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Insecticidal Nature of Ant Venom: Chemical Composition and Applications in Pest Control

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ABSTRACT

Ants (Formicidae), a diverse family of Hymenoptera, exhibit over 13,000 described species classified into 21 subfamilies. Among these, 16 subfamilies possess stinging species, predominantly classified within the poneroid and leptanilloid clades, while the remaining non-stinging subfamilies belong exclusively to the formicoid clade. The venom produced by stinging ants is recognized for its diverse pharmacological effects, encompassing haemolytic, paralytic, cytolytic, antibacterial, insecticidal, allergenic, proinflammatory, and nociceptive qualities. Alkaloids and polypeptides are two principal constituents of ant venom, with significant inter specific variations in their structure and composition. Both of these elements contribute to the insecticidal effects of the venom. Alkaloids including indolizidine, pyrazine, pyrrolidines, and pyrrolizidine are key contributors of ant venom among various genera. The effectiveness of various alkaloids and polypeptides against certain insects varies; they exert their effects through multiple mechanisms such as induction of paralysis, intoxication, reduced reproduction, and rapid mortality in target insect species. Factors such as worker ant age, body size, and seasonal variation influence the quantitative and qualitative venom profile, particularly in terms of alkaloid composition, whereas protein profiles remain relatively stable. Their potential biological activity and mode of action, ant-derived alkaloids and peptides, present a promising source for the development of novel next-generation bioinsecticides and repellents. The present review synthesizes current knowledge on the structural and functional complexity of ant venom, emphasizing its insecticidal properties and potential applications in sustainable pest management strategies.

Keywords Ant, Ant venom, Insecticidal activity, Alkaloids, Polypeptide.

INTRODUCTION

Hymenopterans have long been a focus of scientific research due to their venomous nature. While much of the research centers on bees and wasps because of their potent venom, ants have received less attention

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owing to their small size and the minimal amount of venom they produce. Despite being common and highly diverse insects, ant venom remains underexplored. Ants, belonging to the Formicidae family within Hymenoptera, boast a vast diversity with 13,165 known species (Touchard *et al.* 2016A). Mostly found in most terrestrial environments except cold, wet forests and tundra (Ward 2007). Eusociality underpins their complex social structure, which is key to their evolutionary success, allowing them to divide labor efficiently (Kurane *et al.* 2015), their eusocial behavior also contributes to their venomous characteristics.

Venom is defined as a toxic substance produced by animals, stored in specialized systems, and delivered to a target organism where it disrupts physiological and biochemical processes (Arbuckle 2017). In ants, venom is delivered via a sting, and the composition of this venom has intrigued scientists for centuries. The first venom compound, formic acid, was identified in the 17th century from *Formica rufa,* a member of the subfamily Formicinae (Schmidt 1978). Research has since revealed that ant venom contains a mix of alkaloids, proteins, enzymes, peptides, biogenic amines, and hydrocarbons, with variations in alkaloid types across species (Aili *et al.* 2014). Most allergic reactions to ant venom are caused by its peptide and protein components (King and Spangfort 2000).

Due to the small size of ants, extracting venom is a challenging task, limiting early studies. However, advancements in extraction techniques have allowed for better analysis. Fox *et al.* (2013) developed a novel and simple method that efficiently separates the major components—alkaloids and proteins. Ant venom is now recognized for its insecticidal and antibiotic properties, largely attributed to its alkaloid content, with certain peptides also exhibiting insecticidal effects (Blum *et al.* 1958). Multiple studies have confirmed both the antimicrobial and insecticidal potential of ant venom.

Stinging and non-stinging ants

Ants are believed to have evolved from vespoid wasps, which eventually gave rise to the now-extinct ant subfamily Sphecomyrminae (Blum 1992). Currently, ants are divided into 21 subfamilies and 3 clades, with 16 of these subfamilies containing stinging ants. Over time, four subfamilies lost the ability to sting as part of their evolutionary adaptation. The recently identified subfamily Aenictogitoninae remains uncertain in terms of its venomous capabilities. Formicinae, Dolichoderinae, Aneuretinae, and Dorylinae are non-stinging subfamilies that either have non-functional stings or do not secrete venom (Aili *et al.* 2014), making them less significant for venom studies. In contrast, the remaining 16 subfamilies are key for investigating venom properties. Although the phylogenetic relationships between most subfamilies are well understood, those of Martialinae and Aenictogitoninae remain unresolved. Studying the phylogenetic relationships among ant subfamilies is crucial for understanding the distribution of stinging and non-stinging species across the three clades. Table 1 provides a comprehensive overview of the phylogenetic connections within the Formicidae family (Moreau *et al.* 2006). All non-stinging ant subfamilies are part of the formicoid clade, while stinging ant subfamilies are found within the poneroid and leptanilloid clades. Recently, several subfamilies, including Leptanilloidinae, Cerapachyinae, Ecitoninae, Aenictinae, and Aenictogitoninae, were merged into the Dorylinae subfamily (Brady *et al.* 2014). As a result, the Dorylinae subfamily now includes both

Table 1. Stinging and non-stinging ants in different clades.

Clade	Stinging ant subfamilies	Non-stinging ant subfamilies
1 Formicoid	Myrmicinae	Formicinae
	Heteroponerinae	Dolichoderinae
	Pseudomyrmicinae	Aneuretinae
	Myrmeciinae	Dorylinae
	Ecitoninae	Aenictogitonane
	Cerapachyinae	
	Leptanilloidinae	
	Aenictinae	
	Ectatomminae	
2 Poneroids	Agroecomyrmeciinae	
	Paraponerinae	
	Amblyoponinae	
	Proceratiinae	
	Ponerinae	
	Martialinae	
3 Leptanilloids	Leptanillinae	

stinging and non-stinging ants.

Insecticidal properties of ant venom

In Blum *et al*. (1958) first documented the insecticidal properties of *Solenopsis richetri* ant venom, noting its high toxicity to various insects including *Drosophila melanogaster, Sitophilus oryzae, Anthonomus grandis, Musca domestica, Tetranychus telarius, Tetranychus cinnabarinus,* and *Koleotermes*. The venom was applied topically to these insects. The venom primarily consists of two main components: (i) alkaloids and (ii) polypeptides, both of which contribute to its insecticidal effects.

Insecticidal properties of alkaloids

Different ant subfamilies produce various types of alkaloids, and even ants belonging to different genera within the same subfamily can have distinct alkaloid

Table 2. A checklist of ant venom alkaloids.

Subfamily	Genera	Alkaloids structural classes	References
Myrmicinae			(Leclercq *et al*. 2001)
		Pyridine	(Co *et al*. 2003)
	Messor	Pyrazine	(Cruz-Lopez *et al*. 2006)
			(Brand and Mpuru 1993)
	Aphaenogaster		(Wheeler *et al*. 1981)
			(Adams *et al*. 2015)
			(Wheeler *et al*. 1981)
			(Adams *et al*. 2015)
			(Sozanski *et al*. 2020)
		Pyridine	(Leclercq *et al,* 2001)
		Pyrazine	(Attygalle *et al*. 1998)
			(Wheeler *et al*. 1982)
	Megelomyrmex		(Lenoir *et al*. 2011)
		Pyrrolidine	(Jones *et al*. 1991)
		Piperidine	(Sozanski *et al*. 2020)
		Pyroline	(Adams *et al*. 2015)
		Pyrrolizidine	(Adams *et al*. 2013)
			(Tumlinson *et al*. 1971)
	Atta	Pyrroles	(Evershed and Morgan 1983)
		Pyrazine	(Riley *et al*. 1974)
			(Cross *et al*. 1982)
	Pheidole	Pyrazine	(Ali *et al*. 2007)
		Piperideine	(MacConnell *et al*. 1970)
	Solenopsis	Piperdine	(Torres *et al*. 2001)
		Dialkylpyrrolidine	(Shi *et al*. 2015)
		Indolizidine	(Brand *et al*.1972)
			(Jones *et al*. 1982)
		Pyrrolidine	(Jones *et al*. 1989)
	Monomorium	Piperidine	(Jones *et al*. 1990A)
		Indolizine	(Jones *et al*.1990B)
			(Jones *et al*. 2003)
			(Ritter and Persoons 1974)
		Indolizine	(Francke *et al*. 1995)
	Myrmicaria	Indolizidine	(Jones *et al*. 2007)
		Pyrrolidine	(Schroder *et al*. 1996)
		Lehmizidine	
	Manica	Pyrazines	(Attygalle *et al*. 1986)
	Acromyrmex	Pyrazines	(Cross *et al*. 1982)
	Daceton	Pyrazines	(Morgan *et al*. 1992)
		Pyrrolizidine	(Jones *et al*. 1986)
	Chelaner	Pyrrolidine	(Don and Jones 1993)
		Indolizidine	(Jones *et al*.1988)

Table 2. Continued.

Subfamily	Genera	Alkaloids structural classes	References
	Eutetramorium	Dimethylpyrazine	(Tentschert *et al.* 2000)
	Myrmica	Dimethylpyrazine	(Evershed *et al.* 1982)
			(Evershed *et al.* 1981)
Ponerinae	*Odantomachus*	Pyrazines	(Tursch *et al,* 1976)
Ectatomminae	*Rhytidoponera*	Isopentylpyrazine	
		Citronellypyrazine	(Brophy *et al.* 1981)
Dolichoderinae	*Iridomyrmex*	Propylpyrazine	
		Isopentylpyrazine	(Blum and Hermann 1978)
		Styrylpyrazine	(Cavill *et al.* 1956)
		Iridomyrmecin	(Cavill and Houghton 1974)
Pseudomyrmercinae	*Tetraponera*	Tetraponerine (T_1-T_8)	(Merlin *et al.* 1988)
Dorylinae	*Eciton*	Dimethylpyrazine	
		Trimethylpyrazine	(Keegans *et al.* 1993)
		Indole	
Formicinae	Brachymyrmex	Alkylhydroxyl-Indolizidines	(Saporito *et al.* 2004)

profiles. A comprehensive list of the alkaloid classes found across various genera is provided in Table 2.

Few ant genera have been extensively studied, leaving a limited understanding of alkaloid diversity in ant venom. Key alkaloid families found in ant venom include Pyrazine, Pyrrolidines, Pyrrolizidine, and Indolizidine being the most prevalent across many genera (Fig. 1). Despite the inclusion of some Formicidae genera in studies, the Formicidae family is not typically known for alkaloid production (Smith and Jones 2004).

Alkaloids are crucial defensive compounds contributing to the insecticidal properties of ant venom (Greenberg *et al.* 2008). Research often focuses on the *Solenopsis* genus, particularly fire ants, due to their diverse alkaloid profiles. In *Solenopsis venom,* alkaloids with side chains ranging from C11 to C17, known as solenopsins, are prominent. Common solenopsins include Solenopsin A (C11), Solenopsin B (C13), and Solenopsin C (C15), with Solenopsin A being the most ancestral form (Lai *et al.* 2010, Greenberg *et al.* 2008). Each species has a unique solenopsin composition; for instance, *S. invicta* has six major alkaloids ranging from C11 to C17, while *S.geminata* contains C11 piperidine in both trans and cis forms (Lai *et al*. 2012, Lai *et al.* 2009, Yu *et al.*

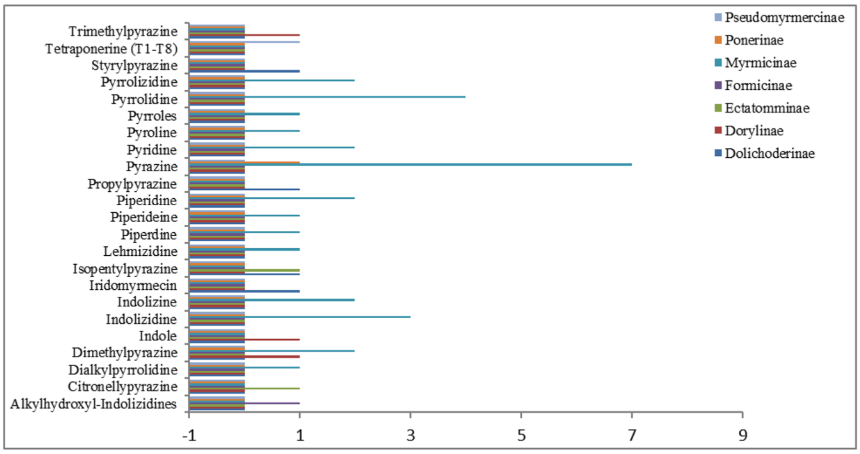

Fig. 1. Ant venom contains several important alkaloid families with pyrazine, pyrrolidines, pyrrolizidine, and indolizidine being the most common among numerous genera,

2014). The proportions of cis and trans-C11 alkaloids vary among species, with smaller amounts found in *S. invicta* (MacConnell *et al.* 1976, Brand *et al.* 1973).

Experiments with fire ant venom on *Spodoptera litura* larvae showed slow mortality with significant discoloration at the sting site. The LT_{50} values for different *Solenopsis* species varied: *S.geminata* had an LT_{50} of 6.55 minutes, while monogynous and polygynous *S.invicta* had LT_{50} values of 14.25 and 29.52 minutes, respectively (Lai *et al.* 2010, Lai *et al.* 2012). Similar results were observed in *Plutella xylostella,* a pest of cruciferous plants. Topical application of *Solenopsis venom* caused paralysis and death, with *S. geminata* being notably faster, killing larvae within 17 minutes compared to 100-130 minutes for *S.invicta* (Lai *et al.* 2012, Yu *et al*. 2014). The variation in LT_{50} values is attributed to differences in side chain length and unsaturation levels. Synthesized alkaloids from fire ants were tested against *Helicoverpa armigera* (cotton bollworm), with different effectiveness based on application method. Compound A showed 45.5% mortality within 24 hours and 75.6% within 48 hours when injected, though it was less effective topically (Wu *et al.* 2022). These findings highlight that solenopsins with shorter side chains and lower unsaturation are more toxic, making *S. geminata* venom more potent than *S. invicta* venom.

Piperidines and piperidine alkaloids also exhibit efficacy against *Myzus persicae* (green peach aphids), with high doses leading to approximately 50% mortality within a few hours and 100% after six hours (Rashid *et al.* 2013). Additionally, piperidines are toxic to *Reticulitermes* termites and house fly larvae (Blum 1988, Sannasi and Blum 1969). *Megalomyrmex peetersi* venom, containing 2-butyl-5-heptylpyrrolidine, has been effective against *Reticulitermes flavipes,* with symptoms of intoxication observed when alkaloids were applied to the termite's head (Sozanski *et al*. 2020).

Insecticidel properties of polypeptides

Ant venom also contains proteins and peptides, which can play a role in insecticidal activity. Pinto *et al.* (2012) identified 46 proteins in the venom of *Solenopsis invicta,* including phospholipase A2, phospholipase A2 inhibitor, allergenic proteins, myotoxins, neurotoxins, thioredoxin peroxidase, cytolytic toxins, and others. These proteins were categorized into four groups: (i) True venom components, (ii) Housekeeping proteins, (iii) Body muscle proteins, and (iv) Proteins for chemical communication. True venom components include (i) Metalloproteins, phospholipase A1, A2, and disintegrin proteins with tissue-damaging properties, (ii) Neurotoxic components like Ctenotoxin, PsTx-60, and Scolopendra toxin, (iii) Atrial natriuretic peptide responsible for vasodilation, (iv) Cytochrome-c oxidase, glutathione-S-transferase, and transferrin for self-protection, and (v) Allergens such as Sol i1 and Sol i3. Additional allergens, Sol i1, Sol i2, Sol i3, and Sol i4, were identified using cation exchange and gel filtration chromatography methods (Hoffman *et al.* 1988). Sol i2 and Sol i4 are strong allergens, while Sol i1 and Sol i4 are less prevalent (Hoffman 1993). Similar allergenic proteins, Sol r1, Sol r2, and Sol r3, were identified in *S. richetri* (Hoffman *et al.* 1990).

In *Pachycondyla goeldii,* insecticidal peptides called ponericins were discovered. Ten peptides identical to ponericins were synthesized, with four (G1, G3, W3-desk, and W4) showing high toxicity to *Acheta domesticus* . Mortality in treated crickets was 50% within 24 hours (Orivel *et al*. 2001).

Touchard *et al.* (2020A) identified fourteen myrmicitoxins in *Manica rubida*. Among these, U10-MYRTX-Mri 1a, 1b, 1c, U13-MYRTX-Mri 1a, and U20-MYRTX-Mri 1a exhibited paralytic effects on blowflies (*Lucilia cuprina*), with weak effects and an LD50 of 75 nMol/g. Novel decapeptide U-MYRTX-MANrl from *M. rubida* was lethal to *Acrothosiphon pisum,* showing 93% and 30% mortality at high and low concentrations, respectively, within 10 days. It also reduced reproduction by 26% (Heep *et al.* 2019B). A similar peptide, U-MYRTX-MYRrub1, from *Myrmica rubra*, was also active against *A. pisum* (Heep *et al.* 2019A). The peptide U-MYRTX-MANrl from *M. rubida* was the most toxic, with a 35% reduction in *A. pisum* survival compared to *M. rubra* peptide.

The peptide Δ-PSDTX-Pp1a (Pseudomyrmecitoxin – Pp1a) from *Pseudomyrmex penetrator* is a heterodimer with a 27-residue A chain and a 33-residue B chain, connected by two disulfide bonds. Synthesized forms included the heterodimer, A-A homodimer, B-B homodimer, and A and B chain monomers. All forms exhibited insecticidal properties on blowflies, causing paralysis and death within 24 hours. Heterodimers and homodimers had strong effects, with complete paralysis observed within 30 minutes, while monomers were less effective (Touchard *et al.* 2020 B). Another peptide, PONTX-Ae1a from *Anochetus emarginatus,* showed poor results on *L. cuprina,* causing only reversible paralysis (Touchard *et al.* 2016B). Δ-PSDTX-Pp1a had the lowest LD_{50} of 3.0 nMol/g, while U20-MYRTX-Mri 1a and G1 peptide had LD_{50} values of 75.45 nMol/g and 25.7 nMol/g, respectively. The LD_{50} for PONTX-Ae was not determined due to its low toxicity.

Ant venom also serves as a repellent to other ant species. *Solenopsis venom* repels non-competing ants that do not produce alkaloids. Even food treated with *Solenopsis* alkaloids repelled Argentine ants (*Linepithema humile*) and odorous house ants, though alkaloid-producing ants were not deterred (Blum *et al.* 1991). *S. invicta* venom is particularly effective against several ant species, with *L. humile* being the most susceptible, followed by *Dorymyrmex bicolor, Liometopum occidentale*, and *S. xyloni.* Interestingly, *S.invicta* itself is highly resistant to its own venom, being 330 times less susceptible than *L. humile.* Trans-C11 piperidine, a synthesized compound, showed similar toxicity to *S. invicta* venom against *L. humile* but was six times more effective against *S. invicta* and *S. xyloni* compared to *S. invicta* venom. Cis-configured piperidines are more effective as repellents than trans-configured ones, making *S. invicta* venom less deterrent compared to other fire ant species containing cis piperidines (Xu and Chen 2023).

Factors affecting ant venom composition

Ant venom composition and volume are influenced by factors such as environmental season, body size, and the age of the worker ants. In a study with *S. geminata,* colonies reared at temperatures of 15°C, 25°C, 35°C, and room temperature showed that the lowest cis-C11 to trans-C11 ratio was at 15°C, while this ratio and the overall alkaloid composition were not significantly affected by temperature. The cis-trans alkaloid ratio also varied with the seasons, being highest in spring and lowest during winter as the temperature dropped to approximately 20°C. In some cases, equal amounts of cis and trans alkaloids were observed during winter (Lai *et al.* 2009). Similar patterns were found in *S. invicta*, where workers produced 55% more venom in spring than in other seasons (Haight and Tshinkel 2003). Additionally, the C13: C13:1 and C15: C15:1 ratio was different between monogynous and polygynous *S. invicta* workers, with the monogynous form having a higher ratio due to the lower presence of unsaturated alkaloids in the polygynous form (Lai *et al.* 2009).

In the genus *Brachymyrmex*, part of the Formicidae family, alkaloid production was not continuous. During the wet season, pumilotoxin (a family of over 80 alkaloids) was detected in the venom of some samples, while it was completely absent during the dry season (Saporito *et al.* 2004).

Body size is another key factor influencing venom composition. Generally, venom volume is positively related to ant body size. Deslippe and Guo (2000) studied the correlation between worker size and alkaloid abundance in *S. invicta* and found that alkaloid abundance was positively correlated with head width. As head width increased, variations in all alkaloids were observed, except for C13:1 alkaloid, which showed minimal variation. The ratios of C13:0:C13:1 and C15:0:C15:1 was also positively correlated with head width. The study confirmed that worker age affects venom quantity and alkaloid composition, with intermediate-aged ants producing more venom than younger or older ants. The C13:0:C13:1 and C15:0:C15:1 ratio also increased with worker age.

While these factors primarily affect alkaloid composition, variations in proteins were not commonly observed. However, a significant difference was noted between the venom proteins of worker and queen ants. The protein Sol i2w in worker ants and Sol i2q in queen ants were 75.6% similar (Chen 2023).

CONCLUSION

Stinging ants produce venom containing a diverse array of alkaloids and peptides, with varying compositions across different species. These venom components confer potent insecticidal effects. Alkaloids in ant venom are primarily responsible for its insecticidal properties, while peptides such as myrmicitoxins and ponericins also contribute to its efficacy. Synthetic versions of these alkaloids and peptides have proven effective against insects, with injected forms generally showing higher lethality compared to topical applications due to better penetration.

The effectiveness of ant venom as a bioinsecticide is supported by its ability to repel competing ant species, although ants are largely unaffected by their own venom. Various factors, including the age of worker ants, body size, and environmental conditions, can influence the composition and potency of ant venom.

Given its complex organic mixture and significant impact on pests, ant venom holds promise for developing future insecticides. By harnessing and synthesizing the structures of venom alkaloids and peptides, it is possible to create natural insecticides that could serve as safer alternatives to chemical insecticides. Further research is needed to explore the full range of alkaloids and their insecticidal potential.

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REFERENCES

Adams, R. M. M., Jones, T. H., Longino, J. T., Weatherford, R. G., & Mueller, U. G. (2015). Alkaloid Venom Weaponry of Three Megalomyrmex Thief Ants and the Behavioral Response of Cyphomyrmex costatus Host Ants. *Journal of Chemical Ecology,* 41(4), 373–385. https://doi.org/10.1007/s10886-015-0565-y

Adams, R. M. M., Liberti, J., Illum, A. A., Jones, T .H., Nash, D. R., & Boomsma, J. J. (2013). Chemically armed mercenary ants protect fungus-farming societies. *The Proceedings of the National Academy of Sciences,* 110(39), 15752–15757. https://doi.org/10.1073/pnas.1311654110

Aili, S. R., Touchard, A., Escoubas, P., Padula, M. P., Orivel, J., Dejean, A., & Nicholson, G. M. (2014). Diversity of peptide toxins from stinging ant venoms. *Toxicon*, 92, 166–178. https://doi.org/10.1016/j.toxicon.2014.10.021

Ali, M. F., Jackson, B. D., & Morgan, E. D. (2007). Contents of the poison apparatus of some species of Pheidole ants. *Biochemical Systematics and Ecology,* 35(10), 641–651. https://doi.org/10.1016/j.bse.2007.03.025

Arbuckle, K. (2017). Evolutionary Context of Venom in Animals. In: Gopalakrishnakone, P., and Malhotra, A. (eds). Evolution of Venomous Animals and Their Toxins. Toxinology. Springer, Dordrecht. pp. 3-31. https://doi.org/10.1007/978-94-007-6458-3_16

Attygalle, A. B., Cammaerts, M., Cammaerts, R., Morgan, E. D., & Ollett, D. G. (1986). Chemical and ethological studies of the trail pheromone of the ant Manica rubida (Hymenoptera: Formicidae). *Physiological Entomology,* 11(2), 125–132. https://doi.org/10.1111/j.1365-3032.1986.tb00399.x

Attygalle, A. B., Kern, F., Huang, Q., & Meinwald, J. (1998). Trail Pheromone of the Myrmicine Ant Aphaenogaster rudis (Hymenoptera: Formicidae). *Naturwissenschaften,* 85(1), 38–41. https://doi.org/10.1007/s001140050450

Blum, M. S. (1988). Biocidal and deterrent activities of nitrogen heterocycles produced by venomous myrmicine ants. In: Cutler H. G. (eds), Biologically Active Natural Products. American Chemical Society, United State, pp, 438–449. https://doi.org/10.1021/bk-1988-0380.ch030

Blum, M. S. (1992). Ant venoms: Chemical and pharmacological properties. *Toxin Reviews*, 11(2), 115–164. https://doi.org/10.3109/15569549209033107

Blum, M. S., Everett, D. M., Jones, T. H., & Fales, H. M. (1991). Arthropod natural products as insect repellents. in: Hadin, P. A. (eds). Naturally Occurring pest Bioregulators. American Chemical Society, United States, pp, 14–26. https://doi.org/10.1021/bk-1991-0449.ch002

Blum, M. S., Walker, J. R., Callahan, P. S., & Novak, A. F. (1958). Chemical, insecticidal, and antibiotic properties of fire ant venom. *Science,* 128 (3319), 306-307. https://doi.org/10.1126/science.128.3319.306.b

Blum, S., & Hermann, H. R. (1978). Venoms and Venom Apparatuses of the Formicidae: Dolichoderinae and Aneuretinae. In: Bettini, S. (eds). Arthropod Venoms. Springer, Berlin, Heidelberg, pp, 871-894. https://doi.org/10.1007/978-3-642-45501-8_26

Brady, S. G., Fisher, B. L., Schultz, T. R., & Ward, P. S. (2014). The rise of army ants and their relatives: Diversification of specialized predatory doryline ants. *BMC Ecology and Evolution*, 14(1), 93. https://doi.org/10.1186/1471-2148-14-93

Brand, J., Blum, Fales, H., & MacConnell, J. (1972). Fire ant venoms: Comparative analyses of alkaloidal components. *Toxicon,* 10(3), 259–271. https://doi.org/10.1016/0041-0101(72)90011-6

Brand, J., Blum, & Ross, H. (1973). Biochemical evolution in fire ant venoms. *Insect Biochemistry,* 3(9), 45–51. https://doi.org/10.1016/0020-1790(73)90017-6

Brand, J. M., & Mpuru, S. P. (1993). Dufour's gland and poison gland chemistry of the myrmicine ant: Messor capensis (Mayr). *Journal of Chemical Ecology,* 19(7), 1315–1321. https://doi.org/10.1007/bf00984878

Brophy, J., Cavill, G., & Plant, W. (1981). Volatile constituents of an Australian ponerine ant Rhytidoponera metallica. *Insect Biochemistry,* 11(3), 307–310. https://doi.org/10.1016/0020-1790(81)90008-1

Cavill, G., Ford, D., & Locksley, H. (1956). The chemistry of ants. I. Terpenoid constituents of some Australian Iridomyrmex species. *Australian Journal of Chemistry,* 9(2), 288. https://doi.org/10.1071/ch9560288

Cavill, G., Houghton, E. (1974). Some pyrazine derivatives from the Argentine ant, Iridomyrmex humilis. *Australian Journal of Chemistry,* 27(4), 879. https://doi.org/10.1071/ch9740879

Chen, J. (2023). Chemistry and functions of imported fire Ant Venom. *Toxins,* 15 (8), 489. https://doi.org/10.3390/toxins15080489

Co, J. E., Jones, T. H., Hefetz, A., Tinaut, A., Snelling, R. R. (2003). The comparative exocrine chemistry of nine Old World species of Messor (Formicidae: Myrmicinae). *Biochemical Systematics and Ecology,* 31(4), 367–373. https://doi.org/10.1016/s0305-1978(02)00155-2

Cross, J. H., West, J. R., Silverstein, R. M., Jutsum, A. R., & Cherrett, J. M. (1982). Trail pheromone of the leaf-cutting ant, Acromyrmex octospinosus (Reich), (Formicidae: Myrmicinae). *Journal of Chemical Ecology,* 8(8), 1119–1124. https://doi.org/10.1007/bf00986982

Cruz-Lopez, L., Jackson, B. D., Hefetz, A., & Morgan, E. D. (2006). Alkaloids in the venom of Messor ants. *Bio-chemical Systematics and Ecology,* 34(3), 199–204. https://doi.org/10.1016/j.bse.2005.10.002

Deslippe, R. J., & Guo, Y. (2000). Venom alkaloids of fire ants in relation to worker size and age. *Toxicon,* 38(2), 223–232. https://doi.org/10.1016/s0041-0101(99)00147-6

Don, A. W., & Jones, T. H. (1993). The stereochemistry of 3-bUtyl-5-(5 -hexenyl) - pyrrolizidine from populations of Monomorium antarcticum (Smith) (Hymenoptera: Formicidae) and its possible role as a unique taxonomic character. *New Zealand Entomologist,* 16(1), 45–48. https://doi.org/10.1080/00779962.1993.9722649

Evershed, R., Morgan, E., & Cammaerts, M. (1982). 3-ethyl-2,5-di methylpyrazine, the trail pheromone from the venom gland of eight species of Myrmica ants. *Insect Biochemistry,* 12(4), 383–391. https://doi.org/10.1016/0020-1790(82)90035-x

Evershed, R. P., & Morgan, E. D. (1983). The amounts of trail pheromone substances in the venom of workers of four species of attine ants. *Insect Biochemistry,* 13(5), 469-474. https://doi.org/10.1016/0020-1790(83)90003-3

Evershed, R. P., Morgan, E. D., & Cammaerts, M. C. (1981). Identification of the trail pheromone of the ant *Myrmica rubra* L., and related species. Naturwissenschaften, 68(7), 374–376. https://doi.org/10.1007/bf01058029

Fox, E. G. P., Solis, D. R., Santos, L. D. D., Pinto, J. R. A. D. S., Da Silva Menegasso, A. R., Silva, R. C. M. C., Palma, M. S., Bueno, O. C., & De Alcântara Machado, E. (2013). A simple, rapid method for the extraction of whole fire ant venom (Insecta: Formicidae: Solenopsis). Toxicon*,* 65, 5–8. https://doi.org/10.1016/j.toxicon.2012.12.009

Francke, W., Schroder, F., Walter, F., Sinnwell, V., Baumann, H., & Kaib, M. (1995). New alkaloids from ants: Identification and synthesis of (3R,5S,9R)-3-butyl,5-(1-oxopropyl) indol izidine and (3R,5R,9R)-3-butyl-5-(1-oxopropyl) indolizidine, constituents of the poison gland secretion in Myrmicariaeu menoides (Hymenoptera:Formicidae). Liebigs Annalen, 1995(6), 965–977. https://doi.org/10.1002/jlac.1995199506138

Greenberg, L., Kabashima, J. N., Allison, C. J., Rust, M. K., Klotz, J. H., Hurvois, J., & Paine, T. D. (2008). Lethality of red imported fire ant venom to Argentine ants and other ant species. *Annals of the Entomological Society of America*, 101(6), 1162–1168. https://doi.org/10.1603/0013-8746-101.6.1162

Haight, K. L., & Tschinkel, W. R. (2003). Patterns of venom synthesis and use in the fire ant, Solenopsis invicta. *Toxicon*, 42(6), 673–682. https://doi.org/10.1016/j.toxicon.2003.09.005

Heep, J., Klaus, A., Kessel, T., Seip, M., Vilcinskas, A., & Skaljac, M. (2019A). Proteomic Analysis of the Venom from the Ruby Ant *Myrmica rubra* and the Isolation of a Novel Insecticidal Decapeptide. *Insects,* 10(2), 42. https://doi.org/10.3390/insects10020042

Heep, J., Skaljac, M., Grotmann, J., Kessel, T., Seip, M., Schmidt berg, H., & Vilcinskas, A. (2019B). Identification and Functional Characterization of a Novel Insecticidal Decapeptide from the Myrmicine Ant Manica rubida. *Toxins*, 11(10), 562. https://doi.org/10.3390/toxins11100562

Hoffman, D. (1993). Allergens in *Hymenoptera venom* XXV: The amino acid sequences of antigen 5 molecules and the structural basis of antigenic cross-reactivity. *Journal of Allergy and Clinical Immunology*, 92(5), 707–716. https://doi.org/10.1016/0091-6749(93)90014-7

Hoffman, D., Dove, D., & Jacobson, R. (1988). Allergens in Hymenoptera venom XX. Isolation of four allergens from imported fire ant (*Solenopsis invicta*) venom. *Journal of Allergy and Clinical Immunology,* 82(5), 818–827. https://doi.org/10.1016/0091-6749(88)90084-x

Hoffman, D. R., Smith, A., Schmidt, M., Moffitt, J. E., & Guralnick, M. (1990). Allergens in Hymenoptera venom XXII. Comparison of venoms from two species of imported fire ants, *Solenopsis invicta* and richteri. *Journal of Allergy and Clinical Immunology,* 85(6), 988–996. https://doi.org/10.1016/0091-6749(90)90042-3

Jones, T. H., Blum, M. S., Fales, H. M., Brandao, C. R. F., & Lattke, J.(1991). Chemistry of venom alkaloids in the ant genus Megalomyrmex. *Journal of Chemical Ecology,* 17(9), 1897–1908. https://doi.org/10.1007/bf00993736

Jones, T. H., Blum, M. S., Howard, R.W., McDaniel, C. A., Fales, H. M., DuBois, M. B., &Torres, J. (1982). Venom chemistry of ants in the genus Monomorium. *Journal of Chemical Ecology,* 8(1), 285–300. https://doi.org/10.1007/bf00984024

Jones, T. H., Blum, M. S., & Robertson, H. G.(1990A). Novel Dialkylpiperidines in the Venom of the Ant Monomorium delagoense. *Journal of Natural Products,* 53(2), 429–435. https://doi.org/10.1021/np50068a022

Jones, T. H., Highet, R. J., Don, A. W., & Blum, M. S. (1986). Alkaloids of the ant Chelaner antarcticus. *The Journal of Organic Chemistry,* 51(14), 2712–2716. https://doi.org/10.1021/jo00364a017

Jones, T. H., Laddago, A., Don, A. W., & Blum, M. S. (1990B). A Novel (5E,9Z)-Dialkylindolizidine from the Ant Monomo rium smithii. *Journal of Natural Products*, 53(2), 375–381. https://doi.org/10.1021/np50068a016

Jones, T. H., Stahly, S. M., Don, A. W., & Blum, M. S. (1988). Chemotaxonomic implications of the venom chemistry of some Monomorium antarcticum populations. *Journal of Chemical Ecology,* 14(12), 2197–2212. https://doi.org/10.1007/bf01014025

Jones, T. H., Voegtle, H. L., Miras, H. M., Weatherford, R. G., Spande, T. F., Garraffo, H. M., Daly, J. W., Davidson, D. W., & Snelling, R. R. (2007). Venom Chemistry of the Ant Myrmicaria melanogaster from Brunei. *Journal of Natural Products*, 70(2), 160–168. https://doi.org/10.1021/np068034t

Jones, T. H., Zottig, V. E., Robertson, H. G., & Snelling, R. R. (2003). The Venom Alkaloids from Some African Monomorium Species. *Journal of Chemical Ecology,* 29(12), 2721–2727. https://doi.org/10.1023/b:joec.0000008015.42254.c3

Jones, T. J., Blum, M. S., Escoubas, P., & Ali, T. M. M. (1989). Novel Pyrrolidines in the Venom of the Ant Monomorium indicum. *Journal of Natural Products,* 52(4), 779–784. https://doi.org/10.1021/np50064a019

Keegans, S. J., Billen, J., Morgan, E. D., & Gokcen O. A. (1993). Volatile glandular secretions of three species of new world army ants, Eciton burchelli, Labidus coecus, and Labidus praedator. *Journal of Chemical Ecology,* 19(11), 2705–2719. https://doi.org/10.1007/bf00980702

King, T. P., & Spangfort, M. D. (2000). Structure and biology of stinging insect venom allergens. *International Archives of Allergy and Immunology,* 123(2), 99–106. https://doi.org/10.1159/000024440

Kurane, S., Sathe, T. V., Bhoje, P. M. (2015). Diversity and economic importance of ants (Hymenoptera: Formicidae) from Kolhapur city, Maharashtra state, India. *International Journal of Development Research,* 5 (3), 3662–3664

Lai, L., Kuo, T., Huang, R., & Wu, W. (2012). The Insecticidal Activities of Fire Ant (Hymenoptera: Formicidae) Venoms Against Plutellaxylostella (Lepidoptera: Plutellidae) Larvae. *Journal of Economic Entomology,* 105(5), 1591–1596. https://doi.org/10.1603/ec12075

Lai, L. C., Chang, Y. Y., Hua, K. H., Wu, W. J., & Huang, R. N. (2010). Comparative Toxicity of Three Fire Ant (Hymenoptera: Formicidae) Venoms to Spodoptera litura Larvae. Sociobiology, (56)3, 653–655.

Lai, L. C., Hua, K. H., Yang, C .C., Huang, R. N., & Wu, W. J. (2009). Secretion Profiles of Venom Alkaloids in Solenopsis geminata (Hymenoptera: Formicidae) in Taiwan. *Environmental Entomology,* 38(3), 879–884. https://doi.org/10.1603/022.038.0342

Leclercq, S., Charles, S., Daloze, D., Braekman, J. C., Aron, S., & Pasteels, J. M. (2001). Absolute configuration of anabasine from Messor and Aphaenogaster ants. *Journal of Chemical Ecology,* 27(5), 945-952. https://doi.org/10.1023/a:1010335003297

Lenoir, A., Benoist, A., Hefetz, A., Francke, W., Cerda, X., & Boulay, R. (2011). Trail-following behaviour in two Aphaenogaster ants. *Chemoecology*, 21(2), 83–88. https://doi.org/10.1007/s00049-011-0071-9

MacConnell, J. G., Blum, M. S., Buren, W. F., Williams, R. N., & Fales, H. M. (1976). Fire ant venoms: Chemotaxonomic correlations with alkaloidal compositions. *Toxicon,* 14(1), 69–78. https://doi.org/10.1016/0041-0101(76)90122-7

MacConnell, J. G., Blum, M. S., & Fales, H. M. (1970). Alkaloid from Fire Ant Venom: Identification and Synthesis. Science, 168 (3933), 840–841. https://doi.org/10.1126/science.168.3933.840

Merlin, P., Braekman, J. C., Daloze, D., Pasteels, J. M. (1988). Tetraponerines, toxic alkaloids in the venom of the Neo-Guinean pseudomyrmecine ant Tetraponera sp. *Journal of Chemical Ecology,* 14(2), 517–527. https://doi.org/10.1007/bf01013903

Moreau, C. S., Bell, C. D., Vila, R., Archibald, S. B, & Pierce, N. E. (2006). Phylogeny of the Ants: Diversification in the Age of Angiosperms. Science, 312 (5770), 101–104. https://doi.org/10.1126/science.1124891

Morgan, E. D., Holldobler, B., Vaisar, T., & Jackson, B. D. (1992). Contents of poison apparatus and their relation to trail-following in the ant Daceton armigerum. *Journal of Chemical Ecology,* 18(12), 2161–2168. https://doi.org/10.1007/bf00984943

Orivel, J., Redeker, V., Caer, J. L., Krier, F., Revol-Junelles, A., Longeon, A., Chaffotte, A., Dejean, A., & Rossier, J. (2001). Ponericins, New Antibacterial and Insecticidal Peptides from the Venom of the Ant Pachycondyla goeldii. *Journal of Biological Chemistry*. 276 (21), 17823–17829. https://doi.org/10.1074/jbc.m100216200

Pinto, J. R. A. D. S., Fox, E. G. P., Saidemberg, D. M., Santos, L. D., Da Silva Menegasso, A. R., Costa-Manso, E., Machado, E. A., Bueno, O. C., & Palma, M. S. (2012). Proteomic View of the Venom from the Fire Ant Solenopsisinvicta Buren. *Journal of Proteome Research*, 11(9), 4643–4653. https://doi.org/10.1021/pr300451g

Rashid, T., Chen, J., & McLeod, P. (2013). Toxicity of newly isolated piperideine alkaloids from the red imported fire ant, Solenopsis invicta Buren, against the green peach aphid, Myzus persicae (Sulzer). *Advances in Entomology,* 01(02), 20–23. https://doi.org/10.4236/ae.2013.12005

Riley, R., Silverstein, R., Carroll, B., & Carroll, R. (1974). Methyl 4-methylpyrrole-2-carboxylate: A volatile trail phero mone from the leaf-cutting ant, Atta cephalotes. *Journal of Insect Physiology,* 20(4), 651–654. https://doi.org/10.1016/0022-1910(74)90186-3

Ritter, F., & Persoons, C. (1974). Recent development in insect pheromone research, in particular in the Netherlands. *Netherlands Journal of Zoology,* 25(3), 261–275. https://doi.org/10.1163/002829675x00281

Sannasi, A., & Blum, M. S. (1969). Pathological effects of fire ant venom on the integument and blood of house fly larvae. *Journal of the Georgia Entomological Society,* 4(3), In prees.

Saporito, R. A., Garraffo, H. M., Donnelly, M. A., Edwards, A. L., Longino, J. T., & Daly, J. W. (2004). Formicine ants: Anarthropod source for the pumiliotoxin alkaloids of dendrobatid poison frogs. *The Proceedings of the National Academy of Sciences,* 101(21), 8045–8050. https://doi.org/10.1073/pnas.0402365101

Schmidt, J. O. (1978). Ant Venoms: A Study of Venom Diversity. in: Shankland, D. L., Hollingworth, R. M., Smyth, T. (eds). Pesticide and Venom Neurotoxicity. Springer, Boston, MA. pp. 247-263. https://doi.org/10.1007/978-1-4615-8834-4_20

Schroder, F., Franke, S., Francke, W., Baumann, H., Kaib, M., Pasteels, J. M., & Daloze, D. (1996). A new family of tricyclic alkaloids from Myrmicaria ants. *Tetrahedron,* 52(43), 13539–13546. https://doi.org/10.1016/0040-4020(96)00834-4

Shi, Q., Hu, L., Wang, W., Meer, R. K. V., Porter, S. D., & Chen, L. (2015). Workers and alate queens of Solenopsis geminata share qualitatively similar but quantitatively different venom alkaloid chemistry. Frontiers in Ecology and Evolution, 3. https://doi.org/10.3389/fevo.2015.00076

Smith, S. Q., & Jones, T. H. (2004). Tracking the cryptic pumiliotoxins. The Proceedings of the *National Academy of Sciences*, 101(21), 7841–7842. https://doi.org/10.1073/pnas.0402599101

Sozanski, K., Prado, L. P. D., Mularo, A. J., Sadowski, V. A., Jones, T. H., & Adams, R. M. M. (2020). Venom function of a new species of Megalomyrmex forel, 1885 (Hymenoptera: Formicidae). *Toxins*, 12(11), 679. https://doi.org/10.3390/toxins12110679

Tentschert, J., Bestmann, H., Holldobler, B., & Heinze, J. (2000). 2,3-Dimethyl-5-(2-methylpropyl) pyrazine, a trail pheromone component of Eutetramorium mocquerysi Emery (1899) (Hymenoptera: Formicidae). Naturwissenschaften, 87(8), 377–380. https://doi.org/10.1007/s001140050745

Torres, J. A., Zottig, V. E., Co, J. E., Roy, T. H., Sneilinge, R., & Jones (2001). Caste Specific Alkaloid Chemistry of Solenopsis maboya and *S. torresi* (Hymenoptera: Formicidae) Sociobiology, 37 (3), 579-583

Touchard, A., Aili, S. R., Fox, E. G. P., Escoubas, P., Orivel, J., Nicholson, G. M., & Dejean, A. (2016A). The biochemical toxin arsenal from ant venoms. *Toxins,* 8 (1), 30. https://doi.org/10.3390/toxins8010030

Touchard, A., Aili, S. R., Tene, N., Barasse, V., Klopp, C., Dejean, A., Kini, R. M., Mrinalini, Coquet, L., Jouenne, T., Lefranc, B., Leprince, J., Escoubas, P., Nicholson, G. M., Treilhou, M., & Bonnafe, E. (2020A). Venom Peptide Repertoire of the European Myrmicine Ant Manica rubida: Identification of Insecticidal Toxins. *Journal of Proteome Research,* 19(4), 1800–1811. https://doi.org/10.1021/acs.jproteome.0c00048

Touchard, A., Brust, A., Cardoso, F. C., Chin, Y. K., Herzig, V., Jin, A., Dejean, A., Alewood, P. F., King, G. F., Orivel, J., & Escoubas, P. (2016B). Isolation and characterization of a structurally unique β-hairpin venom peptide from the predatory ant Anochetus emarginatus. Biochimica et Biophysica Acta, 1860 (11), 2553–2562. https://doi.org/10.1016/j.bbagen.2016.07.027

Touchard, A., Mendel, H. C., Boulogne, I., Herzig, V., Emidio, N. B., King, G. F., Triquigneaux, M., Jaquillard, L., Beroud, R., De Waard, M., Delalande, O., Dejean, A., Muttenthaler, M., & Duplais, C. (2020B). Heterodimeric Insecticidal Peptide Provides New Insights into the Molecular and Functional Diversity of Ant Venoms. *ACS Pharmacology and Translation Science*, 3(6), 1211–1224. https://doi.org/10.1021/acsptsci.0c00119

Tumlinson, J. H., Silverstein, R. M., Moser, J. C., Brownlee, R. G., & Ruth, J. M. (1971). Identification of the Trail Pher omone of a Leaf-cutting Ant, Atta texana. Nature, 234(5328), 348–349. https://doi.org/10.1038/234348b0

Tursch, B., Braekman, J. C., & Daloze, D. (1976). Arthropod alkaloids. *Experientia*, 32(4), 401–407. https://doi.org/10.1007/bf01920762

Ward, P. S. (2007). Phylogeny, classification, and species-level taxonomy of ants (Hymenoptera: Formicidae). Zootaxa, 1668 (1), 549-563. http://dx.doi.org/10.11646/zootaxa.1668.1.26

Wheeler, J., Avery, J., Olubajo, O., Shamin, M., Storm, C., & Duffield, R. (1982). Alkylpyrazines from hymenoptera. Tetrahedron, 38(13), 1939–1948. https://doi.org/10.1016/0040-4020(82)80043-4

Wheeler, J. W., Olubajo, O., Storm, C. B., & Duffield, R. M. (1981). Anabaseine: venom alkaloid of aphaenogaster ants. *Science*, 211(4486), 1051–1052. https://doi.org/10.1126/science.211.4486.1051

Wu, X., Wang, G., Xu, G., & Chen, L. (2022). Synthesis and insecticidal activity of fire Ant venom Alkaloid-Based 2-Methyl-6-alkyl-Δ1,6-piperideines. Molecules, 27 (3), 1107. https://doi.org/10.3390/molecules27031107

Xu, G., & Chen, L. (2023). Biological activities and ecological significance of fire ant venom alkaloids. Toxins, 15(7), 439. https://doi.org/10.3390/toxins15070439

Yu, Y., Wei, H., Fadamiro, H. Y., & Chen, L. (2014). Quantitative analysis of alkaloidal constituents in imported fire ants by gas chromatography. *Journal of Agricultural and Food Chemistry,* 62(25), 5907–5915. https://doi.org/10.1021/jf501423y