NPC Natural Product Communications

2014
Vol. 9
No. 8
1115 - 1122

A List of and Some Comments about the Trail Pheromones of Ants

Xim Cerdá[a*], Louise van Oudenhove[a,b,c], Carlos Bernstein[b] and Raphaël R. Boulay[a,d]

[a]*Department of Ethology and Biodiversity Conservation, Estación Biológica de Doñana, CSIC, E-41092 Sevilla, Spain*

[b]*Laboratoire de Biométrie et Biologie Évolutive, CNRS, UMR5558, Université de Lyon1, F-69622 Villeurbanne, France*

[c]*Present address: INRA, UMR 1355, Institut Sophia Agrobiotech, 400 Route des Chappes, F-06903 Sophia Antipolis, France*

[d]*IRBI, UMR CNRS 7261, Université François Rabelais de Tours, Parc de Grandmont, F-37200 Tours, France*

xim@ebd.csic.es

Received: June 17th, 2014; Accepted: June 30th, 2014

Ants use many different chemical compounds to communicate with their nestmates. Foraging success depends on how efficiently ants communicate the presence of food and thus recruit workers to exploit the food resource. Trail pheromones, produced by different exocrine glands, are a key part of ant foraging strategies. By combing through the literature, we compiled a list of the identity and glandular origin of the chemical compounds found in the trail pheromones of 75 different ant species. Of the 168 compounds identified, more than 40% are amines. In the subfamily Myrmicinae, trail pheromones are mostly produced in the venom gland, while in the subfamily Formicinae, they come from the rectal gland.

Keywords: Ants, Formicidae, Trail pheromone, Glands, Foraging strategies.

There are more than 12,700 known ant species in the world [1]. These species demonstrate many differences at both the colony (society) and individual (worker) level: colony size ranges from only a few workers to 20,000,000 individuals, and ants display a huge variety of foraging strategies that allow them to efficiently exploit their environment. The larger the colony, the less foraging is individually based and the more foraging is chemically coordinated [2].

Some ant species have lost the pheromone-based mechanisms that would allow them to communicate the location of a food resource. However, in some of these species, workers that have encountered a large food resource are still able to prompt their nestmates to exit the nest [3]. Yet, the vast majority of ant species do use chemicals to communicate the location of food and to recruit nestmates [2, 4]. Chemical recruitment mechanisms can be divided into three categories. In tandem running, a forager that has discovered food recruits a single nestmate at a time using an individual-specific trail [5]. As a result, this recruitment mechanism is the least efficient of the three. In group recruitment, a successful forager lays down a trail while returning to the nest and then guides a group of nestmates back to the food resource [6]. In mass recruitment, a successful forager lays down a chemical trail that elicits trail-following and trail-laying behavior by nestmates. This mechanism is the most efficient of the three since it does not require the successful worker to accompany the recruits to the resource. In this review, we broadly define trail pheromones and take into account all three recruitment mechanisms. For example, *Manica rubida* workers do not recruit nestmates but rather mark the ground with chemical trails upon their return to the nest after discovering prey [7]. *Aphaenogaster senilis* workers do the same but subsequently lead a small group of recruits along the trail to the food resource [6a]. Interest in studying and identifying ant trail pheromones has increased exponentially since the first trail pheromone was identified in 1971 [8]. However, trail pheromones have been studied in a very small percentage of ant species because ants are so speciose (Table 1).

Table 1: Number of ant species identified which trail pheromones.

Subfamily	Total number of described species in the World [a]	Total number of species studied	% of total species studied
Myrmicinae (Myr)	6294	45	0.71
Dolichoderinae (Dol)	753	3	0.40
Formicinae (For)	3009	18	0.60
Ponerinae (Pon)	1087	5	0.46
Ectatomminae (Ect)	285	3	1.05
Dorylinae (Doryl)	59	1	1.70

[a]From [1] http://osuc.biosci.ohio-state.edu/hymenoptera/tsa.sppcount?the_taxon=[subfamily name] (21st May 2014).

Some of these studies have been centered on ant species of economic interest, such as leaf-cutter ants (genus *Atta* or *Acromyrmex*), which are major herbivores that cause significant economic losses in agroecosystems, and invasive species, such as the red imported fire ant (*Solenopsis invicta*) and the Argentine ant (*Linepithema humile*). Studying ant pheromones has an applied interest because the knowledge gleaned can be used to help control and reduce the negative effects of these species. Some studies have used trail or alarm pheromones to increase ants' consumption of toxic baits [9]. Other studies have focused on the use of natural or synthetic semiochemicals to disrupt ant trails [10]. Recently, the success of trail pheromone disruption trials in a natural ecosystem (Volcanoes National Park in Hawaii) has underscored the potential that these methods have to control invasive ant species [10c].

Over the last two decades, different publications have reviewed the pheromones found in social insects [11]. Moreover, two excellent reviews have focused specifically on ant trail pheromones [12]: the most recent review [12b] described 54 such compounds. We have added to this list, bringing the total up to 75. In this review, we provide a list of chemical compounds that function as trail pheromones (in a broader sense of the term) and their glandular origin.

Trail pheromones are produced by either one or a few glands located in the gaster, such as the venom gland (in the subfamily Myrmicinae) and the rectal gland (in the subfamily Formicinae) (Table 2). The Dufour, pygidial, post-pygidial, rectal, sternal, and Pavan glands, also found in the abdomen, are other sources of trail pheromones. *Crematogaster castanea* workers are unable to touch the ground with the tip of their heart-shaped abdomens: they use a secretion from their tibial glands to lay down trails [13]. In *Leptogenys diminuta*, workers lay down trails composed of secretions from both the poison and the pygidial glands [14]. The poison gland secretions provide the orientation cues while those from the pygidial gland stimulate recruitment [14]. Trail pheromones generally comprise several compounds (Table 3, Figure 1). The chemical blend is highly variable among species.

Table 2: Number of ant species in the different subfamilies[a] that use chemical compounds from various glands as trail pheromones.

Gland	Myr	Dol	Form	Pon	Ect	Dor
venom (V)	36			1		
Dufour (D)	1				2	
pygidial (Py)	2	1		1		
rectal (R)			15			
sternal (S)						
postpygidial (Pp)						1
tibial (T)	1					
Pavan (Pa)		1				
V+D	4					
V+Py				2		
V+R			1			
Py+Pa		1				

[a] See Table 1 for taxon abbreviations

For example, in *L. diminuta*, a single compound [(3*R*,4*S*)-4-methyl-heptan-3-ol] is enough to provoke trail-following behavior, whereas in *L. peuqueti*, the trail pheromone is composed of 14 compounds; each of them is individually able to elicit some trail-following behavior, but the mixture of all the substances is more effective than any single compound [15]. Closely related species with morphologically similar workers may nonetheless have different trail pheromones. For example, *Tetramorium caespitum* uses a mixture of the pyrazines (or tetramorines) DMP and EDMP, while *T. impurum* uses methyl 6-methylsalicylate [16]. In the army ant *Daceton armigerum*, there are two types of trail pheromone compounds: a mixture of linear alkanes and alkenes secreted by the Dufour gland and a mixture of tetramorines (DMP, TMP, and EDMP) secreted by the poison gland [17]. The linear hydrocarbons might be acting as solvents, "retaining" the more volatile tetramorines [17]. Similarly, the poison gland secretion of the predatory ant *Myrmicaria eumenoides* has a high volatile fraction—which is mostly composed of (+)-limonene, the recruitment pheromone—and a low volatile fraction whose main component is an alkaloid that acts as a fixative and modifies limonene evaporation kinetics, extending the period over which the signal is effective [18]. Chemical communication involves a short-lived excitation signal combined with a long-lasting orientation signal [19]. Some species might also use repellent pheromones to prevent positive feedback when necessary [20]. The complex trail system of *Paratrechina longicornis* demonstrates extraordinary adaptability and integrates signals of different strength and duration: stable routes to either permanent food resources or nest sites are maintained with rectal pheromones, while temporary recruitment trails to unstable but profitable resources are generated with either Dufour or poison gland pheromones [21].

The longevity of trail pheromone signals is highly variable among species. In the army ant *Daceton armigerum*, trails created with poison gland secretions can last for more than seven days [22]. In the Pharaoh's ant, *M. pharaonis*, trail decay is rapid (pheromone half-life is 9 min) and is strongly affected by the substrate upon

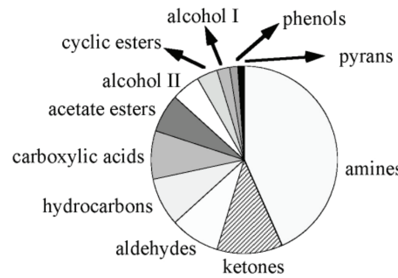

Figure 1: Chemical compounds used as trail pheromones by ants. Data obtained from literature (168 compounds from 75 ant species). See Table 3 for details

which the trail is laid [23]. In this species, there are three types of trail pheromone: a long-lasting attractive pheromone and two short-lived pheromones, one attractive and one repellent [20b]. The use of long-lasting compounds in trails allows workers to re-establish trails after 48 h have passed [24].

Another factor that could affect the longevity of trail pheromone signals is ground surface temperature. Hence, in some Mediterranean environments, hot ground-surface temperatures may accelerate trail pheromone evaporation and thus recruitment decay [25]. Microclimate might therefore explain why many species living in such habitats use individual foraging and lack recruitment pheromones [26]. On the other hand, thermophilic ant species are mainly scavengers, exploiting unpredictable food resources with patchy distributions. Consequently, trail-based worker recruitment may not be advantageous. For example, in contrast to its sister species from North America, the South American seed-harvester ant *Pogonomyrmex vermiculatus* is a solitary forager, probably because it exploits a patchy food resource (seeds occur in low densities in the Chilean desert) in a low-competition environment [27].

Perspectives—Trail pheromone compounds have always been identified indirectly: they are extracted from their glandular sources and bioassays are performed using the extracts or synthesized standards and their mixtures [28]. As Cross *et al* [29] pointed out: "It is an oversimplification to ascribe the complex social behavior of trail following solely to the compound identified as the most active, satisfying though it may be to elicit this response in the laboratory and in the field with a defined chemical". Very recently, Choe *et al.* [28] highlighted a methodological problem concerning the identification of one ant trail pheromone: for more than three decades, different studies have stated that (*Z*)-9-hexadecenal might be a key component of Argentine ant trails because it strongly attracted workers in a multi-choice olfactometer. Using a very original experimental set-up, Choe *et al.* [28] directly studied the substances deposited by living ants as they created their trails. They collected trail chemicals by providing ants with solid-phase microextraction fibers as bridges during foraging (as ants moved from the nest to the feeder). They found that (*Z*)-9-hexadecenal is not present in detectable quantities and that two iridoids, dolichodial and iridomyrmecin, appear to be the primary chemical constituents of the trails. We think that Choe *et al*'s [28] work presents a novel and fruitful approach to study ant trail pheromones: by obtaining them directly from the trail.

Acknowledgments - Alain Lenoir and Abraham Hefetz provided useful comments when LvO was writing her PhD thesis. We thank Pawan K. Agrawal for the invitation and his patience as editor, Jessica Pearce-Duvet for English editing and an anonymous referee for his comments. This study was funded by the Spanish MINECO and FEDER (project CGL2012-36181 to XC and RB).

Table 3: Chemical compounds identified as trail pheromones in the different ant species.

Ant species	Chemical compounds	Gland	Functional group	Chain length	Molecular weight	[reference]
Subfamily MYRMICINAE						
Tribe Dacetini						
Daceton armigerum	2,5-dimethylpyrazine (DMP)	venom	Amine	C03	108.14	[17]
	2,3,5-trimethylpyrazine (TMP	venom	Amine	C04	122.17	[17]
	3-ethyl-2,5-dimethylpyrazine (EDMP)	venom	Amine	C05	136.19	[17]
	9-tricosene	Dufour	Hydrocarbon	C23	324.63	[17]
	tricosane	Dufour	Hydrocarbon	C23	324.63	[17]
	9-pentacosene	Dufour	Hydrocarbon	C25	350.66	[17]
Tribe Solenopsidini						
Mayriella overbecki	methyl 6-methylsalicylate	venom	Phenol	C08	166.17	[30]
Monomorium pharaonis	3-butyl-5-methyloctahydroindolizine (monomorine I)	venom	Amine	C13	195.34	[31]
	2(5'-hexenyl)-5-pentyl pyrrolidine (monomorine III)	venom	Amine	C15	223.4	[32]
	(6*E*,10*Z*)-3,4,7,11-tetramethyl-6,10-tridecadien-1-al (faranal)	Dufour	Carboxylic acid	C13	250.42	[33]
Solenopsis invicta	*Z,E*-alpha-farnesene	Dufour	Hydrocarbon	C12	204.35	[34]
	Z,E-alpha-homofarnesene	Dufour	Hydrocarbon	C12	218.38	[35]
	Z,Z-alpha-homofarnesene	Dufour	Hydrocarbon	C12	218.38	[35]
	Z,Z,Z-allofarnesene	Dufour	Hydrocarbon	C12	204.35	[36]
Tribe Myrmicini						
Eutetramorium mocquerysi	2,3-dimethyl-5-(2-methylpropyl)-pyrazine	venom	Amine	C05	164.25	[37]
Manica rubida	EDMP	venom	Amine	C05	136.19	[38]
Myrmica lobicornis	EDMP	venom	Amine	C05	136.19	[39]
Myrmica rubra	EDMP	venom	Amine	C05	136.19	[39]
Myrmica ruginodis	EDMP	venom	Amine	C05	136.19	[39]
Myrmica rugulosa	EDMP	venom	Amine	C05	136.19	[39]
Myrmica sabuleti	EDMP	venom	Amine	C05	136.19	[39]
Myrmica scabrinodis	EDMP	venom	Amine	C05	136.19	[39]
Myrmica schencki	EDMP	venom	Amine	C05	136.19	[39]
Myrmica sulcinodis	EDMP	venom	Amine	C05	136.19	[39]
Pogonomyrmex barbatus	TMP	venom	Amine	C04	122.17	[40]
	EDMP	venom	Amine	C05	136.19	[40]
	DMP	venom	Amine	C03	108.14	[40]
Pogonomyrmex maricopa	TMP	venom	Amine	C04	122.17	[40]
	EDMP	venom	Amine	C05	136.19	[40]
	DMP	venom	Amine	C03	108.14	[40]
Pogonomyrmex occidentalis	TMP	venom	Amine	C04	122.17	[40]
	EDMP	venom	Amine	C05	136.19	[40]
	DMP	venom	Amine	C03	108.14	[40]
Pogonomyrmex rugosus	TMP	venom	Amine	C04	122.17	[40]
	EDMP	venom	Amine	C05	136.19	[40]
	DMP	venom	Amine	C03	108.14	[40]
Tribe Tetramorini						
Tetramorium caespitum	DMP	venom	Amine	C03	108.14	[16]
	EDMP	venom	Amine	C05	136.19	[16]
Tetramorium impurum	methyl 6-methylsalicylate	venom	Phenol	C08	166.17	[16c, 41]
Tetramorium meridionale	2-methylpyrazine (MP)	venom	Amine	C03	94.11	[42]
	DMP	venom	Amine	C03	108.14	[42]
	TMP	venom	Amine	C04	122.17	[42]
	EDMP	venom	Amine	C05	136.19	[42]
	1-benzo[b]pyrrole (indole)	venom	Amine	C08	117.15	[42]
Tribe Pheidolini						
Aphaenogaster albisetosus	(*S*)-4-methyl-3-heptanone	venom	Ketone	C07	128.21	[43]
	(*R*)-4-methyl-3-heptanone	venom	Ketone	C07	128.21	[43]
Aphaenogaster cockerelli	(*R*)-1-phenylethanol	venom	Alcohol I	C08	122.16	[43]
	(*S*)-4-methyl-3-heptanone	venom	Ketone	C07	128.21	[43]
Aphaenogaster rudis	3-(2-piperidinyl)pyridine (anabasine)	venom	Amine	C09	162.23	[44]
	3,4,5,6-tetrahydro-2,3' -bipyridine (anabaseine)	venom	Amine	C09	160.22	[44]
	2,3'-bipyridyl	venom	Amine	C09	156.18	[44]
	N-isopentyl-2-phenylethylamine	venom	Amine	C08	191.31	[44]
Aphaenogaster senilis	anabaseine	venom	Amine	C09	160.22	[45]
	anabasine	venom	Amine	C09	162.23	[45]
	2,3'-bipyridine	venom	Amine	C09	156.18	[45]
Messor andrei	*n*-tridecane	pygidial	Hydrocarbon	C13	184.36	[46]
Messor bouvieri	anabasine	venom	Amine	C09	162.23	[47]
	anabaseine	venom	Amine	C09	160.22	[47]
	EDMP	venom	Amine	C05	136.19	[47]
	heptadecadiene	Dufour	Hydrocarbon	C17	236.44	[48]
Messor capensis	anabasine	venom	Amine	C09	162.23	[49]
	anabaseine	venom	Amine	C09	160.22	[49]
Messor ebeninus	anabasine	venom	Amine	C09	162.23	[50]
	1-pentadecene	Dufour	Hydrocarbon	C15	210.4	[50]
Messor pergandei	*n*-tridecane	pygidial	Hydrocarbon	C13	184.36	[46]
Pheidole pallidula	EDMP	-	Amine	C05	136.19	[51]
Pristomyrmex pungens	6-*n*-pentyl-2-pyrone	venom	Ketone	C10	166.22	[52]

Tribe Crematogastrini						
Crematogaster castanea	(*R*)-2-dodecanol	tibial	Alcohol II	C12	186.33	[13]
Tribe Attini						
Acromyrmex octospinosus	methyl 4-methylpyrrole-2-carboxylate	venom	Amine	C05	139.15	[29, 53]
	EDMP	venom	Amine	C05	136.19	[29, 53]
	2-ethyl 3,5-dimethyl-pyrazine	venom	Amine	C05	136.2	[29, 53]
	acetaldehyde	venom	Aldehyde	C02	44.05	[53]
Acromyrmex subterraneus molestans	methyl 4-methylpyrrole-2-carboxylate	venom	Amine	C05	139.15	[54]
Acromyrmex subterraneus subterraneus	methyl 4-methylpyrrole-2-carboxylate	venom	Amine	C05	139.15	[55]
Atta bisphaerica	methyl 4-methylpyrrole-2-carboxylate	venom	Amine	C05	139.15	[54, 56]
	EDMP	venom	Amine	C05	136.19	[54, 56]
	2-phenylacetic acid	venom	Carboxylic acid	C08	136.15	[56]
	bornylene	venom	Hydrocarbon	C09	136.23	[56]
	1-octanol	venom	Alcohol I	C08	130.23	[56]
Atta cephalotes	methyl 4-methylpyrrole-2-carboxylate	venom	Amine	C05	139.15	[53, 57]
	EDMP	venom	Amine	C05	136.19	[57]
	acetaldehyde	venom	Aldehyde	C02	44.05	[57]
	acetone	venom	Ketone	C03	58.08	[57]
	methylpropanal	venom	Aldehyde	C04	72.11	[57]
Atta laevigata	methyl 4-methylpyrrole-2-carboxylate	venom	Amine	C05	139.15	[54, 56]
	2-phenylacetic acid	venom	Carboxylic acid	C08	136.15	[54, 56]
	bornylene	venom	Hydrocarbon	C09	136.23	[56]
Atta sexdens	methyl 4-methylpyrrole-2-carboxylate	venom	Amine	C05	139.15	[9a]
Atta sexdens rubropilosa	methyl 4-methylpyrrole-2-carboxylate	venom	Amine	C05	139.15	[53, 58
	EDMP	venom	Amine	C05	136.19	[53, 58]
	acetaldehyde	venom	Aldehyde	C02	44.05	[53]
	acetone	venom	Ketone	C03	58.08	[53]
	methylpropanal	venom	Aldehyde	C04	72.11	[53]
	methyl 2-phenylacetate	venom	Acetate ester	C08	150.17	[58]
	ethyl 2-phenylacetate	venom	Acetate ester	C08	164.2	[58]
Atta sexdens sexdens	methyl 4-methylpyrrole-2-carboxylate	venom	Amine	C05	139.15	[53, 59]
	EDMP	venom	Amine	C05	136.19	[53, 59a]
	DMP	venom	Amine	C03	108.14	[59b]
	TMP	venom	Amine	C04	122.17	[59b]
	acetaldehyde	venom	Aldehyde	C02	44.05	[53, 59b]
	acetone	venom	Ketone	C03	58.08	[53]
	methylpropanal	venom	Aldehyde	C04	72.11	[53]
Atta texana	methyl 4-methylpyrrole-2-carboxylate	-	Amine	C05	139.15	[8, 60]
Tribe Metoponini						
Metapone madagascarica	methyl pyrrole-2-carboxylate	venom	Amine	C05	125.13	[61]
	EDMP	venom	Amine	C05	136.19	[61]
	DMP	venom	Amine	C03	108.14	[61]
	TMP	venom	Amine	C04	122.17	[61]
	acetophenone	venom	Ketone	C08	120.15	[61]
Tribe Myrmicariini						
Myrmicaria eumenoides	(+)- limonene	venom	Hydrocarbon	C08	136.23	[18]
Subfamily DOLICHODERINAE						
Tribe Dolichoderini						
Dolichoderus thoracicus	(*Z*)-9-octadecenal	Pavan	Aldehyde	C18	266.47	[62]
	(*Z*)-9-hexadecenal	Pavan	Aldehyde	C16	238.41	[62]
	(*Z*)-11-eicosenal	Pavan	Aldehyde	C20	294.52	[62]
	(*Z*)-13-docosenal	Pavan	Aldehyde	C22	322.57	[62]
Tribe Tapinomini						
Linepithema humile	(*Z*)-9-hexadecenal	(ventral)	Aldehyde	C16	238.41	[63]
	dolichodial [=2-(1-formylvinyl)-5-methylcyclopentanecarbaldehyde]	pygidial	Aldehyde	C07	166.22	[28]
	iridomyrmecin [=hexahydro-4,7-dimethylcyclopenta[c]pyran-3(1*H*)-one]	pygidial	Ketone	C08	168.23	[28]
Tapinoma simrothi	iridodial [=2-acetyl-5-methylcyclopentanecarbaldehyde]	pygidial	Aldehyde	C07	154.21	[64]
	iridomyrmecin	pygidial	Ketone	C08	168.23	[64]
Subfamily FORMICINAE						
Tribe Formicini						
Formica rufa	mellein [3,4-dihydro-8-hydroxy-3-methylisocoumarin]	rectal	Ketone	C10	178.19	[65]
Tribe Lasiini						
Lasius fuliginosus	mellein	(hindgut)	Ketone	C10	178.19	[66]
	2,3-dihydro-3,5-dihydroxy-6-methyl-4(*H*)-pyran-4-one	(hindgut)	Ketone	C06	144.13	[66]
	hexanoic acid	(rectal fluid)	Carboxylic acid	C06	116.16	[67]
	heptanoic acid	(rectal fluid)	Carboxylic acid	C07	130.19	[67]
	octanoic acid	(rectal fluid)	Carboxylic acid	C08	144.21	[67]
	nonanoic acid	(rectal fluid)	Carboxylic acid	C09	158.24	[67]
	decanoic acid	(rectal fluid)	Carboxylic acid	C10	172.26	[67]
	dodecanoic acid	(rectal fluid)	Carboxylic acid	C12	200.32	[67]
Lasius niger	3,4-dihydro-8-hydroxy-3,5,7-trimethylisocoumarin	rectal	Ketone	C10	206.24	[65]
Tribe Camponotini						
Camponotus atriceps	6-sec-butyl-tetrahydro-3,5-	rectal	Pyran	C08	184.26	[68]

	dimethylpyran-2-one					
Camponotus balzani	3,4-dihydro-8-hydroxy-3,5,7-trimethylisocoumarin	rectal	Ketone	C08	206.24	[69]
Camponotus castaneus	3,5-dimethyl-6-(1'-methylpropyl)-tetrahydro-2*H* -pyran-2-one	rectal	Pyran	C08	184.26	[69]
Camponotus floridanus	nerolic acid [=(*Z*)-3,7-dimethyl-2,6-octadienoic]	rectal	Carboxylic acid	C08	168.23	[68]
Camponotus herculeanus	(2*S*,4*R*,5*S*)-2,4-dimethyl-5-hexanolide	rectal	Cyclic ester	C06	142.2	[70]
Camponotus inequalis	3,4-dihydro-8-hydroxy-3,5,7-trimethylisocoumarin	rectal	Ketone	C10	206.24	[71]
Camponotus ligniperda	(2*S*,4*R*,5*S*)-2,4-dimethyl-5-hexanolide	rectal	Cyclic ester	C06	142.2	[70b]
Camponotus mus	5-hydroxy-4-decanolide	-	Cyclic ester	C10	186.25	[72]
Camponotus pennsylvanicus	(2*S*,4*R*,5*S*)-2,4-dimethyl-5-hexanolide	rectal	Cyclic ester	C06	142.2	[70b]
Camponotus planatus	5-hydroxy-4-decanolide	-	Cyclic ester	C10	186.25	[72]
Camponotus rufipes	3,4-dihydro-8-hydroxy-3,7-dimethylisocoumarin	rectal	Ketone	C10	178.19	[73]
Camponotus sericeiventris	3,4-dihydro-8-hydroxy-3,5,7-trimethylisocoumarin	rectal	Ketone	C08	206.24	[69]
Camponotus silvicola	3,4-dihydro-8-hydroxy-3,5,7-trimethylisocoumarin	rectal	Ketone	C08	206.24	[73]
Camponotus socius	(2*S*,4*R*,5*S*)-2,4-dimethyl-5-hexanolide	rectal	Cyclic ester	C06	142.2	[70b]
	2,3-dihydro-3,5-dihydroxy-6-methyl-4(*H*)-pyran-4-one	rectal	Ketone	C06	144.13	[74]
	formic acid [=methanoic acid]	venom	Carboxylic acid	C01	46.03	[74]
Camponotus vagus	((2*S*,4*R*,5*S*)-2,4-dimethyl-5-hexanolide	rectal	Cyclic ester	C06	142.2	[70b]
Subfamily PONERINAE						
Tribe Ponerini						
Leptogenys diminuta	(3*R*,4*S*)-4-methyl-3-heptanol	venom	Alcohol II	C07	130.23	[14, 75]
	cis-isogeraniol	pygidial	Alcohol I	C08	154.25	[14b, 75]
Leptogenys peuqueti	1-ethyl-4-methylheptyl acetate	venom	Acetate ester	C08	200.32	[15]
	1-isopropyl-4-methylheptyl acetate	venom	Acetate ester	C08	214.34	[15]
	1-propyl-4-methylheptyl acetate	venom	Acetate ester	C09	214.34	[15]
	4-methyl-7-dodecanol	venom	Alcohol II	C11	200.36	[15]
	3,9-dimethyl-6-dodecanol	venom	Alcohol II	C12	214.39	[15
	1-pentyl-4-methylheptyl acetate	venom	Acetate ester	C11	242.4	[15]
	4-methyl-7-tridecanol	venom	Alcohol II	C13	214.39	[15]
	4-methyl-7-tetradecanol	venom	Alcohol II	C14	228.41	[15]
	4,10-dimethyl-7-tridecanol	venom	Alcohol II	C13	228.41	[15]
	1-(3-methylhexyl)-4-methylheptyl acetate	venom	Acetate ester	C13	270.45	[15]
	1-(3-methylhexyl)-octyl acetate	venom	Acetate ester	C14	270.45	[15]
	1-heptyloctyl acetate	venom	Acetate ester	C15	270.45	[15]
	4-methyl-7-hexadecanol	venom	Alcohol II	C16	256.47	[15]
	1-(3-methylhexyl)-decyl acetate	venom	Acetate ester	C16	298.5	[15]
Megaponera foetens (= *Pachycondyla analis)*	*N,N*-dimethyluracil	venom	Amine	C03	140.14	[76]
	actinidine	pygidial	Amine	C08	147.22	[76b]
Pachycondyla marginata	citronellal [=3,7-dimethyl-6-octenal]	pygidial	Aldehyde	C08	154.25	[77]
Pachycondyla tarsata	9-heptadecanone	sternal	Ketone	C17	254.45	[78]
Subfamily ECTATOMMINAE						
Tribe Ectatommini						
Gnamptogenys striatula	4-methylgeranyl decanoate	Dufour	Carboxylic ester	C10	322.53	[79]
	4-methylgeranyl dodecanoate	Dufour	Carboxylic ester	C12	350.58	[79]
Ectatomma ruidum	geranylgeraniol acetate	Dufour	Acetate ester	C16	332.52	[80]
	geranylgeraniol	Dufour	Alcohol I	C16	290.48	[80]
Rhytidoponera metallica	isogeraniol [=(*Z*)-3,7-dimethyl-3,6-octadien-1-ol	pygidial	Alcohol I	C08	154.25	[81]
	3-hydroxybenzaldehyde	pygidial	Aldehyde	C06	122.12	[81]
Subfamily DORYLINAE						
Tribe Aenictini						
Aenictus sp	methyl anthranilate [=methyl 2-aminobenzoate]		Carboxylic ester	C07	151.16	[82]
	methyl nicotinate [=methyl 3-pyridinecarboxylate]		Amine	C05	137.14	[82]

References

[1] http://osuc.biosci.ohio-state.edu/hymenoptera/tsa.sppcount?the_taxon=Formicidae (accessed 21st May 2014). The exact number is 12,795.

[2] Beckers R, Goss S, Deneubourg JL, Pasteels JM. (**1989**) Colony size, communication, and ant foraging strategy. *Psyche*, ***96***, 239-256.

[3] (a) Wehner R. (**1987**) Spatial organization of foraging behavior in individually searching desert ants, *Cataglyphis* (Sahara desert) and *Ocymyrmex* (Namib desert). In *From Individual to Collective Behavior in Social Insects*. Pasteels JM, JL Deneubourg JL (Eds). Birkhauser, Basel, Switzerland, 15-42. Comment in the page 33: "Finally let me mention one observation made by S. Wehner and myself (26-07-76). It indicates that, under certain circumstances, *Cataglyphis* might exploit a rich food patch not exclusively by chance encounters. ....". (b) Amor F, Ortega P, Cerdá X, Boulay R. (**2010**) Cooperative prey-retrieving in the ant *Cataglyphis floricola*: an unusual short-distance recruitment. *Insectes Sociaux*, ***57***, 91-94; (c) Razin N, Eckmann JP, Feinerman O. (**2013**) Desert ants achieve reliable recruitment across noisy interactions. *Journal of the Royal Society Interface*, ***10***, 201330079.

[4] (a) Hölldobler B, Wilson EO. (**1990**) *The Ants*. Belknap Press of Harvard University Press, Cambridge. 1-732; (b) Passera L, Aron S. (**2005**) *Les Fourmis. Comportement, organisation sociale et évolution*. Les Presses scientifiques du CNRC, Ottawa, Canada. 1-480.

[5] Jessen K, Maschwitz U. (1**986**) Orientation and recruitment behavior in the ponerine ant *Pachycondyla tesserinoda* (Emery): laying of individual-specific trails during tandem running. *Behavioral Ecology and Sociobiology*, ***19***, 151-155.

[6] (a) Cerdá X, Angulo E, Boulay R, Lenoir A. (**2009**) Individual and collective foraging decisions: a field study of worker recruitment in the gypsy ant *Aphaenogaster senilis*. *Behavioral Ecology and Sociobiology*, ***65***, 551-562; (b) Sommer S, Weibel D, Blaser N, Furrer A, Wenzler NE, Rössler W, Wehner R (**2013**) Group recruitment in a thermophilic desert ant, *Ocymyrmex robustior*. *Journal of Comparative Physiology A*, ***199***, 711-722.

[7] Jackson BD, Cammaerts MC, Morgan ED, Attygalle AB. (**1990**) Chemical and behavioral studies on Dufour gland contents of *Manica rubida*. *Journal of Chemical Ecology*, ***16***, 827-840.

[8] Tumlinson JH, Silverstein RM, Moser JC, Brownlee RG, Ruth JM. (**1971**) Identification of the trail pheromone of a leaf-cutting ant, *Atta texana*. *Nature*, ***234***: 348–349.

[9] (a) Robinson SW, Cherrett JM. (**1978**) The possible use of methyl 4-methylpyrrole-2- carboxylate, an ant trail pheromone, as a component of an improved bait for leaf-cutting ant (Hymenoptera: Formicidae). *Bulletin of Entomological Research*, ***68***, 159–170; (b) Vilela EF, Howse PE. (**1988**) Pheromone performance as an attractive component in baits for the control of the leafcutting ant *Atta sexdens rubropilosa* Forel, 1908 (Hymenoptera: Formicidae). *Anais da Sociedade de Entomologia do Brasil*, ***17***, 107–124; (c) Greenberg L, Klotz JH. (**2000**) Argentine ant (Hymenoptera: Formicidae) trail pheromone enhances consumption of liquid sucrose solution. *Journal of Economic Entomology*, ***93***, 119-122; (d) Hughes WOH, Goulson D (**2002**) The use of alarm pheromones to enhance bait harvest by grass-cutting ants. *Bulletin of Entomological Research*, ***92***, 213-218.

[10] (a) Shorey HH, Gaston LK, Gerber RG, Phillips PA, Wood DL. (**1992**) Disruption of foraging by Argentine ants, *Iridomyrmex humilis* (Mayr) (Hymenoptera: Formicidae), in citrus trees through the use of semiochemicals and related. *Journal of Chemical Ecology*, ***18***, 2131-2142; (b) Suckling DM, Peck RW, Manning LM, Stringer LD, Cappadonna J, El-Sayed AM. (**2008**) Pheromone disruption of Argentine ant trail integrity. *Journal of Chemical Ecology*, ***34***, 1602-1609; (c) Suckling DM, Peck RW, Stringer LD, Snook K, Banko PC. (**2010**) Trail pheromone disruption of Argentine ant trail formation and foraging. *Journal of Chemical Ecology*, ***36***, 122-128; (d) Nishisue K, Sunamura E, Tanaka Y, Sakamoto H, Suzuki S, Fukumoto T, Terayama M, Tatsuki S. (**2010**) Long-term field trial to control the invasive Argentine ant (Hymenoptera: Formicidae) with synthetic trail pheromone. *Journal of Economic Entomology*, ***103***, 1784–1789.

[11] (a) Ali MF, Morgan ED. (**1990**) Chemical communication in insect communities: a guide to insect pheromones with special emphasis on social insects. *Biological Reviews*, ***65***, 227-247; (b) Billen J, Morgan ED. (**1998**) Pheromone communication in social insects: sources and secretions. In *Pheromone Communication in Social Insects. Ants, Wasps, Bees, and Termites*. Vander Meer RK, Breed MD, Espelie KE, Winston ML (Eds). Westview Press, Boulder, Colorado, USA. pp 3-33; (c) Jackson BD, Morgan ED. (**1993**) Insect chemical communication: pheromones and exocrine glands of ants. *Chemoecology*, ***4***, 125-144; (d) El-Sayed AM. (**2008**). The Pherobase: Database of Insect Pheromones and Semiochemicals. <http://www; (e) Morgan ED (**2008**) Chemical sorcery for sociality: exocrine secretions of ants (Hymenoptera: Formicidae). *Myrmecological News*, ***11***, 79-90.

[12] (a) Morgan ED. (**2009**) Trail pheromones of ants. *Physiological Entomology*, ***34***, 1-17; (b) Jaffe K, Issa S, Sainz-Borgo C (**2012**) Chemical recruitment for foraging in ants (Formicidae) and termites (Isoptera): a revealing comparison. *Psyche*, ***2012***, 694910. doi:10.1155/2012/694910.

[13] Morgan ED, Brand JM, Mori K, Keegans SJ. (**2004**) The trail pheromone of the ant *Crematogaster castanea*. *Chemoecology*, ***14***, 119–120.

[14] (a) Attygalle, AB, Vostrowsky O, Bestmann, HJ, Steghaus-Kovac S, Maschwitz U. (**1988**) (3*R*,4*S*)-4-Methyl-3-heptanol, the trail pheromone of the ant *Leptogenys diminuta*. *Naturwissenschaften*, ***75***, 315–317; (b) Attygalle AB, Steghaus-Kovac, S, Ahmad VU, Maschwitz U, Vostrowsky O, Bestmann HJ. (**1991**) *cis*-Isogeraniol, a recruitment pheromone of the ant *Leptogenys diminuta*. *Naturwissenschaften*, ***78***, 90–92.

[15] Janssen E, Übler E, Bauriegel L, Kern F, Bestmann HJ, Attygalle AB, Steghaus- Kovac S, Maschwitz U. (**1997**) Trail pheromone of the ponerine ant *Leptogenys peuqueti* (Hymenoptera: Formicidae): a multicomponent mixture of related compounds pheromones. *Naturwissenschaften*, ***84***, 122–125.

[16] (a) Attygalle AB, Morgan ED. (**1983**) Trail pheromone of the ant *Tetramorium caespitum* L. *Naturwissenschaften*, ***70***, 364–365; (b) Attygalle AB, Morgan ED. (**1984**) Identification of trail pheromone of the ant *Tetramorium caespitum* L. (Hymenoptera: Myrmicinae). *Journal of Chemical Ecology*, ***10***,1453–1468; (c) Morgan ED, Ollett DG. (**1987**) Methyl 6-methylsalicylate, trail pheromone of the ant *Tetramorium impurum*. *Naturwissenschaften*, ***74***, 596–597.

[17] Morgan ED, Hölldobler B, Vaisar T, Jackson BD. (**1992**) Contents of poison apparatus and their relation to trail-following in the ant *Daceton armigerum*. *Journal of Chemical Ecology*, ***18***, 2161–2168.

[18] Kaib M, Dittebrand H. (**1990**) The poison gland of the ant *Myrmicaria eumenoides* and its role in recruitment communication. *Chemoecology*, ***1***, 3-11.

[19] Dussutour A, Nicolis SC, Shephard G, Beekman M, Sumpter DJT. (2009). The role of multiple pheromones in food recruitment by ants. *Journal of Experimental Biology*, ***212***, 2337–2348.

[20] (a) Robinson EJH Jackson DE, Holcombe M, Ratnieks FLW. (**2005**) "No entry" signal in ant foraging. *Nature*, ***24***, 438–442; (b) Robinson EJH, Green KE, Jenner EA, Holcombe M, Ratnieks FLW. (**2008**) Decay rates of attractive and repellent pheromones in an ant foraging trail network. *Insectes Sociaux*, ***55***, 246–251.

[21] Witte V, Attygalle AB, Meinwald J. (**2007**) Complex chemical communication in the crazy ant *Paratrechina longicornis* Latreille (Hymenoptera: Formicidae). *Chemoecology*, ***17***, 57-62.

[22] Hölldobler B, Palmer JM, Moffett MW. (**1990**) Chemical communication in the dacetine ant *Daceton armigerum* (Hymenoptera: Formicidae). *Journal of Chemical Ecology*, ***16***, 1207-1219.

[23] Jeanson R, Ratnieks FLW, Deneubourg J.-L. (**2003**). Pheromone trail decay rates on different substrates in the Pharaoh's ant, *Monomorium pharaonis*. *Physiological Entomology*, ***28***, 192–198.

[24] Jackson DE, Martin SJ, Holcombe M, Ratnieks FLW. (**2006**) Longevity and detection of persistent foraging trails in Pharaoh's ants, *Monomorium pharaonis* (L.). *Animal Behaviour*, ***71***, 351-359.

[25] van Oudenhove L, Billoir E, Boulay R, Bernstein C, Cerdá X. (**2011**) Temperature limits trail following behaviour through pheromone decay in ants. *Naturwissenschaften*, ***98***, 1009-1017.

[26] Ruano F, Tinaut A, Soler JJ. (**2000**) High surface temperatures select for individual foraging in ants. *Behavioral Ecology*, ***11***, 396–404.

[27] Torres-Contreras H, Olivares-Donoso R, Niemeyer HM. (**2007**) Solitary foraging in the ancestral South American ant, *Pogonomyrmex vermiculatus*. Is it due to constraints in the production or perception of trail pheromones? *Journal of Chemical Ecology*, ***33***, 435-440.

[28] Choe DH, Villafuerte DB, Tsutsui ND. (**2012**) Trail pheromone of the Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae). *PLoS ONE 7*: e45016.

[29] Cross JH, West JR, Silverstein, RM, Jutsum AR, Cherrett JM. (**1982**) Trail pheromone of the leaf-cutting ant, *Acromyrmex octospinosus* (Reich) (Formicidae: Myrmicinae). *Journal of Chemical Ecology*, ***8***, 1119–1124.

[30] Kohl E, Hölldobler B, Bestmann, HJ. (**2000**) A trail pheromone component of the ant *Mayriella overbecki* Viehmeyer (Formicidae: Myrmicinae). *Naturwissenschaften*, ***87***, 320–322.

[31] Ritter FJ, Rotans IE, Talman E, Verwiel PE, Stein E (**1973**) 5-Methyl-3- butyloctahydroindolizine, a novel type of pheromone attractive to pharaoh's ants *Monomorium pharaonis* (L.). *Experientia*, ***29***, 530-531.

[32] Ritter FJ, Bruggemann-Rotgans IEM, Verkuil E, Persoons CJ. (**1975**) The trail pheromone of the Pharaoh's ant: components of the odour trail and their origin. In *Pheromones and Defensive Secretions in Social Insects*. Noirot CH, Howse PE, Le Masne G. (Eds). French section of the IUSSI, University of Dijon, France, 99-103.

[33] Ritter FJ, Bruggemann-Rotgans IE, Verwiel PE, Persoons CJ, Talman E. (**1977**) Trail pheromone of the pharaoh's ant, *Monomorium pharaonis*: isolation and identification of faranal, a terpenoid related to juvenile hormone II. *Tetrahedron Letters*, ***30***, 2617–2618.

[34] Vander Meer RK, Alvarez FM, Lofgren CS. (**1988**) Isolation of the trail recruitment pheromone of *Solenopsis invicta*. *Journal of Chemical Ecology*, ***14***, 825–838.

[35] (a) Vander Meer RK, Williams FD, Lofgren CS. (**1981**) Hydrocarbon components of the trail pheromone of the red imported fire ant, *Solenopsis invicta*. *Tetrahedron Letters*, ***22***, 1651–1654; (b) Alvarez FM, Vander Meer RK, Lofgren CS. (**1987**) Synthesis of homofarnesenes: trail pheromone components of the fire ant, *Solenopsis invicta*. *Tetrahedron*, ***43***, 2897-2900.

[36] Williams HJ, Strand MR, Vinson SB. (**1981**) Trail pheromone of the red imported fire ant *Solenopsis invicta* (Buren). *Experientia*, ***37***, 1159–1160.

[37] Tentschert J, Bestmann HJ, Hölldobler B, Heinze J. (**2000**) 2,3-Dimethyl-5-(2- methylpropyl)pyrazin, a trail pheromone component of *Eutetramorium mocquerysi* Emery (1899) (Hymenoptera: Formicidae). *Naturwissenschaften*, ***87***, 377–380.

[38] Attygalle AB, Cammaerts MC, Cammaerts R, Morgan ED, Ollett DG. (**1986**). Chemical and ethological studies of the trail pheromone of the ant *Manica rubida* (Hymenoptera: Formicidae). *Physiological Entomology*, ***11***, 125–132.

[39] Evershed RP, Morgan ED, Cammaerts MC. (**1981**) Identification of the trail pheromone of the ant *Myrmica rubra* L., and related species. *Naturwissenschaften*, ***68***, 374–376.

[40] Hölldobler B, Morgan ED, Oldham NJ, Liebig J. (**2001**). Recruitment pheromone in the harvester ant genus *Pogonomyrmex*. *Journal of Insect Physiology*, ***47***, 369–374.

[41] Morgan ED, Jackson BD, Ollett DG, Sales GW. (**1990**) Trail pheromone of the ant *Tetramorium impurum* and model compounds: structure-activity comparisons. *Journal of Chemical Ecology*, ***16***, 3493–3510.

[42] Jackson BD, Keegans SJ, Morgan ED, Cammaerts MC, Cammaerts R. (**1990**) Trail pheromone of the ant *Tetramorium meridionale*. *Naturwissenschaften*, ***77***, 294–296.

[43] Hölldobler B, Oldham NJ, Morgan ED, König WA (**1995**) Recruitment pheromones in the ants *Aphaenogaster albisetosus* and *A. cockerelli* (Hymenoptera: Formicidae). *Journal of Insect Physiology*, ***41***, 739-744.

[44] Attygalle AB, Kern F, Huang Q, Meinwald J. (**1998**) Trail pheromone of the myrmicine ant *Aphaenogaster rudis* (Hymenoptera: Formicidae). *Naturwissenschaften*, ***85***, 38–41.

[45] Lenoir A, Benoist A, Hefetz A, Francke W, Cerdá X, Boulay R. (**2011**) Trail-following behaviour in two *Aphaenogaster* ants. *Chemoecology*, ***21***, 83-88.

[46] Hölldobler B, Plowes NJR, Johnson RA, Nishshanka U, Liu C, Attygalle AB. (**2013**) Pygidial gland chemistry and potential alarm-recruitment function in column foraging, but not solitary, Nearctic *Messor* harvesting ants (Hymenoptera: Formicidae: Myrmicinae). *Journal of Insect Physiology*, ***59***, 863-869.

[47] Jackson BD, Wright PJ, Morgan ED. (**1989**). 3-Ethyl-2,5-dimethylpyrazine, a component of the trail pheromone of the ant *Messor bouvieri*. *Experientia*, ***45***, 487–489.

[48] Ali MF, Billen JPJ, Jackson BD, Morgan ED (**1989**) The Dufour gland contents of three species of Euro-African *Messor* ants and a comparison with those of North American *Pogonomyrmex* (Hymenoptera: Formicidae). *Biochemical Systematics and Ecology*, ***17***, 469-477.

[49] Brand JM, Mpuru SP. (**1993**) Dufour's gland and poison gland chemistry of the myrmicine ant, *Messor capensis* (Mayr). *Journal of Chemical Ecology*, ***19***, 1315–1321.

[50] Coll M, Hefetz A, Lloyd HA. (**1987**). Adnexal gland chemistry of *Messor ebeninus* Forel (Formicidae: Myrmicinae). *Zeitschrift für Naturforschung C*, ***42***, 1027–1029.

[51] Ali MF, Morgan ED, Detrain C, Attygalle AB. (**1988**) Identification of a component of the trail pheromone of the ant *Pheidole pallidula* (Hymenoptera: Formicidae). *Physiological Entomology*, ***13***, 257–265.

[52] Janssen E, Hölldobler B, Kern F, Bestmann HJ, Tsuji K. (**1997**). Trail pheromone of myrmicine ant *Pristomyrmex pungens*. *Journal of Chemical Ecology*, ***23***, 1025–1034.

[53] Evershed RP, Morgan ED. (**1983**) The amounts of trail pheromone substances in the venom of workers of four species of Attine ants. *Insect Biochemistry*, ***13***, 469–474.

[54] Mosquera OM, de Oliveira JS. (**1990**) Identificación de las feromonas de trilla de hormigas cortadoras (Formicidae: Attini). *Revista Colombiana de Química*, ***19***, 73-79

[55] do Nascimento RR, Morgan ED, Moreira DDO, Della Lucia TMC. (**1994**). Trail pheromone of leaf-cutting ant *Acromyrmex subterraneus subterraneus* (Forel). *Journal of Chemical Ecology*, ***20***, 1719–1724.

[56] de Oliveira JS, Martínez OMM, Carnieri N, Vilela EF, Reis HO. (**1990**) Componentes do feromônio de trilha das formigas cortadeiras *Atta laevigata* F. Smith e *Atta bisphaerica* Forel (Formicidae: Attini). *Anais da Sociedade Entomologica do Brasil,* ***19***, 143-154

[57] Riley RG, Silverstein RM, Carroll B, Carroll R. (**1974**) Methyl 4-methylpyrrole-2-carboxylate: a volatile trail pheromone from the leaf-cutting ant, *Atta cephalotes*. *Journal of Insect Physiology*, ***20***, 651-654.

[58] Cross JH, Byler RM, Ravid U, Silverstein RM, Robinson SW, Baker PM, de Oliveira JS, Jutsum AR, Cherrett, JM. (**1979**) The major component of the trail pheromone of the leaf-cutting ant, *Atta sexdens rubropilosa* Forel: 3-ethyl-2,5-dimethylpyrazine. *Journal of Chemical Ecology*, ***5***, 187–203.

[59] (a) Billen J, Beeckman W, Morgan ED. (**1992**) Active trail pheromone compounds and trail following in the ant *Atta sexdens sexdens* (Hymenoptera Formicidae). *Ethology Ecology and Evolution*, ***4***, 197–202; (b) Morgan ED, Keegans S, Tits J, Wenseleers T, Billen J. (**2006**). Preferences and differences in the trail pheromone of the leaf-cutting ant *Atta sexdens sexdens* (Hymenoptera: Formicidae). *European Journal of Entomology*, ***103***, 553–558.

[60] Tumlinson JH, Moser JC, Silverstein RM, Brownlee RG, Ruth JM. (**1972**) A volatile trail pheromone of the leaf-cutting ant, *Atta texana*. *Journal of Insect Physiology*, ***18***, 809–814.

[61] Hölldobler B, Oldham NJ, Alpert GD, Liebig J. (**2002**) Predatory behavior and chemical communication in two *Metapone* species (Hymenoptera: Formicidae). *Chemoecology*, ***12***, 147–151.

[62] Attygalle AB, Mutti A, Rohe W, Maschwitz U, Garbe W, Bestmann HJ. (**1998**) Trail pheromone from the Pavan gland of the ant *Dolichoderus thoracicus* (Smith). *Naturwissenschaften*, ***85***, 275–277.

[63] (a) Cavill GWK, Robertson PL, Davies NW. (**1979**) An Argentine ant aggregation factor. *Experientia*, ***35***, 989–990; (b) Van Vorhis Key SE, Baker TC. (**1982**) Trail-following responses of the Argentine ant *Iridomyrmex humilis* (Mayr), to a synthetic trail pheromone component and analogs. *Journal of Chemical Ecology*, ***8***, 3–14; (c) Van Vorhis Key SE, Baker TC. (**1982**) Specificity of laboratory trail following by the Argentine ant, *Iridomyrmex humilis* (Mayr), to a (*Z*)-9-hexadecenal, analogs, and gaster extract. *Journal of Chemical Ecology*, ***8***, 1057–1063.

[64] Simon T, Hefetz A. (**1991**) Trail-following responses of *Tapinoma simrothi* (Formicidae: Dolichoderinae) to pygidial gland extracts. *Insectes Sociaux*, ***38***, 17–25.
[65] Bestmann HJ, Kern F, Schäfer D, Witschel MC. (**1992**) 3,4-Dihydroisocoumarins, a new class of ant trail phromone. *Angewandte Chemie International Edition*,***31***, 795–796.
[66] Kern F, Klein RW, Janssen E, Bestmann HJ, Attygalle AB, Schäfer D, Maschwitz U. (**1997**) Mellein, a trail pheromone component of the ant *Lasius fuliginosus*. *Journal of Chemical Ecology*, ***23***, 779-792.
[67] (a) Huwyler S, Grob K, Viscontini M. (**1975**) The trail pheromone of the ant, *Lasius fuliginosus*: identification of six components. *Journal of Insect Physiology*, ***21***, 299–304; (b) Akino T, Yamaoka, R. (**1996**) Purification of the trail pheromone of *Lasius fuliginosus* Latreille. *Japanese Journal of Applied Entomology and Zoolology*, ***40***, 233–238. [In Japanese with English abstract]
[68] Haak U, Hölldobler B, Bestmann HJ. (**1996**) Species-specificity in trail pheromones and Dufour 's gland contents of *Camponotus atriceps* and *C. floridanus* (Hymenoptera: Formicidae). *Chemoecology*, ***7***, 85-93.
[69] Kohl E, Hölldobler B, Bestmann, HJ. (**2003**) Trail pheromones and Dufour gland contents in three *Camponotus* species (*C. castaneus*, *C. balzani*, *C. sericeiventris*: Formicidae, Hymenoptera). *Chemoecology*, ***13***, 113–122.
[70] (a) Bestmann HJ, Haag U, Kern F, Hölldobler B. (**1995**) 2,4-Dimethyl-5-hexanolide, a trail pheromone component of the carpenter ant *Camponotus herculeanus*. *Naturwissenschaften*, ***82***, 142-144; (b) Bestmann HJ, Liepold B, Kress A, Hofmann A. (**1999**) (2*S*, 4*R*, 5*S*)-2,4-dimethyl-5-hexanolide: ants of different species *Camponotus* can distinguish the absolute configuration of their trail pheromone. *Chemistry - a European Journal*, ***5***, 2984–2989.
[71] Bestmann HJ, Übler E, Hölldobler B. (**1997**) First biosynthetic studies on trail pheromones in ants. *Angewandte Chemie International Edition*, ***36***, 395-397.
[72] Bestmann HJ, Kohl E, Hölldobler B. in prep., cited in [69]
[73] Übler E, Kern F, Bestmann HJ, Hölldobler B, Attygalle AB. (**1995**) Trail pheromone of two formicine ants, *Camponotus silvicola* and *C. rufipes* (Hymenoptera: Formicidae). *Naturwissenschaften*, ***82***, 523–525.
[74] Kohl E, Hölldobler B, Bestmann, HJ. (**2001**) Trail and recruitment pheromones in *Camponotus socius* (Hymenoptera: Formicidae). *Chemoecology*, ***11***, 67–73.
[75] Kern F, Bestmann HJ (**1993**) Antennal electrophysiological responsiveness of the ponerine ant *Leptogenys diminuta* to trail and recruitment pheromones and its structure analogs. *Naturwissenschaften*, ***80***, 424-427
[76] (a) Longhurst C, Bakers R, Howse PE (**1979**) Termite predation by *Megaponera foetens* (Fab.) (Hymenoptera: Formicidae). Coordination of raids by glandular secretions. *Journal of Chemical Ecology*, ***5***, 703-719; (b) Janssen E, Bestmann HJ, Hölldobler B, Kern F. (**1995**) *N,N*-dimethyluracil and actinidine, two pheromones of the ponerine ant *Megaponera foetens* (Fab.) (Hymenoptera: Formicidae). *Journal of Chemical Ecology*, ***21***, 1947–1955.
[77] Hölldobler B, Janssen E, Bestmann HJ, Leal IR, Oliveira PS, Kern F, König WA. (**1996**) Communication in the migratory termite-hunting ant *Pachycondyla* (=*Termitopone*) *marginata* (Formicida, Ponerinae). *Journal of Comparative Physiology A*, ***178***, 47-53
[78] Janssen E, Hölldobler B, Bestmann HJ. (**1999**) A trail pheromone component of the African stink ant, *Pachycondyla (Paltothyreus) tarsata* Fabricius (Hymenoptera: Formicidae: Ponerinae). *Chemoecology*, ***9***, 9–11.
[79] Blatrix R, Schulz C, Jaisson P, Francke W, Hefetz A. (**2002**) Trail pheromone of ponerine ant *Gnamptogenys striatula*: 4-methylgeranyl esters from Dufour's gland. *Journal of Chemical Ecology*, ***28***, 2557–2567.
[80] Bestmann HJ, Janssen E, Kern F, Liepold B, Hölldobler B. (**1995**). All-*trans* geranyl- geranyl acetate and geranylgeraniol, recruitment pheromone components in the Dufour gland of the ponerine ant *Ectatomma ruidum*. *Naturwissenschaften*, ***82***, 334–336.
[81] Meinwald J, Wiemer DF, Hölldobler B. (**1983**) Pygidial gland secretions of the ponerine ant *Rhytidoponera metallica*. *Naturwissenschaften*, ***70***, 46-47.
[82] Oldham NJ, Morgan ED, Gobin B, Billen J. (**1994**) First identification of a trail pheromone of an army ant (*Aenictus* species). *Experientia*, ***50***, 763–765.

Article dedicated to Prof. Josep Coll Toledano on the Occasion of his 70th Birthday