense of the colony. This study aimed to describe the state-of-the-art on extraction methods, chemical characterization and the antibiotic potential of glandular secretions of ants. This is a review of the scientific literature between 1989 and 2017. A total of 52 articles were selected. These addressed the behavior, chemical characterization, the antimicrobial effect and evaluated methods of extraction. The most investigated genera are *Atta, Acromyrmex*and *Crematogaster*. The glands most reported in the articles involving extraction of secretions were Dufour, mandibular and metapleural. The most reported methods of extraction were gland maceration and extraction with (organic) solvents and direct extraction of the gland. Most studies evaluated secretions with respect to ant behavior. There is a paucityin the literature about the chemical characterization of most glandular secretions of ants, as well as for most taxa. The same deficiency is observed with regard to prospecting the antibiotic and antifungal potential of these secretions.

Introduction

Ants represent a group of social insects found in all terrestrial ecosystems, with the exception ofthe poles (Hölldobler & Wilson, 1990; Fernández, 2003). In the tropics, these insects present the higher richness, abundance and number of endemic species (Guenard et al., 2012; Baccaro et al., 2015). Formicidae is composed of 20 subfamilies, 474 genera, 16,029 species (AntWeb, 2018). The ubiquity of these organisms and their multiple interactions with other species make them one of the dominant insect families in tropical terrestrial ecosystems (Campos, 2011; Morreau & Bell, 2013).

Formicids construct subterranean nests (soil and subsoil), as well as in the litter, tree cavities and plant roots (Baccaro et al., 2015; Billen et al., 2016). They live in symbiosis with other insects, plants, fungi and bacteria, play a vital role in enriching the soil in many ecosystems. When attacking plants or animals, they act as natural agricultural pest enemies and participate in a multitude of additional interactions that shape terrestrial ecosystems (Morreau & Bell, 2013). In Brazil, 1,458 species have been cataloged, distributed in 111 genera, which means that the country has one of the largest diversity of these organisms in the world (Baccaro et al., 2015).

Ants are social insects that live in colonies characterized by a dense aggregation of related individuals interacting with each other (Tragust, 2016; Penick et al., 2018). Their activities are regulated by climatic factors, such as temperature and humidity (Lutinski et al., 2017). These factors, within the colony, generateideal microenvironments for the development of symbiotic microorganisms or that expose the colony to potentially lethal diseases (Hölldobler; Wilson, 1990; Tranter et al., 2015; Penick et al., 2018).

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As an adaptation and survival strategy, ants present mechanisms to defend their colonies (Junqueira et al., 2014; Penick et al., 2018). Protection against pathogens can occur through behaviors, production of antibiotics (chemical defense) and immune defenses (Yek & Mueller, 2011; Penick et al., 2018).

Ant colonies need to be kept clean. Valuable resources such as stored foods need to be preserved and group members, including immature forms, have to be protected. These ecological and life history characteristics of insect societies probably increased the selective pressure to develop external immune defenses (Tragust, 2016; Penick et al., 2018). Ants are known to have the largest number of exocrine glands, with 84 glands already described (Billen & Sobotník, 2015), most of which are used in defense against pathogens (Yek & Mueller, 2011; Vander Meer, 2012). The glands most cited in the scientific literature are metapleural, mandibular, venom gland and Dufour (Tragust, 2016; Billen, 2017).

The metapleural gland is of special importance (Pech & Billen, 2017), it is exclusive to ants and consists of pair structures located in the posterolateral region of the thorax (Bot et al., 2002; Junqueira et al., 2014, Pech & Billen, 2017). It is known mainly for the production of antibiotics capable of inhibiting fungi and bacteria that develop within the colonies (Yek et al., 2012; Tragust et al., 2013; Tranter et al., 2015). Its unique presence in ants suggests a decisive role in the origin and ecological success of these insects (Hölldobler; Wilson, 1990; Ward, 2010, Tranter et al., 2015). The metapleural gland is absent only in species of the genus *Camponotus*, suggesting that its secretions are used in the recognition of colonies or species and in the marking of nest entrances (Yek & Mueller, 2011).

The Dufour and venom glands are abdominal exocrine glands which occur in association with the reproductive tract (Hölldobler & Wilson, 1990; Zhou et al., 2018). The Dufour gland produces trail, recruitment and mating pheromones (Mitra, 2013). The venom gland releases alarm and trail pheromones and especially acts on the capture and defense of prey as an integral part in the topical application of venom (Mitra, 2013; Billen, 2017; Zhou et al., 2018). The mandibular gland occurs in the anterior region of the head, near the basal margin of the compound eye (Billen et al., 2016). It is responsible for secreting compounds that are part of an alarm and recruitment system, sex pheromones and antibiotic substances (Billen et al., 2016; Billen & Al-Khalifa, 2018).

Most studies with the metapleural, mandidular, venom and Dufour glands have the objective of studying the evolutionary origin and morphology of the gland (Yek & Mueller, 2011; Viera et al., 2011; Pech & Billen, 2017; Billen, 2017; Zhou et al., 2018). Only a few ant species have been studied in detail to identify active chemical compounds and their function (Ortius-Lechner et al., 2000; Yek & Mueller, 2011; Tranter et al., 2015, Tragust, 2016). This provides support to state that ants depend on antimicrobial secretions for defense against pathogens (Penick et al., 2018). However, if all or most species of ants produce secretions with antibiotic potential, this is not known, remaining a gap in the scientific literature.

People are daily exposed to pathogenic microorganisms that have the potential to cause disease. The bacterial genera responsible for causing the highest frequency of nosocomial infections are *Escherichia* Castellani and Chalmers, 1919, *Staphylococcus* Rosenbach 1884, *Enterobacter* Hormaeche and Edwards 1960, *Klebsiella* Trevisan, 1885 and fungi of the genera *Candida* Berkin, 1923 and *Aspergillus* Micheli, 1729 (ANVISA, 2004; Maciel & Cândido, 2010; Almeida & Farias, 2014). However, the increasing development of resistance of microorganisms to conventional antibiotics has become a worldwide concern (Loureiro et al., 2016). Given the above, there is a need to prospect new antibiotics for human needs. Ants represent a promising and relatively unexplored alternative (Melo & Fortich, 2013; Song et al., 2012; Penick et al., 2018). In this context, the study aimed to describe the state-of-the-art on extraction methods, chemical characterization and the antibiotic potential of glandular secretions of ants.

Methodology

Characterization of the study

In this study, we conducted an integrative review of the literature on what was scientifically produced on the extraction and use of glandular secretions of ants. The integrative review consists of the analysis of the theoretical and empirical literature (Mendes et al., 2008; Souza et al., 2010). The main objective of the integrative review is to provide an understanding of the phenomenon analyzed, with the potential to build a scientifically grounded knowledge in previous studies (Mendes et al., 2008; Souza et al., 2010).

Search, selection and inclusion of articles

The search for articles was performed in CAPES journals portal, in an advanced search using the terms “gland secretion” and “ants”, without selecting a specific database. Two articles found in the Biblioteca Virtual emSaúde (BVS) and three selected in the Scientific Electronic Library Online (SCIELO) were included because they directly met the criteria determined for analysis, as follows:Attygalle et al. (1998), Nascimento et al. (1996), Marsaro-Júnior et al. (2001), Quinet et al. (2012) as well as Melo and Fortich (2013). Time series included articles published between 1989 and 2017.

The selection of articles was based on searches in the CAPES Journals Portal database. The search was carried out from March to June 2018. Only articles were selected, not including theses, dissertations, monographs and abstracts. The selection included works published in national and international journals, in Portuguese, Spanish and English. All articles have been downloaded to an electronic directory in the Portable Document Format (.pdf) extension and identified. In all, 329 articles were found.

The preliminary analysis was based on the reading of the titles, abstracts and keywords. According to the selection criteria the selected articles were those that presented in their scope: a) extraction of glandular secretions or ant compounds; b) chemical characterization of glandular secretions of ants and; c) test or application of ant secretions. From this pre-analysis, we selected the articles of the review.

Articles that met the selection criteria were read in full. Information was extracted and tabulated in a database in Excel for Windows (.xlsx) (Microsoft Inc., 2010). The information extracted was year of publication, scientific journal, authors, title, objective, study focus, taxon, studied gland, extraction method, chemical characterization and application.

Analysis

Data were explored for frequency and results presented through graphs and tables constructed in Excel for Windows (.xlsx) (Microsoft Inc., 2010).

Results

In all, 52 articles were included in the review. There was an upward trend in the frequency of studies using substances extracted from ants during the evaluated period. The highest number was observed in 2012 (n = 7), followed by the year 2000 (n = 6). However, there was a fluctuation in the frequency in the period (Figure 1).

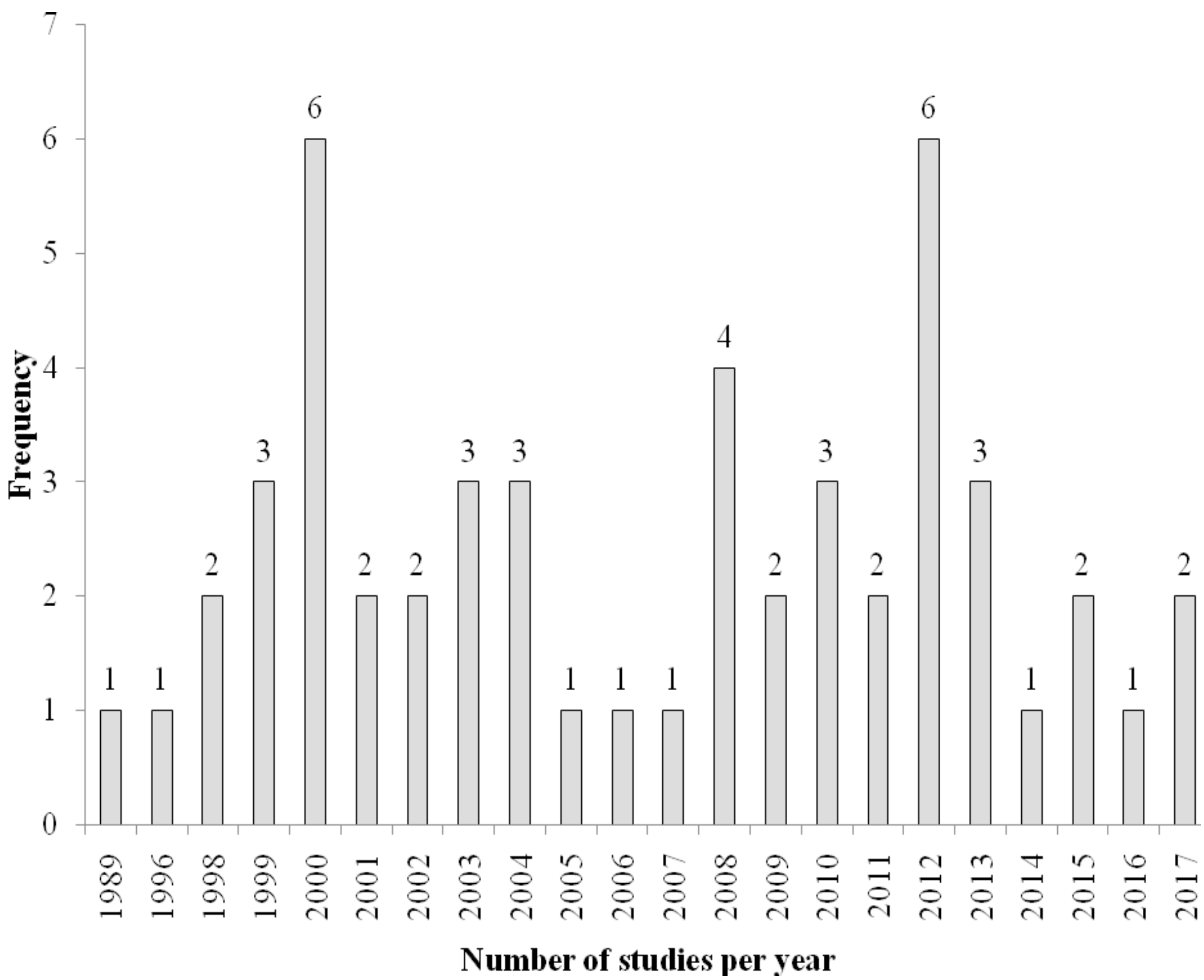

Fig 1. Historical series and frequency of the studies performed for the extraction of substances from ants, between 1989 and 2017.

A total of 26 (50%) studies aimed to analyze behavior, 20 (38.46%) performed chemical characterization, six (11.54%) tested the antimicrobial effect and two (3.85%) evaluated extraction methods. Only five of the articles selected were developed in Brazil. The ant genera most cited in the reviewed articles were *Crematogaster* Lund, 1831 (9), followed by *Atta* Fabricius, 1804 (8), *Acromyrmex* Mayr, 1865 (6), *Solenopsis* Westwood, 1840 (5), *Cataglyphis* Foerster, 1850 (4), *Camponotus* Mayr, 1861 (3), *Pogonomyrmex* Mayr 1868(3) and *Polyergus* Latreille, 1804 (3) (Appendix).

The glands most frequently reported in the articles involving extraction of ant secretions were Dufour (21.15%), metapleural (15.38%) and mandibular (11.53%). It is worth mentioning that many studies have reported a combination of glands, parts of the ant or the whole ant in the studies (Table 1).

Table 1. Glands and/or tissues used in the studies conducted for the extraction of substances from ants.

Glands and/or tissues	Frequency (n)	Percentage
Dufour	11	21.15
Metapleural	8	15.38
Mandibular	6	11.53
Dufour and venom gland	5	9.61
Venom gland	5	9.61
Whole ant and trisected	4	7.69
Post-pharyngeal	3	5.76
Mandibular and gastric	2	3.84
Whole ant, Dufour and venom gland	1	1.92
Head capsule	1	1.92
Mandibular and post-pharyngeal	1	1.92
Mandibular, labial, Dufour, venom gland and ovaries	1	1.92
Mandibular and metapleural	1	1.92
Mandibular, Dufour and venom gland	1	1.92
Intramandibular.	1	1.92
Post-pharyngeal and Dufour	1	1.92

The extraction methods most reported in the articles were maceration of the gland and extraction with solvents such as acetone, chloroform, dichloromethane, hexane, methanol, pentane, ethanol, direct extraction of the gland and maceration of the gland in water. In most articles, the main objective is to evaluate the behavior of ants. Only 11.54% of the articles tested the antimicrobial effect of substances extracted from ants (Table 2).

Discussion

The majority (50%) of the selected articles analyzed the action of glandular substances on the behavioral interaction of ants. A minority evaluated antimicrobial activity and methods forextracting glandular secretions. The genera *Crematogaster*, *Atta*, *Acromyrmex* and *Solenopsis* were mentioned in the largest number of studies related to the extraction, identification and application of secretions. The most reported glands involving substance extraction were Dufour, metapleural and mandibular. The most reported methods of extraction were maceration of the gland and extraction with (organic) solvents and direct extraction of the gland.

Ants present 85 exocrine glands secreting chemical substances (Adams et al., 2012; Billen & Sobotník, 2015). The evolutionary origin suggests that most of these glands are used in defense against pathogens (Yek & Mueller, 2011; Vander Meer, 2012). The ecological niche and selective pressure may influence the amount and composition of the glandular secretions produced (Yek & Mueller, 2011; Billen, 2017).

Table 2. Articles with different methods of extraction and evaluations to test the origin and functions of substances extracted from ants.

Authors	Extractionmethod	Evaluation
Attygale et al. (1989); Nascimento et al. (1996); Leclercq et al. (2000); Ortius et al. (2000); Yek et al. (2012); Quinet et al. (2012); Liu et al. (2017)	Direct extraction from the gland	Repellent, antimicrobial and chemical.
Mori et al. (2000); Ortius-Lechner et al. (2003); Hölldobler et al. (2004); Rojas et al. (2004)	Maceration of the gland and extraction in water	Behavioral and chemical.
Cammaerts & Cammaerts (1998); Dahbi & Lenoir (1998); Marsaro-Junior et al. (2001)	Maceration of the gland and extraction in acetone	Behavioral and antimicrobial
Lahav et al. (1998); Lahav et al. (1999)	Maceration of the gland and extraction in chloroform and methanol	Compounds as recognition discriminators.
D'ettore et al. (2000); Ruando et al. (2005); Dahbiet al. (2008)	Maceration of the gland and extraction in pentane	Behavior of aggression, repellent and chemical
Kohl et al. (2000)	Maceration of the gland and extraction in diethyl ether	Origin of the trail pheromone
Hölldobler et al. (2002); I'Allemand et al. (2010);	Maceration of the gland and extraction in dichloromethane	Behavior of aggression and trail pheromone.
Vieira et al. (2012);	Fixed and stained glands	Histochemical
Cruz-Lopez et al. (2000); Fujiwara-tsujii et al. (2007); Brindis et al. (2008); Lommelena et al. (2008); Nikbakhtzadeh et al. (2009); Vander Meeret al. (2010); Rifflet et al. (2011); Plowes et al. (2014); Wang et al. (2014); Martins et al. (2015); Campos et al.(2016); Norman et al. (2017)	Maceration of the gland and extraction in hexane	Response of workers to the extract of queens' glands, behavior; Chemical and the presence of egg marking pheromones

Table 2. Articles with different methods of extraction and evaluations to test the origin and functions of substances extracted from ants. (Continuation)

Authors	Extractionmethod	Evaluation
Ruelet al. (2013);	Maceration of the whole ant, glands and eggs, extraction in dichloromethane	Behavioral
Castella et al. (2010)	Thorax and abdomen, extraction in cacodylate sodium and calcium chloride	Antimicrobial
Liu et al. (2017)	Maceration of the gland and part of the ant, extraction in hexane	Chemical
Mendonça et al. (2009)	Synthetic substances	Antimicrobial
Castracani et al. (2003)	Maceration of the gland and extraction in solvent (not identified)	Chemical
Vieira et al. (2012)	Gland extraction, direct analysis	Chemical
Sainz-Borgo et al. (2013)	Maceration of the head capsule and direct analysis	Behavioral
Hernandez et al. (1999)	Maceration of the head capsule and extraction in hexane	Behavioral of the mandibular gland secretion
Wood et al. (2002); Wood et al. (2011)	Maceration of the head capsule and extraction in dichloromethane	Behavioral; Repellent and Chemical
Voegtle et al. (2008)	Maceration of the head capsule, thorax and gaster, extraction in methanol	Chemical
Jones et al. (2007); Adams et al. (2012)	Maceration of the whole ant and trisected ant, extraction in methanol	Chemical in phylogenetic context
Laurent et al. (2003)	Maceration of the whole ant e extraction in dichloromethane and methanol	Chemical
Melo & Fortich (2013)	Maceration of whole ant and extraction in ethanol	Antimicrobial
Jones et al. (2004)	Maceration of whole ant and extraction	Chemical
Song et al. (2012)	Ant powder and extraction in dichloromethane	Antimicrobial

The same compound can be produced by different glands and have several functions. Ants are able to use a unique mixture of compounds and varying concentrations to alter the function of their glandular substances (Adams et al., 2012). However, the synergies and interactions of multiple glandular products are far from being fully understood. For these reasons, the products of the exocrine glands of the ants remain an exciting and challenging field of research (Adams et al., 2012).

In the secretion of the metapleural gland, more than 20 compounds have been isolated. Most substances are acids (Ortius-Lechner et al., 2000; Yek & Mueller, 2011; Yek et al., 2012; Fernández-Marin et al., 2015) and protein substances (Yek et al., 2012), with antimicrobial function (Yek et al., 2012; Mendonça et al., 2009; Pech & Billen, 2017). The mandibular glands, venom gland and Dufour gland also present a broad spectrum of chemical compounds with proven toxic, repellent and antimicrobial effects (Mendonça et al., 2009; Quinet et al., 2012; Tragust, 2016).

Crematogaster ants have well developed metapleural glands (Attygalle et al. 1989; Vander Meer, 2012; Tranter et al., 2015). *C. inflata* that occurs in Southeast Asia has the largest known metapleural glands (measured by counting secretory cells) (Billen et al., 2011). The amount of secretion produced by the metapleural gland and the greater ease of extraction due to size may justify the number of studies performed with *Crematogaster* ants. The chemical characterization of the secretions of this gland (although different from Attines) presents carboxylic and phenolic acid moieties associated with the antibiotic role (Yek& Mueller, 2011) and negative effects on predatory arthropods (Vander Meer, 2012). Thus, species of *Crematogaster* or other ants nesting in tree cavities, in myrmecophytic epiphytes and related habitats have a need for protection against pathogens and predators (Vander Meer, 2012). However, if the other ant taxa with similar ecological characteristics have antimicrobial glandular secretions and with particularities as to their composition, this has not been investigated yet.

Species of *Atta* and *Acromyrmex* (tribe Attini) occur in the Neotropical region and live in colonies formed by a large number of individuals and in obligatory mutualism with a genetically homogeneous culture. Evidence indicates the evolution of individual immune defenses increased or more elaborated in the form of an active antimicrobial secretion of the metapleural gland (Vander Meer, 2012; Tragust, 2016).

The metapleural gland that varies in size among species, and in many taxa, produces an antimicrobial secretion that flows freely on the cuticle or can be spread by movements of the legs and thorax in some species (Holldobler & Wilson 1990; Yek & Mueller 2011). For these reasons, fungus-growing ants have encouraged research aimed at identifying antimicrobial substances from gland secretions, with special attention to the metapleural gland.

Ants of the genus *Solenopsis* live in colonies in the soil (Vander Meer, 2012). In the secretion of venom and metapleural glands of species of this genus were identified compounds used as external immune defense, in the individual protection of the other members of the group and developing descendants (Vander Meer, 2012). Some species of this genus are known for their invading potential and called fire ants due to the burning sensation associated with their bites (Vander Meer, 2012; Liu et al., 2017). Identifying the action of the venom that can cause allergies in humans and testing different extraction methods have been the main objectives of the research conducted with *Solenopsis* ants. Venom alkaloids of ants of this genus are basic and have comprehensive physiological activities that include antimicrobial activity. In turn, the secretion of the metapleural gland produces acidic antibiotics (Vander Meer, 2012. Yek & Muller, 2011). The effects of the combination of acidic and basic compounds as antimicrobials need to be better understood.

A higher frequency of selected articles addresses glandular secretions of ants with the objective of evaluating the origin and action of the pheromones in the intra- and inter-specific behavior of the ants (Cammaerts & Cammaerts, 1998; Jones et al., 2004; Norman et al., 2017). The chemical characterization of the substances present in the secretions was the second goal that most motivated the investigation of glandular secretions of ants (Castricani et al., 2003; Wood et al., 2011; Martins et al., 2015). Antimicrobial activity of glandular secretions of ants appears as the third most cited objective in the literature consulted (Attygale et al., 1989; Quinet et al., 2012; Song et al., 2012). Evidence in the studies consulted suggests that investment in antimicrobial substances has evolved repeatedly in social strains and may be particularly important for species living in large, complex societies such as ants of the tribe Attini (*Atta* and *Acromyrmex*), made up of large numbers of individuals living in obligatory mutualism with a homogeneous culture of fungi (Penick et al., 2018). Nevertheless, only a minority of species have been studied to identify the chemical composition and to test the antimicrobial effect of the secreted compounds (Song et al., 2012; Penick et al., 2018). It is observed the need to increase the number of ant species investigated (Penick et al., 2018).

The Dufour gland is an exocrine gland that occurs associated with the sting apparatus, mainly produces compounds of lipid character, where the long chain hydrocarbons are among the main compounds. This gland plays a key role in the behavior of ant species. Since many of the compounds produced are involved in the chemical communication mechanism of the species (Serrão et al., 2015). The results found in this review indicate that most of the studies tested the secretions of the Dufour gland in the behavioral interaction of ants.

Metapleural gland products have acidic characteristics, expressed as moieties of carboxylic acid or phenol (Yek & Mueller 2011; Vander Meer 2012). The antimicrobial activity of the metapleural gland secretion has been repeatedly demonstrated in several species of ants of different ant subfamilies (Tragust, 2016; Penick et al., 2018). In the present review, it is observed that the studies developed with the purpose of identifying substances with antibiotic potential used mainly secretions of the metapleural gland.

The mandibular glands are typically formed by a reservoir in which glandular cells release their secretory products (Billen & Al-Khalifa, 2017). The secretions of the mandibular gland of leaf-cutting ants contain alcohols and low molecular weight ketones that induce alarm behavior related to inter-colony recognition (Mendonça et al., 2009). In the secretion produced by the mandibular gland of *Atta sexdens*, inhibitory activities were confirmed against bacteria and fungi, including those that are resistant to conventional antibiotics (Mendonça et al., 2009). It is observed that the studies using mandibular glands had a behavioral approach, chemical characterization and antimicrobial effect.

The dissection of the glands and subsequent extraction with organic solvents, such as hexane, was the most used method among the selected studies. This technique allows the extraction of secretions in larger quantities, allowing the extraction of alkaloids and proteins successively from multiple ants, including those of smaller sizes like *Solenopsis* (Melo & Fortich, 2013; Liu et al., 2017).

The direct extraction of the gland with capillaries or through suction with the use of needle and syringe allows the extraction of pure and individual secretions for direct use, although the quantity is quite limited and the method is laborious (Liu et al., 2017). It was identified the use of this technique primarily for the chemical characterization of the secretions, in order to reduce possible contaminations that could interfere with the results.

There is a lack in literature about the chemical characterization of most glandular secretions of ants, as well as for most taxa. The same lack is found with regard to prospecting the antibiotic and antifungal potential of such secretions.

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Table 1. Authors, publication period, ant taxon used and objective of articles involving extraction of ant secretions in the period between 1989 and 2017.

Author	Journal	Taxon	Objective
Attygalle et al. (1989)	Journal of Chemical Ecology	*Crematogaster physotothorax* Emery,1889 (*C. deformis*)	To describe the chemical composition and function of the secretion of the metapleural gland.
Nascimento et al. (1996)	Journal of Chemical Ecology	*Atta sexdens rubropilosa* Forel, 1908 *A. cephalotes* (Linnaeus, 1758)	To test the antimicrobial effect of secretions of the metapleural gland.
Cammaerts & Cammaerts (1998)	Behavioural Processes	*Pheidolepallidula* (Nylander, 1849)	To demonstrate the neighborhood marking on the nest entrance of *P. pallidula*.
Dahbi & Lenoir (1998)	Behavioral Ecology and Sociobiology	*Cataglyphisiberica* (Emery, 1906)	To analyze the consequences of the separation of nests in the presence of hydrocarbons of the post-pharyngeal gland and the effect of the mixture of individuals after their separation.
Lahav et al. (1998)	Behavioral Ecology and Sociobiology	*Cataglyphisniger* (Andre, 1881)	To evaluate the role of hydrocarbons as recognition discriminators.
Lahav et al. (1999)	Naturwissenschaften	*Cataglyphisniger* (Andre, 1881)	To compare the composition of post-pharyngeal gland secretions; Investigate the biosynthesis and hydrocarbon exchange of this gland between queens and workers.
Hernandez et al. (1999)	Journal of Chemical Ecology	*Atta laevigata* (Smith, 1858)	To carry out chemical analysis of the secretion of the mandibular gland of the different castes of the ant *A. laevigata*.
Ortius-Lechner et al. (2000)	Journal of Chemical Ecology	*Acromyrmex octospinosus* (Forel, 1899)	To perform chemical analysis of the secretions of the metapleural gland of *Acromyrmex octospinosus*.
Leclercq et al. (2000)	Tetrahedron	*Crematogaster brevispinosarochai*	To perform chemical analysis of the secretion of the Dufour gland in *Crematogaster*.
D'ettore et al. (2000)	Chemoecology	*Polyergus rufescens* (Latreille, 1798)	To chemically characterize the secretions of the Dufour gland in queen and worker of *P. rufescens*.
Leclercq et al. (2000)	Tetrahedron Letters,	*Crematogaster rochai* Forel, 1903 (*Crematogaster brevispinosarochai*)	To identify venom compounds in the secretions of the *C. brevispinosarochai* Dufour gland.
More et al. (2000)	Insectes sociaux	*Polyergus rufescens* (Latreille, 1798)	To verify the effect of the secretion of the main tissue and the mandibular gland of *P. rufescens* on the behavior of the workers of the host species.
Kohl et al. (2000)	Naturwissenschaften	*Mayriella overbecki* Viehmeyer, 1925	Identify whether the trail pheromone originates from the venom gland.
Cruz-Lopez et al. (2001)	Journal of Chemical Ecology	*Solenopsis geminata* (Fabricius, 1804)	To evaluate the response of *S. geminate* workers to queen venom gland extract.
Marsaro-Júnior et al. (2001)	Neotropical Entomology	*Atta sexdens rubropilosa* Forel, 1908	To investigate the effect of the secretion of the mandibular gland of *A. sexdens* on the germination of conidia of the fungus *Botrytiscinerea* Pers.
Wood et al. (2002)	Biochemical Systematics and Ecology	*Crematogaster mimosa* Santschi, 1914 *Crematogaster nigriceps* Emery, 1897 and *Crematogaster Gerstaeckeri sjostedti* Mayr, 1907	To identify the chemical composition of secretions of the mandibular gland of three *Crematogaster* species.
Hölldobler et al. (2002)	Chemoecology	*Metapone madagascarica* Gregg, 1958 and *Metapone quadridentata* Eguchi, 1998	To evaluate predatory behavior and communication in two species of *Metapone* and to present the first record of a trail pheromone in this genus.
Laurent et al. (2003)	Tetrahedron Letters	*Crematogaster nigriceps* Emery, 1897	To investigate the defensive mechanisms in the genus *Crematogaster* and to evaluate the composition of the secretion of the Dufour gland.
Castricani et al. (2003)	Journal of mass spectrometry	*Polyergus rufescens* (Latreille, 1798)	Chemical characterization of the *P. rufens* mandibular gland.

Appendix. Authors, publication period, ant taxon used and objective of articles involving extraction of ant secretions in the period between 1989 and 2017. (Continuation)

Author	Journal	Taxon	Objective
Ortius-Lechner et al. (2003)	Insectes Sociaux	*Acromyrmex octospinosus* (Forel, 1899)	To test whether the offspring of more diverse workers can produce a more variable spectrum of compounds of metapleural glands.
Hölldobler et al. (2004)	Chemoecology	*Pogonomyrmex barbatus* (Smith, 1858), *Pogonomyrmex rugosus* Emery, 1895 and *Pogonomyrmex maricopa* Wheeler, 1914.	Carry out a chemical analysis of the secretions of the Dufour glands *P.barbatus, P. rugorus* and *P. maricopa*.
Rojas et al. (2004)	*PhysiologicalEntomology*	*Solenopsis geminata* (Fabricius, 1804)	To evaluate whether the difference in attractiveness of the queen with the workers results from a variation in the components of the recognition pheromone in *S. germinata*.
Jones et al. (2004)	Journal of Chemical Ecology	*Camponotus* Mayr, 1861	To perform chemical analysis of the mandibular gland of nine species of *Camponotus*.
Ruano et al. (2005)	Journal of Insect Physiology	*Rossomyrmex minuchae* Tinaut, 1981	To evaluate the secretion of the Dufour gland of *R. minuchae*, which has a repellent used to stop and pacify during nest usurpation.
Fujiwara-Tsujii et al. (2006)	Zoological Science	*Camponotus obscuripes* Mayr, 1879	Perform chemical analysis of secretions of the venom and Dufour glands.
Jones et al. (2007)	Journal of natural products	*Myrmicaria melanogaster* Emery, 1900	Perform chemical analysis of the venom of *M. melanogaster.*
Brindis et al. (2008)	Neotropical Entomology	*Solenopsis geminata* (Fabricius, 1804)	To evaluate behavioral differences caused by the secretion of the Dufour gland and set a relationship between the chemical profile of the Dufour gland and the different sizes of workers.
Dahbi et al. (2008)	Biochemical Systematics and Ecology	*Cataglyphis viaticus* Crawley, 1920, *Cataglyphis mauritanicus* (Emery, 1906)	To describe the chemical content of post pharyngeal and Dufour glands of *C. viaticus, C. mauritanicus.*
Lommelenaet al. (2008)	Journal of Insect Physiolog	*Gnamptogenys striatula* Mayr, 1884	To identify the chemical compounds on the surface of eggs of *G. striatula* and the secondary source of these compounds.
Voegtle et al. (2008)	Journal of Chemical Ecology	*Camponotus irritibilis* and *Camponotus quadrisectus* (Smith, F., 1858)	To describe three compounds from the mandibular gland of *C. quadrisectus* and *C. irritibilis.*
Nikbakhtzadeh et al. (2009)	*Toxicon*	*Pachycondyla sennaarensis* (Mayr, 1862)	To characterize the secretions of venom glands of the ant *P. sennaarensis*.
Mendonça et al. (2009)	Antonie van Leeuwenhoek	*Atta* Fabricius, 1804	To perform antimicrobial tests using synthetic components of the main components of the mandibular and metapleural glands.
Vander Meer et al. (2010)	Journal of Chemical Ecology	*Solenopsis invicta* Buren, 1972	To isolate and identify the source of a component of the alarm pheromone of the fire ant worker.
Castella et al. (2010)	Insectes Sociaux	*Formica selysi* Bondroit, 1918	To evaluate whether the social or ecological variation at the colony level has an impact on the individuals' immunological investment.
I'Allemand & Witte (2010)	Biological Invasions	*Anoplolepis gracilipes* (Smith, F., 1857)	To analyze the trail communication of *A. gracilipes* using methods established for *P. longicornis*.
Rifflet et al. (2011)	Plos One	*Crematogaster striatula* Emery, 1892	To evaluate the toxicity of Dufour gland secretions of *C. striatula.*
Wood et al. (2011)	Biochemical Systematics and Ecology	*Cephalotes alfaroi* (Emery, 1890) and *Cephalotes cristatus* (Emery, 1890)	Chemical characterization of the mandibular gland.
Yek et al. (2012)	Proceedings of the Royal Society B	*Acromyrmex octospinosus* (Reich, 1793)	To analyze whether the secretions of the metapleural gland of *A. octospinosus* ants can be adjusted according to the fungal conidia to which they are exposed.

Table 1. Authors, publication period, ant taxon used and objective of articles involving extraction of ant secretions in the period between 1989 and 2017. (Continuation)

Author	Journal	Taxon	Objective
Vieira et al. (2012)	Journal of Chemical Ecology	*Trachymyrmex fuscus*, *Atta laevigata* (Smith, 1858) and *Acromyrmex coronatus* (Fabricius, 1804) *Apterostigma pilosum* Mayr, 1865 and *Mycetarotes parallelus* (Emery, 1906) *Ectatomma brunneum* Smith, 1858 and *Pogonomyrmex naegeli* Forel, 1878	To identify the chemical composition of the metapleural gland of fungus-growing and non-growing ants.
Adams et al. (2012)	Biochemical Systematics and Ecology	*Trachymyrmex* Forel, 1893 and *Sericomyrmex* Mayr, 1865	To perform chemical comparison of a set of species of *Sericomyrmex* from *Trachymyrmex* in a phylogenetic context.
Song et al. (2012)	Bioorganic & Medicinal Chemistry Letters	*Tetramorium*, Mayr, 1855	To test antimicrobial activity of extracts of ants of the genus *Tetramorium.*
Vieira et al. (2012)	PLoS ONE	*Trachymyrmex fuscus*, *Atta laevigata* (Smith, 1858) and *Acromyrmex coronatus* (Fabricius, 1804) *Apterostigma pilosum* Mayr, 1865 and *Mycetarotes parallelus* (Emery, 1906) *Ectatomma brunneum* Smith, 1858 and *Pogonomyrmex naegeli* Forel, 1878	To compare morphological differences in the metapleural gland of fungus-growing and non-growing ant species.
Quinet et al. (2012)	The journal of Venomous Animals and Toxins including Tropical Diseases	*Cremetogaster distans* Mayr, 1870, *Crematogaster pygmaea* Forel, 1904 and *Crematogaster rochai* Forel, 1903	To test the antibacterial property of the venom of three species of *Crematogaster*.
Ruel et al. (2013)	Naturwissenschaften	*Aphaenogaster senilis* Mayr, 1853	To identify whether the eggs of *A. senilis* can act as means to prevent the development of future queens.
Sainz-Borgo et al. (2013)	Revista de biologia tropical	*Acromyrmex landolti* (Forel, 1885)	To identify the origin of the recognition signal in the ant body and the effect of the isolation on the recognition ability.
Melo & Fortich (2013)	Revista colombiana de ciências químico-farmacéuticas	*Crematogaster* and *Solenopsis*	To evaluate antimicrobial activity of extracts produced with *Crematogaster* and *Solenopsis* ants.
Plowes et al. (2014)	Journal of Comparative Physiology	*Messorandrei* and *Messorpergandei* (Mayr, 1886)	To identify whether the venom gland of *M. pergandei* and *M. andrei* species is a source of chemical recruitment compounds.
Wang & Chen (2015)	Journal of Chemical Ecology	*Monomorium minimum* (Buckley, 1866)	To evaluate whether the defensive secretions can contribute to *M. minimum* competitive ability.
Martins et al. (2015)	Chemoecology	*Neoponera villosa* (Fabricius, 1804)	To identify the compounds of the intramandibular gland and the cuticle.
Campos et al. (2016)	Journal of Insect Physiology	*Atta opaciceps* Borgmeier, 1939	To identify the components of the venom gland of *A. opaciceps* involved in trail marking.
Liu et al. (2017)	Florida Entomologist	*Solenopsis invicta* Buren, 1972	To evaluate the efficacy in the of venom alkaloid extraction using different methods.
Norman et al. (2017)	Journal of Chemical Ecology	*Atta colombica* Guérin-Méneville, 1844, *Atta cephalotes* (Linnaeus, 1758), *Acromyrmex echinatior, Ac. octospinosus),* *Sericomyrmex amabilis, Trachymyrmex cornetzi* and *Apterostigma pilosum.*	To identify and compare the chemical composition of the alarm pheromones of two species of *Atta*, two species of *Acromyrmex*, two "higher" attines and the "lower" Attine.

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