

# Semiochemistry of the Scarabaeoidea

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**Abstract** The superfamily Scarabaeoidea comprises a large and diverse monophyletic group. Members share ancestral characteristics, but often exhibit considerable differences in their ecology, physiology, or mating strategies. A large number of species are regarded as pests of crop or amenity plants, while others are beneficial to humans and even may be extremely rare as a result of anthropogenic activities. A significant number of chemical ecology-based studies have been conducted with the Scarabaeoidea in order to characterize semiochemicals influencing their behavior, such as pheromones and plant-derived allelochemicals. These may be used either to control or preserve populations of the beetles, depending upon pest or beneficial status. This paper is a review of the role and identity of the semiochemicals of the Scarabaeoidea, with comments on possible future research and applied opportunities in the field of chemical ecology.

**Keywords** Integrated pest management · Attractant · Lamellicornia · Conservation · Monitoring traps · Chemical communication

## Introduction

The monophyletic superfamily Scarabaeoidea (Coleoptera) comprises about 31,000 species worldwide that share common characters, including adult antennae with the last 3–7 segments forming a lamellate club, and C-shaped larvae with

well-developed antennae and legs (Grimaldi and Engel 2005; Lawrence and Britton 1991). Composition of the Scarabaeoidea (here also termed as ‘scarabaeoid beetles’) into higher categories is still unresolved, and conclusions about phylogenetic relationships and the number of families are subjects of debate (e.g., Browne and Scholtz 1999; Löbl and Smetana 2006; Smith et al. 2006). Here, we follow the classification by Bouchard et al. (2011).

It is thought that the ancestral larval habitat of scarabaeoid beetles was soil, and the ancestral larval food was fungus-rich humus, which also served as food for the adults (Krell 2006). Adaptation to various food sources then led to the extensive radiation of the group (Browne and Scholtz 1999). Feeding habits now include necrophagy, coprophagy, saprophagy, fungivory, carnivory, and herbivory (Browne and Scholtz 1999; Endrődi 1956). In some of the most derived groups (Krell 2006), there can be considerable differences between the diet of the larval and adult stages. For example, in *Anoxia* spp. (Scarabaeidae: Melolonthinae), the larvae feed on plant roots, while the adults do not feed at all. Adult flower chafers of the genus *Cetonia* (Scarabaeidae: Cetoniinae) are herbivores, whereas the larvae are saprophagous (Hurpin 1962).

Many species, whether as adults, larvae, or both, attack crop plants and, therefore, are of economic importance, making them a focus of research aimed at the development of environmentally benign pest control strategies (Jackson and Klein 2006). Such investigations have been undertaken on the chemical ecology of chafers to exploit their semiochemicals (behavior-modifying chemical signals, Nordlund and Lewis 1976) in plant protection. Other driving forces behind such research efforts are (i) the ability to detect and monitor the occurrence and distribution of endangered saprophylic species, so as to aid conservation decisions (Larsson and Svensson 2009), and (ii) the evaluation of the ecological status of dung beetles associated with large mammals via monitoring their distribution (Burger et al. 2008). Semiochemicals of the

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Scarabaeidae family have been reviewed earlier (Francke and Dettner 2005; Leal 1998, 1999), with a focus on pheromones (intraspecific chemical signals). However, study of pheromones has advanced those reviews, and there also has been considerable progress in understanding the role of allelochemicals (interspecific chemical signals) in scarab behavior. Here, we give a comprehensive, family-by-family review of the semiochemicals of both pest and non-pest scarabaeoid beetles studied from the 1970s to the present.

### Glaphyridae

Also known as bumble bee scarabs, species in this family are distributed worldwide (Löbl and Smetana 2006). The larvae feed on humus, while the adults often visit flowers and may even function as pollinators. Beetle attraction to flowers of a broad range of colors is well known (Keasar et al. 2010), with the preference of certain species for red flowers being mediated by vision, via red-sensitive photoreceptors (Briscoe and Chittka 2001; Martinez-Harms et al. 2012). However, floral volatiles also may be important in the attraction of species in this group to flowers. In a field trial targeted on species of the Cetoniinae (Scarabaeidae), light blue traps baited with combinations of either (*E*)-anethol and (*E*)-cinnamyl alcohol, or (*E*)-anethol, 1-phenylethanol, 3-methyleugenol and (*RS*)-lavandulol, caught a total of 16 and 10 individuals of *Amphicoma* spp. (Amphicominae, Glaphyridae), respectively, compared to three individuals caught in fluorescent yellow traps baited with a mixture of (*RS*)-lavandulol and 2-phenylethanol (J. Vuts and M. Tóth, unpublished). The relative importance of color and odor in the attraction of bumble bee scarabs remains to be clarified. *Lichnanthe vulpina* Hentz (Glaphyrinae, Glaphyridae) is an economically important pest of cranberries in the USA. (*Z*)-7-Hexadecenol has been identified as a female-derived sex pheromone, of yet unknown anatomical origin, by coupled gas chromatography/electroantennogram detection (GC/EAG; Wadhams 1990), and proven to be sufficient for attracting this insect for monitoring (Robbins et al. 2006a). The corresponding aldehyde, (*Z*)-7-hexadecenol, also is electrophysiologically active but, when added to the alcohol, does not enhance attraction in the field.

### Lucanidae

The diverse and widespread family of the stag beetles features larvae that usually burrow into rotting wood and adults that feed on sap and decaying fruit (Endrődi 1956). There are also occasional reports of anthophilous lucanids (Endrődi 1956). Investigations into the chemical ecology of *Lucanus cervus* L., an iconic species of the West Palearctic region, revealed a

female-produced sex pheromone, longifolene, of unknown chirality (Harvey et al. 2011). Interestingly, adult males approach larvae and attempt to mate with them; longifolene has been detected in larval extracts prepared by dynamic headspace collection or air entrainment (Birkett 2010). Such behavior also has been reported in the Scarabaeidae (Haynes and Potter, 1995). This suggests the evolutionary development of sex pheromones from non-communication chemicals that previously played a role in larval physiology or behavior. The production of such chemicals is assumed to be lost in adult males, but retained in females and larvae, because of a possible primary function or because production does not represent a cost (Haynes et al. 1992).

When testing a wide range of vegetable material and synthetic odors, Harvey et al. (2011) found that ginger, avocado, and mango were highly attractive to adult *L. cervus*.  $\alpha$ -Copaene, a common constituent of these and other fruits, also is attractive to this insect and is a known attractant for a number of saprophylic insects (Vrkocova et al. 2000).

### Geotrupidae

Species in this monophyletic, relatively small family are commonly called earth-boring dung beetles, and are either detritivores feeding on underground fungi, herbivores, or are coprophagous, similar to dung beetles in the subfamily Scarabaeinae (Scarabaeidae) (Endrődi 1956). Members of the coprophagous Geotrupinae burrow tunnels under dung piles, where they accumulate organic matter for the larvae (paracoprid lifestyle) (Hanski and Cambefort 1991). Inouchi et al. (1988) performed detailed electrophysiological studies on *Geotrupes auratus* Motschulsky, using single cell recording (Wadhams 1990), to measure electrophysiological responses from individual antennal receptor neurons to components of cow dung headspace. Olfactory cells responded strongly to a range of volatile chemicals, with a mixture of these, in field trapping trials, attracting individuals of *G. auratus* at a level comparable to that of cow dung (Table 1).

### Scarabaeidae

Approximately 91 % of all scarabaeoids belong to this family. It has been proposed recently that the Scarabaeidae might have undergone an evolutionary transition from a coprophagous (dung beetles) to a phytophagous (chafers) lifestyle (Schiestl and Dötterl 2012). Biological and ecological aspects of the family are discussed briefly for each subfamily.

**Table 1** Behaviorally active semiochemicals of the Scarabaeoidea

Family	Subfamily	Species	Female sex pheromone or pheromone-related attractant	Allelochemicals (with attraction effect)	References
Glaphyridae	Glaphyrinae	<i>Lichnanthe vulpina</i> Hentz	(Z)-7-Hexadecenol		Robbins et al. 2006a
Lucanidae	Lucaninae	<i>Lucanus cervus</i> L.	Longifolene	$\alpha$ -Copaene	Harvey et al. 2011
Geotrupidae	Geotrupinae	<i>Geotrupes auratus</i> Motschulsky		Butan-2-one, Phenol, <i>p</i> -Cresol, Indole, Skatole	Inouchi et al. 1988
Scarabaeidae	Aphodiinae	<i>Aphodius alternatus</i> Horn, <i>A. floridanus</i> Robinson, <i>A. gracilis</i> Boheman, <i>A. imbricatus</i> Melsheimer, <i>A. simulator</i> Harold <i>A. pseudolividus</i> Balthasar <i>A. tasmaniae</i> Hope <i>Canthon morsei</i> Howden		$\beta$ -Neerodol (repellent)	Eisner et al. 1986
	Scarabaeinae	<i>Onthophagus bartosi</i> Balthasar, <i>O. chinonophilus</i> Krell, <i>O. chlomoderus</i> D'Orbigny, <i>O. imbellis</i> D'Orbigny, <i>O. latigibber</i> D'Orbigny, <i>O. trinommatius</i> Goidanich <i>Pachylomerus femoralis</i> Kirby		DEET Skatole Benzaldehyde Toluquinone, 2-methoxy-3-methyl-1,4-benzoquinone	Krell and Simon 2003 Osborne et al. 1975 Bedoussac et al. 2007 Schmitt et al. 2004
	Melolonthinae	<i>Amphimallon solstitiale</i> L. <i>Costelytra zealandica</i> White <i>Dasytelpida ishigakiensis</i> Nijijima and Kinoshita <i>Heptophylla picea</i> Motschulsky <i>Holotrichia consanguinea</i> Blanchard <i>H. loochooana loochooana</i> Sawada <i>H. oblita</i> Falderman <i>H. parallela</i> Motschulsky <i>H. reynaudi</i> Blanchard <i>Hoplia communis</i> Waterhouse <i>Hoplia equina</i> LeConte <i>Liparetrus atriceps</i> Macleay	(R)-Acetoin Phenol (R)-Butan-2-ol (R,Z)-7,15-Hexadecadien-4-olide Anisole <sup>a</sup> Anthranilic acid L-Isoleucine methyl ester, (R)-Linalool Anisole Tetradecan-2-one (E)-Anethole, eugenol	Methyl propanoate, ethyl propanoate, methyl butanoate, ethyl butanoate, methyl pentanoate, ethyl pentanoate, methyl 4-pentenoate, ethyl 4-pentenoate Butan-1-ol, methyl butanoate, ethyl butanoate, ethyl 2-methylpropanoate, butyl ethanoate, ethyl 2-methylbutanoate, propyl butanoate, butyl propanoate, methyl hexanoate, butyl 2-methylpropanoate, butyl butanoate	Burger et al. 1995a Burger and Petersen 1991 Tolasch et al. 2003 Henzell and Lowe 1970 Wakamura et al. 2009 Leal et al. 1996c Leal et al. 1996b Yasui et al. 2003 Li et al. 2013 Leal et al. 1992b, Leal et al. 1993b Li et al. 2013 Ward et al. 2002 Imai et al. 1998 Zhang et al. 2003 Allsopp 1992

**Table 1** (continued)

Family	Subfamily	Species	Female sex pheromone or pheromone-related attractant	Allelochemicals (with attraction effect)	References
		<i>Macrobrachyus</i> spp. ( <i>murinus</i> Bates, <i>nigripes</i> Bates, <i>subspinosus</i> Fabricius)		Caproic acid; valeric acid; octyl butyrate (1:1:1), 1-octanol; octyl butyrate (1:1)	Williams et al. 1990; Arredondo-Bernal et al. 1995
		<i>Maladera matrida</i> Argaman		Eugenol	Ben-Yakir et al. 1995
		<i>Maladera orientalis</i> Motschulsky		(Z)-3-Hexen-1-ol; benzyl alcohol (1.6:1)	Li et al. 2013
		<i>Melolontha hippocastani</i> Fabricius	1,4-Benzoquinone, phenol	(Z)-3-Hexen-1-ol (for adults); Anisole, eucalyptol (1,3,3-trimethyl-2-oxabicyclo[2.2.2]octane) (for larvae)	Ruther et al. 2001a, 2002a,b
		<i>M. melolontha</i> L.	Toluquinone, phenol	(Z)-3-Hexen-1-ol	Weisssteiner et al. 2012
		<i>Phyllophaga anxia</i> LeConte	L-Valine methyl ester, L-isoleucine methyl ester	Caproic acid	Reinecke et al. 2002; Ruther et al. 2002b
		<i>Ph. apicata</i> Reinhard, <i>lissopyge</i> Bates, <i>menetriesi</i> Blanchard, <i>tristis</i> Fabricius	Methyl 2-(methylthio)benzoate <sup>b</sup>		Ruther et al. 2002a
		<i>Ph. congrua</i> LeConte		Phenyl propionate, eugenol; geraniol (1:1), linalool	Zhang et al. 1997
		<i>Ph. crassissima</i> Blanchard	L-Valine methyl ester, L-isoleucine methyl ester <sup>b</sup>	Butyl sorbate (repellent)	Crocker et al. 1999
		<i>Ph. crinita</i> Burmeister	Methyl 2-(methylthio)benzoate	(E)-Anethole	Zhang et al. 1997
		<i>Ph. cuyabana</i> Moser	<i>p</i> -Cresol, phenol		Crocker et al. 1999
		<i>Ph. elenans</i> Saylor	L-Isoleucine methyl ester		Robbins et al. 2003
		<i>Phyllophaga</i> spp. <sup>c</sup>	L-Valine methyl ester, L-isoleucine methyl ester <sup>b</sup>		Zarbin et al. 2007
		<i>Ph. georgiana</i> Horn	L-Valine methyl ester		Leal et al. 2003
		<i>Ph. gracilis</i> Burmeister, <i>Ph. postrema</i> Horn	L-Isoleucine methyl ester <sup>b</sup>		Zhang et al. 1997; Alm et al. 2004; Robbins et al. 2006b
		<i>Ph. lanceolata</i> Say	L-Leucine methyl ester, L-isoleucine, L-valine methyl ester		Robbins et al. 2009
		<i>Ph. squamipilosa</i> Saylor	L-Leucine methyl ester <sup>b</sup>		Robbins et al. 2009
		<i>Phyllotocus navicularis</i> Blanchard		(E)-Anethole, eugenol, 2-phenylethylpropionate; eugenol; geraniol (10:22:11)	Nojima et al. 2003b
		<i>Rhizotrogus majalis</i> Razoumowsky		Butyl sorbate, propyl 1,4-benzodioxan-2-carboxylate	Nojima et al. 2003b
		<i>Rhizotrogus vernus</i> Germar	1,4-Benzoquinone <sup>b</sup>		Allsopp and Cherry 1991
		<i>Trigonopeltastes delta</i> Forster			Tashiro et al. 1964; McGovern et al. 1970
		<i>Adoretus tessulatus</i> Burmeister		(E)-Anethole	Imrei et al. 2002
Rutelinae				(E)-Cinnamyl alcohol	Cherry et al. 1996
					Donaldson et al. 1990

Table 1 (continued)

Family	Subfamily	Species	Female sex pheromone or pheromone-related attractant	Allelochemicals (with attraction effect)	References
		<i>Anomala albopilosa albopilosa</i> Hope	(R)-Buiulactone [(R)-(Z)-5-(oct-1-enyl)oxacyclopentan-2-one], (E)-2-nonen-1-ol, (E)-2-nonenal, methyl benzoate		Leal et al. 1996a
		<i>A. albopilosa sakishimana</i> Nomura, <i>A. cuprea</i> Hope	(R)-Buiulactone, (R)-Japonilure		Leal 1991; Leal et al. 1993c, 1994b
		<i>A. corpulenta</i> Motschulsky		(Z)-3-Hexen-1-ol: dibutyl phthalate (1: 19), (Z)-3-hexen-1-ol: benzyl alcohol (16: 10), (E)-cinnamaldehyde: benzyl alcohol (4:1)	Li et al. 2013
		<i>A. daimiana</i> Harold	(R)-Buiulactone, (E)-2-nonen-1-ol		Leal et al. 1993a
		<i>A. dubia</i> Scopoli	(E)-2-nonen-1-ol <sup>b</sup>		Tóth et al. 1994
		<i>A. exoleta</i> Faldeman		(Z)-3-Hexen-1-ol: dibutyl phthalate (1: 19), dibutyl phthalate: 2-phenylethanol (37: 1), (Z)-3-hexen-1-ol: (E)-cinnamaldehyde (10:25), (E)-cinnamaldehyde: benzyl alcohol (4:1)	Li et al. 2013
		<i>A. marginata</i> Robinson		(E)-Anethole	Cherry et al. 1996
		<i>A. octiescostata</i> Burmeister	(R)-Buiulactone, (E)-2-nonen-1-ol	(Z)-3-Hexenyl acetate : benzaldehyde : Phenylacetaldehyde: benzyl alcohol: 2-phenylethanol: 2-phenylacetoneitrile: benzyl benzoate (4: 8: 14: 3: 5: 19: 11)	Leal et al. 1994c
		<i>A. osakana</i> Sawada	(S)-Japonilure	(E)-anethole: geraniol: phenethyl propionate (18: 1: 1)	Leal 1996
		<i>A. rufocuprea</i> Motschulsky	Methyl (Z)-5-tetradecenoate	Methyl anthranilate	Tamaki et al. 1985
		<i>A. schonfeldii</i> Ohaus	(E)-2-Nonen-1-ol		Imai et al. 1997
		<i>A. solida</i> Erichson	(R)-Buiulactone		Leal et al. 1992a
		<i>A. transvalensis</i> Arrow		(E)-Cinnamyl alcohol, $\beta$ -ionone	Tóth et al. 2003a
		<i>A. vitis</i> Fabricius	(E)-2-Nonen-1-ol <sup>b</sup>		Donaldson et al. 1990
		<i>Anoplognathus</i> spp.			Tóth et al. 1994
		<i>Exomala orientalis</i> Waterhouse	(Z)-7-Tetradecen-2-one	Eucalyptol, sideroxylonals (feeding deterrents)	Matsuki et al. 2011
		<i>Hylamorphia elegans</i> Burmeister	1,4-Benzoquinone		Leal et al. 1994d;
		<i>Parastasia bimaculata</i> Guerin		Butan-2-ol, veratrole (1,2-dimethoxybenzene)	Rodriguez-Saona et al. 2009
		<i>Phyllopertha diversa</i> Waterhouse	1,3-Dimethyl-2,4-(1H,3H)-quinazolinedione		Quiroz et al. 2007
		<i>Ph. horticola</i> L.			Kumano-Nomura and Yamaoka 2009
		<i>Popillia japonica</i> Newman	(R)-Japonilure	(Z)-3-Hexen-1-ol: geraniol: eugenol: phenethyl propionate (50: 11.5: 27: 11.5)	Leal et al. 1997
				Phenethyl propionate: eugenol: geraniol (3: 7: 3), linalool, 2-phenylethanol, etc.	Ruther and Mayer 2005
					Tumlinson et al. 1977

**Table 1** (continued)

Family	Subfamily	Species	Female sex pheromone or pheromone-related attractant	Allelochemicals (with attraction effect)	References
Dynastinae		<i>P. lewisii</i> Arrow		Wintergreen and Peppermint oil (repellents)	Ladd and McGovern 1980; Loughrin et al. 1996; Theiss 2006; Youssef et al. 2009
		<i>P. atrocoerulea</i> Bates, <i>P. indigonacea</i> Motschulsky, <i>P. quadriguttata</i> Fabricius, <i>P. taiwana</i> Arrow	( <i>R</i> )-Japonilure <sup>b</sup>	Phenethyl propionate: eugenol: geraniol (3: 7: 3) ( <i>Z</i> )-3-Hexen-1-ol: dibutyl phthalate (1: 19), ( <i>Z</i> )-3-hexen-1-ol: benzyl alcohol (16: 10)	Klein and Edwards 1989 Li et al. 1995; Chow 1986 Li et al. 2013
		<i>Cyclocephala atricapilla</i> Mannerheim, <i>C. vestita</i> Höhne		4-Methyl-5-vinylthiazole	Maia et al. 2012
		<i>C. cearae</i> Höhne		( <i>S</i> )-2-Hydroxy-5-methyl-3-hexanone	Maia et al. 2013
		<i>C. celata</i> Dechambre		4-Methyl-5-vinylthiazole, ( <i>S</i> )-2-hydroxy-5-methyl-3-hexanone	Maia et al. 2012, 2013
		<i>C. guttata</i> Bates		Methyl acetate, ethyl acetate	Canino-Lavin et al. 1996
		<i>C. insulicola</i> Arrow		Phenol	Gruner and Marival 1974
		<i>C. literata</i> Burnmeister		Methyl 2-methylbutyrate	Gottisberger et al. 2012
		<i>C. lurida</i> Bland		Phenyl propionate, eugenol, geraniol	Crocker et al. 1999
		<i>Cyphonistes tuberculifrons</i> Quedenfeldt		1,4-Benzoquinone, 2-methyl-1,4-benzoquinone, 2-methoxy-3-methyl-1,4-benzoquinone, 2,3-dimethoxy-1,4-benzoquinone	Krell et al. 1999
		<i>Erioscelis emarginata</i> Mannerheim	( <i>RS</i> )-Ethyl 4-methyloctanoate (male aggregation pheromone)	4-Methoxystyrene	Dötterl et al. 2012
		<i>Oryctes monoceros</i> Olivier	( <i>RS</i> )-Ethyl 4-methyloctanoate (male aggregation pheromone)		Gries et al. 1994
		<i>O. rhinoceros</i> L.		Ethyl dihydrochrysanthemumate, (±)-des- <i>N</i> -morphinan	Hallet et al. 1995 Barber et al. 1971; Vander Meer et al. 1979
		<i>O. elegans</i> Prell	( <i>RS</i> )-4-methyloctanoic acid (male aggregation pheromone)		Rochat et al. 2004
		<i>Scapanes australis</i> Boisduval	( <i>RS</i> )-Butan-2-ol, acetoin, ( <i>RS</i> )-butane-2,3-diol (male aggregation pheromone)		Rochat et al. 2000
		<i>Strategus aloeus</i> L.	Butan-2-one, pentan-3-one, 2-Butyl acetate (male aggregation pheromone)		Rochat et al. 2000
		<i>Arrichelaiphinis tigrina</i> Olivier		Methyl benzoate, linalool	Steenhuisen et al. 2013
		<i>Cetonia a. aurata</i> L.		( <i>E</i> )-Anethole: 1-phenylethanol: 3-methyleugenol (1: 1: 1), ( <i>E</i> )-anethole: 1-phenylethanol: 3-methyleugenol: ( <i>RS</i> )-lavandulol (1: 1: 1: 1)	Toth et al. 2005; Vuts et al. 2010a



Table 1 (continued)

Family	Subfamily	Species	Female sex pheromone or pheromone-related attractant	Allelochemicals (with attraction effect)	References
		<i>Clinteroides permutans</i> Burmeister		Isosafrole (unspecified isomer)	Donaldson et al. 1990
		<i>Cotinix nitida</i> L.		Isopropanol, phenylacetaldehyde: 2-phenethyl alcohol: ( <i>R</i> )-limonene: methyl-2-methoxybenzoate: methyl salicylate (21: 22: 23: 18: 1)	Landolt 1990; Johnson et al. 2009
		<i>Dyspilophora trivittata</i> Schaum		Linalool	Donaldson et al. 1990
		<i>Epicomotis hirta</i> Poda		( <i>E</i> )-Cinnamyl alcohol: ( <i>E</i> )-anethole (1: 1), ( <i>E</i> )-cinnamyl alcohol: ( <i>E</i> )-anethole: 4-methoxyphenethyl alcohol (1: 1: 1)	Tóth et al. 2004; Vuts et al. 2010b
		<i>Euphoria sepulchralis</i> Fabricius		Eugenol, geraniol	Cherry and Klein 1992; Cherry et al. 1996
		<i>Eupoecila australastae</i> Donovan		( <i>E</i> )-Anethole	Allsopp and Cherry 1991
		<i>Oplostomus haroldi</i> Witte		( <i>Z</i> )-9-Pentacosene (contact pheromone)	Fombong et al. 2012
		<i>Osmoderma eremita</i> Scopoli		( <i>R</i> )- $\gamma$ -Decalactone (male sex pheromone)	Larsson et al. 2002
		<i>Oxyctenia jucunda</i> Falderman		Phenethyl propionate : eugenol: geraniol (3: 7: 3)	Klein and Edwards 1989
		<i>Oxythyrea cinctella</i> Schaum		2-Phenethyl alcohol: ( <i>RS</i> )-lavandulol (1: 1)	Vuts et al. 2012a
		<i>O. funesta</i> Poda		( <i>E</i> )-Anethole, 2-phenethyl alcohol: ( <i>RS</i> )-lavandulol (1: 1)	Tóth et al. 2003b; Vuts et al. 2008
		<i>O. testaceoguttata</i> Blanchard, <i>Plaesiorrhina recurva</i> plana Wiedemann		Isosafrole (unspecified isomer)	Donaldson et al. 1990
		<i>Pachnoda interrupta</i> Olivier		( <i>RS</i> )-Butane-2,3-diol	Bengtsson et al. 2010
		<i>Potosia cuprea</i> Fabricius		Phenylacetaldehyde	Bengtsson et al. 2009
		<i>Protaetia brevitarsis</i> Lewis		( <i>E</i> )-Anethole: 1-phenylethanol: 3-methyleugenol (1: 1: 1), ( <i>E</i> )-anethole: 1-phenylethanol: 3-methyleugenol: ( <i>RS</i> )-lavandulol (1: 1: 1: 1)	Tóth et al. 2005; Vuts et al. 2010a
		<i>P. ishigakia okinawana</i> Kurosawa		Propan-1-ol, 2-phenylethanol	Chen and Li 2011
		<i>Thopinota squalida</i> Scopoli		Phenethyl propionate : eugenol : geraniol (3: 7: 3)	Klein and Edwards 1989
		<i>Ulugus hemipterus</i> L.		( <i>E</i> )-Cinnamyl alcohol, ( <i>E</i> )-anethole, ( <i>E</i> )-cinnamyl alcohol: ( <i>E</i> )-anethole (1: 1)	Ortu et al. 2003; Tóth et al. 2009
				( <i>E</i> )-Cinnamyl alcohol, ( <i>E</i> )-anethole: 1-phenylethanol: 3-methyleugenol: ( <i>RS</i> )-lavandulol (1: 1: 1: 1)	Tóth et al. 2003b; Vuts et al. 2010c

<sup>a</sup> Attracts females and males in a 1: 1 ratio; hereto referred to as an aggregation pheromone

<sup>b</sup> Sex attractant: compound found to be attractive to a species, but has not been identified from it

<sup>c</sup> *Phyllophaga aemula* Horn, *affabilis* Horn, *balia* Say, *bipartita* Horn, *clypeata* Horn, *corrota* LeConte, *crenulata* Frölich, *curialis* Reinhard, *davisi* Langston, *diffinis* Blanchard, *drakei* Kirby, *epiphila* Say, *fervida* Fabricius, *forbesi* Glasgow, *forsteri* Burmeister, *foxii* Davis, *fraterna* Harris, *fusca* Frölich, *fulvis* LeConte, *glaberrima* Blanchard, *glabricula* LeConte, *hirsuta* Knoch, *hirticula* Knoch, *hirtiventris* Horn, *ilicis* Knoch, *implicata* Horn, *inversa* Horn, *kenrickiana* Richer, *latifrons* LeConte, *longispina* Smith, *lota* Lugibill, *luctuosa* Horn, *marginalis* LeConte, *mariana* Fall, *micans* Knoch, *mississippiensis* Davis, *nitida* LeConte, *obsoleta* Blanchard, *perlonga* Davis, *postrema* Horn, *praetermissa* Horn, *profunda* Blanchard, *quercus* Knoch, *rubiginosa* LeConte, *rugosa* Melsheimer, *soror* Davis, *submucida* LeConte, *sylvatica* Sanderson, *taxodii* Langston, *torta* LeConte, *ulkei* Smith, *uniformis* Blanchard, *vehemens* Horn

### Aphodiinae

Both larvae and adults of the genus *Aphodius* live in dung, on which they also feed (endocoprid lifestyle) (Hanski and Cambefort 1991). Unfed gravid females of *A. tasmaniae* Hope are attracted to poultry dung, as well as to one of its characteristic compounds, skatole (Osborne et al. 1975). Anecdotal evidence reports that an ethanolic formulation of the commercial insect repellent, DEET [*N,N*-diethyl-*m*-toluamide], is attractive to *A. pseudolividus* Balthasar (Krell and Simon 2003). Several *Aphodius* species are repelled by  $\beta$ -necrodoal [((1*R*,3*S*)-2,2,3-trimethyl-4-methylidenecyclopentyl) methanol], a monoterpene found in the defensive secretion of the carrion beetle species *Necrodes surinamensis* Fabricius (Coleoptera: Silphidae) (Eisner et al. 1986) (Table 1). Some *Arum* spp. (Araceae) use deceptive volatile chemicals that attract *Aphodius* spp. for pollination (Schiestl and Dötterl 2012). However, the identity of the floral compounds mimicking the scent of the oviposition substrates of these scarabs is unknown.

### Scarabaeinae

Dung beetles are either paracoprids, or form balls, which they then roll and bury a distance from the dung (telecoprid lifestyle) (Hanski and Cambefort 1991). The coprophagous fauna associated with large herbivores plays an important role in the recycling of nutrients and in the habitat destruction of dung-breeding flies (Heinrich and Bartholomew 1979).

Females of the telecoprid genus *Kheper* produce only one or two eggs per year and remain underground for several months to care for their offspring (Burger et al. 2008). Increasing their chances of finding a mate, males release a proteinaceous secretion into the air from an abdominal filamentous organ that attracts females, with each particle containing a complex mixture of more than 150 volatile organic compounds (Burger et al. 2008). Using GC/EAG, several putative sex pheromone compounds present in the proteinaceous carrier material were identified, including propanoic acid, butanoic acid, indole, skatole, and methyl (*RR*)-cascarillate [methyl 2-((1*R*,2*R*)-2-hexylcyclopropyl)acetate] for *K. bonelli* MacLeay (Burger et al. 2008), butanoic acid, skatole, and subaeneol [(*E*)-2,6-dimethyl-6-octen-2-ol] for *K. subaeneus* Harold (Burger et al. 2002), skatole and (*R*)-3-methylheptanoic acid for *K. nigroaenus* Boheman (Burger and Petersen 2002), and palmitic acid, 2,6-dimethyl-5-heptenoic acid, (*E*)-nerolidol [(*RS*)-3,7,11-trimethyl-1,6,10-dodecatrien-3-ol], and skatole for *K. lamarcki* MacLeay (Burger et al. 1983). Behavioral activity of the identified compounds, however, is yet to be demonstrated. Interestingly, Burger et al. (1995a) observed that both sexes of *Pachylomerus femoralis* Kirby were attracted to individual males of *K. lamarcki* during courtship. In GC/EAG experiments with *P. femoralis*, several chemicals were

identified from the excretion of male *K. lamarcki*. In subsequent field tests, mixtures of these compounds were found to be almost as attractive as horse dung to *P. femoralis* (Burger et al. 1995a; Table 1). The authors hypothesized that these esters enable individuals of *P. femoralis*, which do not form dung balls, to detect and utilize dung balls formed by *K. lamarcki*. *Pachylomerus femoralis* also was attracted to fruit of *Strychnos* spp. trees (Loganiaceae), as well as to a synthetic mixture of volatiles identified from the fruit (Burger and Petersen 1991) (Table 1).

*Canthon morsei* Howden was attracted to freshly dead millipedes (Diplopoda: Polydesmida) in field tests in a Mexican tropical forest. It was proposed that *C. morsei* is adapted to detect volatiles from fresh arthropod cadavers with high levels of defensive substances, thereby exploiting unusual resources that are not in great demand (Bedoussac et al. 2007). Among the compounds identified from fresh millipede carcasses, benzaldehyde was highly attractive to individuals of *C. morsei*. Similarly, in tropical Africa, a few specialized species of *Onthophagus* feed on fresh carcasses of juliform millipedes (Schmitt et al. 2004). Because of a strong quinooid smell, fresh carcasses are unattractive to most necrophagous animals. However, six *Onthophagus* species were attracted to crude extracts of defensive millipede secretions, as well as to a synthetic mixture of toluquinone and 2-methoxy-3-methyl-1,4-benzoquinone, the most common constituents isolated from the extracts (Schmitt et al. 2004) (Table 1). Finally, similar to the aforementioned *Arum-Aphodius* pollination system, inflorescences of several species of *Amorphophallus* (Araceae) in India deceptively attract *Onthophagus* and *Heliocopris* dung beetles for pollination (Punekar and Kumaran 2010), although the odors responsible for this remain to be identified.

When disturbed, some copronecrophagous telecoprid scarabs in the genus *Canthon* discharge small droplets with defensive properties from a pair of glands on the posterior margins of the elytra (Aliabadi et al. 2000). Volatile constituents, assumed to be putative allomones (Nordlund and Lewis 1976), of this odorous secretion were identified as indole, *m*-cresol, phenol, and creosol. *Oniticellus egregius* Klug also secretes a defensive fluid from the lateral edges of the anterior abdominal segments when attacked by predators, from which methyl salicylate and 1,4-benzoquinone are the presumed volatile defense compounds (Burger et al. 1995b).

### Melolonthinae

Adult chafers in this phylogenetically basal subfamily (Krell 2006) generally are foliage feeders (e.g., *Melolontha* spp.), while some are florivores (e.g., *Hoplia* spp.), or do not feed at all (e.g., *Anoxia* spp.) (Endrödi 1956). The rhizophagous larvae, together with those of the Rutelinae and Dynastinae, are popularly known as white grubs, and cause damage to a



vast range of food (e.g., McLeod et al. 1999) and amenity (Held and Potter 2012) crops.

The first scarab pheromone was identified as phenol, some four decades ago, from *Costelytra zealandica* White (Henzell and Lowe 1970) (Table 1). Structurally related compounds later were identified from females of *Holotrichia consanguinea* Blanchard (anisole) (Leal et al. 1996b) and *Phyllophaga cuyabana* Moser (*p*-cresol, together with phenol) (Zarbin et al. 2007). Female *H. parallela* Motschulsky, on the other hand, produce L-isoleucine methyl ester and (*R*)-linalool (Leal et al. 1992b, 1993b). L-Isoleucine methyl ester is a key component of the sex pheromone of *Ph. elenans* Saylor (Leal et al. 2003). Its *N*-formyl and *N*-acetyl derivatives also are present in gland extracts of calling females (Leal et al. 2003). The same author proposed a common biosynthetic origin for these phenolic, amino acid, and terpenoid compounds from amino-acid precursors, which would be unique among scarabaeoid beetles. The above semiochemicals are produced in large amounts, and their enantiomeric purities are not crucial for mate attraction. Moreover, most exhibit antimicrobial activities, leading Leal (1997, 1998) to argue that they may have evolved into sex pheromones from a primary defensive role. Further examples of compounds with antimicrobial and antifungal activities used in the chemical communication of melolonthine scarabs include 1,4-benzoquinone and toluquinone, which, in addition to phenol, are female-produced sex pheromone components of *Melolontha melolontha* L. and *M. hippocastani* Fabricius (Reinecke et al. 2002; Ruther et al. 2001a,b; 2002a).

It is still unknown how sexual isolation is ensured in the case of sympatric *M. melolontha* and *M. hippocastani*. Toluquinone, the female sex pheromone of *M. melolontha*, is not attractive to males of *M. hippocastani*, nor is 1,4-benzoquinone, produced by female *M. hippocastani*, attractive to male *M. melolontha*. However, these compounds elicit EAG responses from males of both species. Reinecke et al. (2002) suggested two possibilities: (i) the emission, rather than the production, of sex pheromone components is species-specific, or (ii) a species-specific blend of the identified compounds, or a still unknown chemical, allows for species-specific mate recognition and sexual isolation.

As described above, female-produced sex pheromones are widespread among the Melolonthinae. However, *H. consanguinea* females produce a pheromone to which both females and males are attracted (Leal et al. 1996b); thus, this pheromone functions similarly to the aggregation pheromones commonly found among the Dynastinae. The same authors argued that the mating-related chemical communication of *H. consanguinea* represents an intermediate evolutionary step, in which the signal is yet to evolve into a sex-specific chemical cue. It also is noteworthy that pheromone release in *H. consanguinea* is restricted to a short period of the day (~1 h). This also is similar to that observed (15 min, Leal

et al. 1993b) among individuals of the congeneric *H. parallela*. These short release periods may be a mechanism to reduce predation pressure (Leal et al. 1996b).

A suite of long-chain allenic cuticular hydrocarbons was identified in hexane extracts of *Antitrogus consanguineus* Blackburn, *Lepidiota negatoria* Blackburn, *L. crinita* Brenske, *L. picticollis* Lea, and *Dermolepida albohirtum* Waterhouse (McGrath et al. 2003). These allenes are represented by the formula  $\text{CH}_3(\text{CH}_2)_n\text{CH}=\text{CH}(\text{CH}_2)_7\text{CH}_3$ , with *n* being 11–15, 17, and 19 and may play a role in mate recognition in these species. Their biological relevance, however, is yet to be demonstrated. (*R*)-Acetoin, butane-(2*R*,3*R*)-diol, and butane-(2*R*,3*S*)-diol were identified from the abdominal glands of female *Rhizotrogus majalis* Razoumowsky (= *Amphimallon majale*) and found to be electrophysiologically (but not behaviorally) active to conspecific males (Nojima et al. 2003a). In *Rh. solstitialis* L. (= *A. solstitialis*), however, (*R*)-acetoin is a female-produced sex pheromone (Tolasch et al. 2003), the activity of which can be completely blocked by the (*S*)-enantiomer.

There is evidence for the use of a female-produced sex pheromone by *Maladera matruda* Argaman. Males are attracted to field traps baited with live females (Falach and Shani 2000), and laboratory bioassays also have suggested the existence of a sex pheromone of female origin (Falach et al. 2003). Previously, Yarden et al. (1996) identified (3*Z*,6*E*)- $\alpha$ -farnesene from female *M. matruda* and found it to be electrophysiologically active in males, but no behavioral activity of this compound has been demonstrated.

To date, three main pheromone production types have been described in the Melolonthinae. Compounds are produced either by symbiotic bacteria in the collateral gland of females (*C. zealandica*, Hoyt et al. 1971), or synthesized in glands in the anal plate and the two apical sternites (*Heptophylla picea* Motschulsky), or in an eversible abdominal ball-shaped sac (*H. parallela*) (Tada and Leal, 1997). Melolonthinae pheromones generally are derived from phenolic, isoprenoid, and even amino acid precursors (Leal 1999). The first fatty acid derivative identified for the Melolonthinae was the sex pheromone of *H. picea*, (*R,Z*)-7,15-hexadecadien-4-olide (Leal et al. 1996c).

Some nectar-feeding scarab species from Australia, including *Phyllotocus* spp., were observed to “swarm around beehives, apparently attracted by the smell of honey” (Allsopp and Cherry 1991). No compounds mediating this behavior have been identified, but similar studies with *Aethina tumida* Murray (Coleoptera: Nitidulidae) (Torto et al. 2007) could be the key to understanding the role of such allelochemicals.

It is interesting to note that the semiochemistry of below-ground interactions between plant roots and the larvae of Melolonthinae also is being elucidated, and such efforts already have identified some chemical signals from oak tree roots that mediate host finding in *M. hippocastani* larvae

(Weissteiner et al. 2012; Table 1). Above ground, males of this species are guided to the host canopy by plant stress-signaling compounds [e.g., (Z)-3-hexen-1-ol] triggered by feeding conspecifics, with males being able to discriminate unspecific leaf damage from leaves with feeding females via the female sex pheromone, 1,4-benzoquinone (Ruther and Hilker 2003).

### Rutelinae

The shining leaf chafers received early attention from chemical ecologists because many species damage crop plants (Leal 1998). The larvae live in soil, where they feed on roots of living plants, while the adults are either foliage feeders (e.g., *Anomala* spp.) or florivores (e.g., *Popillia* or *Adoretus* spp.) (Hurpin 1962).

Intensive research conducted on the chemical ecology of *Popillia japonica* Newman, an introduced pest in North America (Potter and Held 2002), led to the identification of the first female-produced sex pheromone in this group in the late 1970s. The discovery of japonilure [(R)-(Z)-5-(dec-1-enyl)oxacyclopentan-2-one] highlighted the importance of chirality in scarab chemical communication systems (Table 1). Only the *R*-enantiomer evoked behavioral responses from male *P. japonica*, while addition of the *S*-enantiomer, in even as little as 1 % relative amount, significantly reduced catches (Tumlinson et al. 1977). On the other hand, *Anomala osakana* Sawada uses (*S*)-japonilure as a female sex pheromone, with inhibition by its antipode being as dramatic as in *P. japonica* (Leal 1996). Males of these two species possess olfactory receptor neurons tuned to each enantiomer, which is thought to aid sexual isolation (Leal 1999). However, sexual isolation by chemical communication channels can also be achieved in other ways. In contrast to single-constituent sex pheromones, in which chirality aids species-specificity, closely related species of Rutelinae sharing the same pheromone components may either use minor components that are antagonistic to the main component, or may be isolated geographically or temporally, thereby ‘escaping’ from the selection pressure to develop pheromone systems comprising different constituents (Leal 1999). Leal et al. (1992a), using a coupled GC-behavioral bioassay, reported (*E*)-2-nonen-1-ol as the female-produced sex pheromone of *A. schonfeldti* Ohaus, a species native to Japan. In field-screening tests in Hungary, (*E*)-2-nonen-1-ol was highly attractive to male *A. vitis* Fabricius and *A. dubia* Scopoli (Tóth et al. 1994; Voigt and Tóth 2002). This compound cannot be classified a “sex pheromone” for the latter two species until it is isolated from conspecific females (Dethier et al. 1960; Dicke and Sabelis 1988). If females of both *A. vitis* and *A. dubia* produce (*E*)-2-nonen-1-ol, geographical isolation may preclude inter-mating of the two species with *A. schonfeldti*.

Female sex pheromone glands of several species of the Rutelinae have been identified as “sex-specific epithelial cells lining the inner surfaces of anal plates and two apical sternites,

connected through many pores to the cuticle surface” (Tada and Leal 1997). It has been proposed that the majority of rutelin sex pheromones are biosynthesized from fatty acids (Leal 1997, 1998). However, 1,3-dimethyl-2,4-(1*H*,3*H*)-quinazolidinedione, the female sex pheromone of *Phyllopertha diversa* Waterhouse (Leal et al. 1997), is an alkaloid. This compound possesses medicinal (anti-inflammatory and analgesic) properties, which might also support the hypothesis of the origin of scarab sex pheromones from compounds with primary defensive roles.

Efforts toward the development of plant allelochemical-based lures for the Rutelinae have followed two main approaches: ecological orientation (e.g., Leal et al. 1994a) and trial-and-error (e.g., Donaldson et al. 1986, 1990). Although probably less sophisticated, trial-and-error programs proved no less efficient than the ecologically orientated approach, with field screening of plant compounds, individually or in combination, successfully leading to the development of synthetic lures. For example, in order to survey the spread of *P. japonica*, different plant essential oils and their constituents were field-tested in the USA and found to attract the beetles (Leal 1998). These efforts eventually evolved into the optimization of a lure comprising phenethyl propionate, eugenol, and geraniol in the relative ratio of 3:7:3 (Ladd and McGovern 1980; Table 1). Loughrin et al. (1996) proposed a host location scenario for *P. japonica*, whereby beetles that emerge early in the season respond to odors from a wide range of plants. If a plant is accepted as a host, the beetles start feeding on it, thereby inducing volatile release from damaged leaves. Induced volatiles then serve as a more efficient means of host location for conspecifics emerging later in the season.

Electrophysiology can help us better understand the underlying mechanisms of semiochemical perception and the interactions between plant allelochemicals and pheromones, thus serving as a crucial step in attractant development (Pickett et al. 2012). Using single cell recordings, Larsson et al. (2001) discovered a clear spatial separation between sensory cells responsible for the detection of pheromone compounds and plant volatiles on the antennae of *A. cuprea* Hope. Receptor cells for green leaf volatiles [GLV, e.g., (Z)-3-hexenyl acetate] appeared to be 1000-times more sensitive to their respective key compound than to any other compound, resembling the sensitivity of many pheromone receptors.

### Dynastinae

Commonly called rhinoceros beetles, after the males’ conspicuous horns and other appendages, members of this group are distributed worldwide, mostly in the tropics, and show a considerable variation in size, ranging between ca. 10 and 150 mm (Endrödi 1985). The larvae usually feed on decaying wood, while adults feed on nectar, plant sap, and fruits (Endrödi 1985). Some species are highly specialized flower

visitors and form intimate mutualistic relationships with the plants they pollinate (e.g., *Cyclocephala* spp.) (Schiestl and Dötterl 2012). Adults of some subtropical and tropical species of the genus *Oryctes* are serious pests of coconut, oil, or date palm plantations both directly, by feeding on the foliage, and indirectly, by providing entry points for diseases and other pests (Bedford 1980, 2013).

(*RS*)-Ethyl 4-methyloctanoate was reported as the male-derived aggregation pheromone of *O. monoceros* Olivier (Gries et al. 1994) and *O. rhinoceros* L. (Hallet et al. 1995). Males of both species also produce (*RS*)-4-methyloctanoic acid, which apparently has no behavioral function for either species. Hallet et al. (1995) argued that the utilization of the same compound is likely to be based on geographical isolation of the two species, given that *O. monoceros* occurs in tropical Africa and *O. rhinoceros* in South and Southeast Asia. However, Rochat et al. (2004) demonstrated that males of *O. elegans* Prell, distributed in the Near- and Middle-East and in North Africa, also produce a mixture of (*RS*)-ethyl 4-methyloctanoate and (*RS*)-4-methyloctanoic acid although, contrastingly, only the acid is active in this species. Another difference between *O. elegans* and the aforementioned congeners is that the pheromone of *O. elegans* is only weakly attractive by itself, but highly synergistic with the odor emitted by freshly cut and macerated shoot tissue of date palm (*Phoenix dactylifera* L; Arecaceae). This is not the case for the aggregation pheromones of its tropical congeners, which are highly attractive alone (Rochat et al. 2004). Specific pheromone receptor neurons on the antennae of female *O. rhinoceros* are randomly distributed over the surface of the lamellae (Renou et al. 1998), in contrast to the well-structured receptor distribution in *A. cuprea* (Rutelinae) (Larsson et al. 2001), and they respond only to the respective pheromone compound, and not to the pheromone of the closely related *O. elegans*. Males of *Scapanes australis* Boisduval and *Strategus aloeus* L., coconut and oil palm pests in Papua New Guinea/Melanesia and South America, respectively (Bedford 1980), release mixtures of low molecular weight, ubiquitous compounds (Rochat et al. 2000) (Table 1). In the case of *S. australis*, pheromonal activity can be enhanced with host plant volatiles (Rochat et al. 2002), but the active plant compounds are unknown.

There are no data available on the anatomical origins of the pheromone production site in the Dynastinae. However, it is known that males of *S. australis* secrete droplets from the tip of the abdomen from which pheromone vapor can be collected, and also that feces contain traces of the pheromone compounds (Rochat et al. 2000).

Similar to what is observed in some species of Lucanidae, adult males of some species of *Cyclocephala* are attracted to extracts of 1st-3rd instars of both sexes (Haynes and Potter 1995). A wider survey may reveal the distribution of such

behavior across the different lineages of the Scarabaeoidea, and allow better insight into the evolution of these chemical communication systems.

In field tests, several synthetic compounds were effective attractants for *Cyclocephala* spp. (Camino-Lavin et al. 1996; Crocker et al. 1999; Gruner and Marival 1974; Table 1). Different quinones were found serendipitously to attract *Cyphonistes tuberculifrons* Quedenfeldt (Krell et al. 1999). Krell et al. (1999) argued that the activity of these chemicals is a case of primary attraction of beetles to the larval microhabitat (rotting wood), or to food resources essential for the adults. In a USDA trap-development program for pest Dynastinae, ethyl dihydrochrysanthemumate (ethyl 3-isobutyl-2,2-dimethylcyclopropanecarboxylate) (Barber et al. 1971) and ( $\pm$ )-des-N-morphinan [ $l(\pm)$ -4b,5,6,7,8,8a $\beta$ ,3,9,10-octahydro-9 $\beta$ 4b  $\beta$ -propanophenanthrene] (Vander Meer et al. 1979) appeared to be attractive to both sexes (presumably) of *O. rhinoceros*. A number of receptor cells later were demonstrated to respond to ethyl chrysanthemumate, and also to 2-phenylethanol, phellandrene, isoamyl acetate, (*Z*)-3-hexenol, and phenol (Renou et al. 1998).

Nocturnal *Cyclocephala* scarabs are a good example of how the activity of insect pollinators and the phenology of their host plants may be synchronized, leading to mutualistic relationships (Moore and Jameson 2013). For example, beetle emergence from soil is synchronized with the flowering of host plants at the beginning of the rainy season in the Neotropics (Gottsberger et al. 2012). During the female phase of anthesis, flowers become thermogenic, a phenomenon that enhances floral volatile emission and, thus, beetle attraction. Beetles feed and mate inside the flowers, which offer them energy (i.e., warmth and food) to maintain their activities (Gottsberger et al. 2012). During the following night, floral thermogenesis decreases, encouraging beetles to leave flowers with pollen loads and reducing the chances of other scent-oriented beetles finding that particular flower. Table 1 lists floral compounds that are supposed to play a key role in long-range plant signaling for feeding and/or mating sites for scarabs, including pollinating systems such as *C. literata* Burmeister - *Magnolia ovata* (A. St.-Hil.) Spreng (Magnoliaceae) (Gottsberger et al. 2012), *C. atricapilla* Mannerheim/*C. celata* Dechambre/*C. vestita* Hohné - *Annona* spp. (Annonaceae)/*Caladium bicolor* (Aiton) Vent. (Araceae) (Maia et al. 2012), *Erioscelis emarginata* Mannerheim - *Philodendron selloum* K.Koch (Araceae) (Dötterl et al. 2012), and *C. cearae* Hohné/*C. celata* - *Taccarum ulei* Engl. & K.Krause (Araceae) (Maia et al. 2013).

#### Cetoniinae

Flower chafers are most abundant in tropical and subtropical areas, but some genera also are found at high latitudes (e.g., *Cetonia* in the northern hemisphere) (Hurpin 1962). Larvae of

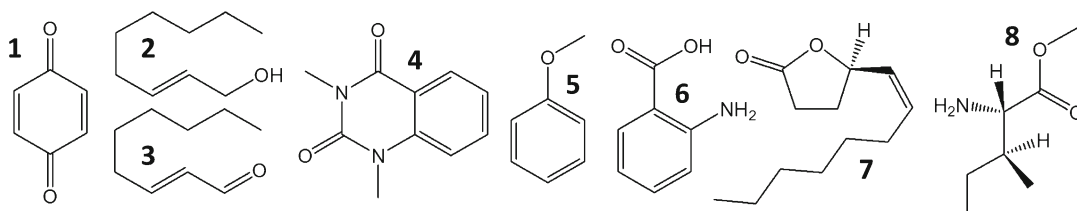
these species consume decomposing organic matter in the soil, in ant nests, or in the substrate at the bottom of tree hollows (Endrődi 1956), and some may even be carnivorous (Koshiyama et al. 2012; Mynhardt and Wenzel 2010). Day-

flying adults feed on sap of wounded trees (e.g., *Cetonischaema* spp.), flower tissues (e.g., *Tropinota* spp.) (Endrődi 1956), or ripening and rotting fruit (e.g., *Cotinis* spp.) (Johnson et al. 2009), and can also be pollinators (e.g.,

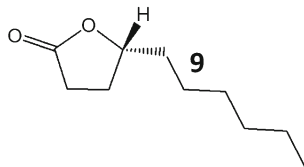
## PHEROMONES

### Sex pheromones

Emitting sex: females

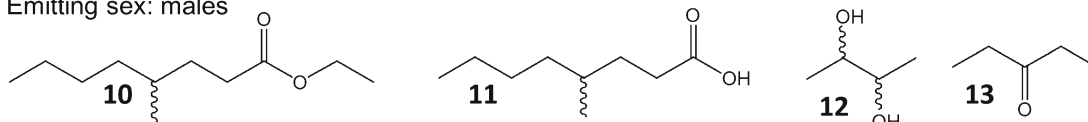


Emitting sex: males



### Aggregation pheromones

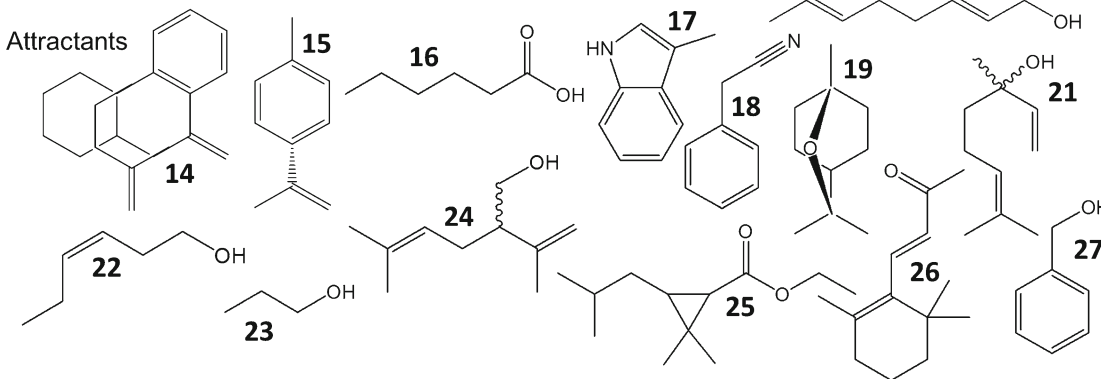
Emitting sex: males



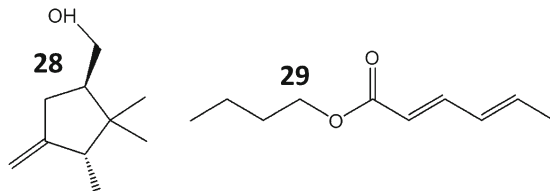
## ALLELOCHEMICALS

### Kairomones

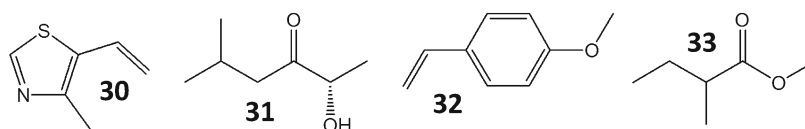
Attractants



Repellents



### Synomones





*Atrichelaphinis*, *Cyrtothyrea*, *Protaetia*, or *Eucetonia* spp.) (Hurpin 1962; Ollerton et al. 2003; Steenhuisen and Johnson 2012).

Pheromonal communication in the Cetoniinae is largely unexplored, but recent progress in this field may unveil more information. Bengtsson et al. (2010) showed that males of *Pachnoda interrupta* Olivier, a sorghum pest of the Sahel in Africa, are attracted to caged virgin females, but not to males, and females are not attracted to either sex, indicating the presence of a female-produced pheromone. Because beetles of this species are polyphagous, the authors used banana as a common food source, in order to study the interactions between volatiles emitted by females and those from plant material. They found that “unmated females combined with banana attracted significantly more males and females than did unmated females alone”; thus, “aggregation behavior appears to be guided by a combination of pheromone and host volatiles” (Bengtsson et al. 2010). Solvent extracts of females contained 19 sex-specific compounds, of which phenylacetaldehyde isolated from the abdominal tip caught more beetles than any other compound, alone or in combination. Bengtsson et al. (2010) proposed that phenylacetaldehyde is a putative female pheromone.

Similarly, promising results have been reported on the orchard pest *Tropinota hirta* Poda, the adults of which

damage flowers of fruit trees (Hurpin 1962). Individuals of each sex were placed in cages on funnel traps with a piece of apple (as a food source; Tóth et al. 2005). In field trapping tests, males were attracted to traps baited with females+apple, but not to those baited with males+apple, or apple alone. Females were not attracted to either sex or to apple baits. Whole body solvent extracts and air entrainment samples obtained from female beetles evoked EAG responses from male antennae that were stronger than those to the solvent control (Imrei et al. 2012). Identification of EAG-active compounds is underway.

Sex pheromones of scarabs are not only long-range or female-produced volatile compounds. The discovery of (Z)-9-pentacosene as a contact sex pheromone for *Oplostomus haroldi* Witte is a good example of a high molecular weight cuticular compound detected by the maxillary palps of males (Fombong et al. 2012), as opposed to the general long-range, volatile sex pheromones that are perceived by antennae. *Oplostomus haroldi* is often found in bee hives, where it feeds on pollen. Fombong et al. (2012) argued that the use of contact pheromones may be an essential, cryptic mechanism for this flower chafer, associated with eusocial insects, in order to find mates in a chemically complex environment. In *Osmoderma eremita* Scopoli, the male produces a sex pheromone, (R)- $\gamma$ -decalactone, a compound with a characteristic peach-like smell (Larsson et al. 2002). It has been proposed that exploitation of this compound by males is a sexually selected trait used to compete for females, whereby males advertise a resource (tree hollows) with a patchy distribution.

Plant-derived allelochemicals are widely described for members of the Cetoniinae (Table 1). Field screening of synthetic volatiles, independently identified from flower headspace samples, led to the discovery of effective lures (Donaldson et al. 1986, 1990; Tóth et al. 2003b) that are now in use for detection and monitoring (Cowell et al. 2012; Subchev et al. 2011, 2012; Tóth et al. 2009; Vuts et al. 2010c). Furthermore, EAG-screening of common floral compounds has proved to be useful in attractant development (Vuts et al. 2010a, 2010b). Efficacy of lures can further be enhanced synergistically by adding visual stimuli (color) for the target species (Schmera et al. 2004; Tóth et al. 2005; Vuts et al. 2012a). In some cases, attractant-baited traps were sufficient for direct population control by mass trapping of damage-causing adult Cetoniinae (Razov et al. 2008), or by attract-and-kill methods (Chen and Li 2011). Mixtures of ubiquitous floral scent compounds (Knudsen et al. 2006) are believed to indicate the presence of food (e.g., flowers) to the foraging beetles (Steenhuisen and Johnson 2012). It may be noteworthy that *Scolia hirta* Schrank wasps (Hymenoptera: Scoliidae), parasitoids of *Cetonia a. aurata* L. and *Potosia cuprea* Fabricius, are particularly attracted to the odor/color combination of their hosts (Vuts et al. 2012b). This might only be because these wasps, similar to the scarabs, are day-flying

**Fig. 1** A functional classification of selected compounds involved in the chemical communication of the Scarabaeoidea. **1** 1,4-benzoquinone (*Hylamorpha elegans*, *Melolontha hippocastani*), **2** (E)-2-nonen-1-ol (*Anomala* spp.), **3** (E)-2-nonenal (*Anomala* spp.), **4** 1,3-dimethyl-2,4-(1H,3H)-quinazolinedione (*Phyllopertha diversa*), **5** anisole (*Holotrichia consanguinea*), **6** anthranilic acid (*Holotrichia l. lochooana*), **7** (R)-butyl lactone (*Anomala* spp.), **8** L-isoleucine methyl ester (*Holotrichia parallela*, *Phyllophaga* spp.), **9** (R)- $\gamma$ -decalactone (*Osmoderma eremita*), **10** (RS)-ethyl 4-methyloctanoate (*Oryctes monoceros*, *O. rhinoceros*), **11** (RS)-4-methyloctanoic acid (*Oryctes elegans*), **12** (RS)-butane-2,3-diol (*Scapanes australis*), **13** pentan-3-one (*Strategus aloeus*), **14** ( $\pm$ )-des-N-morphinan (*Oryctes rhinoceros*), **15** (R)-limonene (*Cotinis nitida*), **16** caproic acid (*Macrodactylus* spp., *Phyllophaga anxia*), **17** skatole (*Geotrupes auratus*, *Aphodius tasmaniae*), **18** phenylacetone nitrile (*Anomala octiescostata*), **19** eucalyptol (*Melolontha hippocastani*, *Anoplognathus* spp.), **20** geraniol (*Phyllophaga congrua*, *Phyllotocus navicularis*, *Anomala octiescostata*, *Phyllopertha horticola*, *Popillia japonica*, *P. lewisii*, *Cyclocephala lurida*, *Euphoria sepulchralis*, *Oxyctonia jucunda*, *Protaetia ishigakia okinawana*), **21** linalool (*Phyllophaga congrua*, *Popillia japonica*, *Atrichelaphinis tigrina*), **22** (Z)-3-hexen-1-ol (*Holotrichia oblita*, *H. parallela*, *Maladera orientalis*, *Melolontha hippocastani*, *M. melolontha*, *Anomala corpulenta*, *A. exoleta*, *Phyllopertha horticola*, *Popillia* spp.), **23** propan-1-ol (*Protaetia brevitarsis*), **24** (RS)-lavandulol (*Cetonia a. aurata*, *Oxythyrea cinctella*, *O. funesta*, *Potosia cuprea*, *Valgus hemipterus*), **25** ethyl dihydrochrysanthemumate (*Oryctes rhinoceros*), **26**  $\beta$ -ionone (*Anomala transvaalensis*), **27** benzyl alcohol (*Holotrichia oblita*, *H. parallela*, *Maladera orientalis*, *Anomala* spp., *Popillia* spp.), **28**  $\beta$ -necrodol (*Aphodius* spp.), **29** butyl sorbate (*Phyllophaga congrua*, *Rhizotrogus majalis*), **30** 4-methyl-5-vinylthiazole (*Cyclocephala* spp.), **31** (S)-2-hydroxy-5-methyl-3-hexanone (*Cyclocephala cearae*, *C. celata*), **32** 4-methoxystyrene (*Erioscelis emarginata*), **33** methyl 2-methylbutyrate (*Cyclocephala literata*)

flower visitors, but it might also reflect yet undiscovered indirect host/parasitoid interactions.

Different types of fruit also are important food sources for several cetoniin scarabs. Stensmyr et al. (2001) and Bengtsson et al. (2009, 2011), while screening numerous synthetic compounds by single cell recording, found highly specialized fruit odor-detecting receptor cells in *P. interrupta* and *P. marginata* Drury. Of these, (*RS*)-butane-2,3-diol attracted *P. interrupta* in the field (Bengtsson et al. 2009). For *Cotinis nitida* L., fermentation volatiles are powerful attractants (Johnson et al. 2009; Landolt 1990). Studies by Johnson and Vishniac (1991) also shed light on the interactions between the beetles and their gut yeast flora, which they pick up from peach fruits. After feeding for 2 days, attraction of the feeding complex to conspecifics increases, indicating the release of aggregation semiochemicals. Johnson et al. (2009) identified several volatile fermentation compounds from such complexes and, indeed, found a mixture of these chemicals to be attractive to *C. nitida* (Table 1).

Research efforts also have started to unravel the role that symbiotic microorganisms play in the chemical ecology of scarabs. Microorganisms can be involved in the production of pheromones and, possibly, of allomones, the latter having antimicrobial properties, similar to what has been observed in some species of Staphylinidae (Piel 2002). Cetoniacytone A, (1*R*,5*S*,6*R*)-4-amino-5-hydroxy-1-(hydroxymethyl)-7-oxabicyclo[4.1.0]hept-3-en-2-one, and B, N-[(1*R*,2*S*,6*R*)-2-hydroxy-6-(hydroxymethyl)-5-oxo-7-oxabicyclo[4.1.0]hept-3-en-3-yl]acetamide, moderate antitumor agents produced by an endosymbiotic strain of *Actinomyces* sp., were isolated from the intestines of *C. aurata* (Schlörke et al. 2002). Genetic and biochemical approaches have been pursued to gain further information regarding the biosynthesis of these compounds (Wu et al. 2009). *Cremastocheilus* species live in ant nests, where they feed on ant larvae and pupae (Mynhardt and Wenzel 2010). *Cremastocheilus castaneus* Knoch, when disturbed by ants, secretes an odorous viscous fluid from the anal opening that repels the attackers (Kloft et al. 1979).

**Table 2** Semiochemicals utilized by multiple taxa of the Scarabaeoidea (P: pheromone, A: allelochemical)

Chemical class	Compound	Taxon						
		Geotrupidae	Scarabaeidae					
			Aphodiinae	Scarabaeinae	Melolonthinae	Rutelinae	Dynastinae	Cetoniinae
Aliphatics	( <i>RS</i> )-Butane-2,3-diol					P	A	
	( <i>RS</i> )-Butan-2-ol				A	P		
	Butan-2-one	A				P		
Aromatics	( <i>Z</i> )-3-Hexen-1-ol			A	A			
	( <i>E</i> )-Anethole			A	A		A	
	Benzaldehyde		A		A			
	1,4-Benzoquinone			P	P	A		
	Benzyl alcohol			A	A			
	( <i>E</i> )-Cinnamyl alcohol				A		A	
	<i>p</i> -Cresol	A		P				
	Dibutyl phthalate			A	A			
	Eucalyptol			A	A			
	Eugenol			A	A	A	A	
	2-Methoxy-3-methyl-1,4-benzoquinone		A			A		
	Methyl benzoate				P		A	
	Phenol	A		P		A		
	Phenylacetaldehyde				A		P, A	
	2-Phenylethanol			A	A		A	
	Phenyl propionate			A		A		
	Toluquinone			A	P			
Heterocyclic compounds	Skatole	A	A					
Terpenes	Geraniol			A	A	A	A	
	Linalool			A	A		A	



Compounds in this secretion with allomonal properties have not been identified so far.

### Interactions at Other Trophic Levels

To our knowledge, there are no reports of chemically mediated multi-trophic interactions (Vet and Dicke 1992) among the Scarabaeoidea. However, there are a few examples of bi-trophic relationships governed by chemical signals. Damage by foliage feeders can induce stress-related volatile emission from the attacked plant, as in the case of *Melolontha hippocastani* (Melolonthinae). Feeding by this species on oak leaves increases the emission of GLVs after 1.5 h of damage (Ruther et al. 2002a). GLVs then serve as kairomones (Nordlund and Lewis 1976) for conspecifics to find hosts and mates. Grubs of this species exploit constitutively emitted root volatiles to orientate toward plants (Weissteiner et al. 2012). Another example of the utilization of plant-derived kairomones by herbivorous chafers is the attraction of *Anomala octiescostata* to dandelion (*Taraxacum officinale* F.H. Wigg; Asteraceae) through a blend of volatiles released by (and identified in) the flowers (Leal et al. 1994a).

Moving to higher trophic levels, a predator of *Osmoderma eremita* (Cetoniinae), the click beetle *Elater ferrugineus* L. (Coleoptera: Elateridae), exploits its host's sex pheromone as a kairomone to locate suitable breeding sites for its larvae, which then prey on *O. eremita* eggs and grubs (Svensson et al. 2004). Behavioral evidence shows that egg-laying *Tiphia vernalis* Rohwer and *T. pygidialis* Allen wasps (Hymenoptera: Tiphidae) in North America can follow soil scent trails of their respective larval hosts, *Popillia japonica* and *Cyclocephala* spp. (Rogers and Potter 2002). The attractive chemicals involved are still unknown, but results suggest that they are present both in the larval cuticle and in frass. *Cyclocephala* spp. grubs in Argentina are parasitized by larvae of the robber fly *Mallophora ruficauda* Wiedemann (Diptera: Asilidae) (Groba and Castelo 2012). Fly larvae actively search for hosts in the soil, and use semiochemicals to locate 3<sup>rd</sup> instars. Extracts of the grub's fermentation chamber (proctodeum) were particularly attractive to fly larvae, indicating that behavior-eliciting chemical signals are associated with this region of the digestive tract.

### Conclusions

The diversity of semiochemicals utilized by scarabaeoid beetles (Fig. 1) is truly remarkable among the Coleoptera, probably due to the rich variety of lifestyles found within this superfamily. The same compound can play a role in interspecific chemical communication of numerous taxa, as well as function as an allelochemical and pheromone, even in groups

with quite different ecologies (semiochemical parsimony, Blum 1996; Table 2).

Scarabaeoid beetles, as members of many coleopteran taxa (Francke and Dettner 2005), use female sex pheromones for intraspecific communication. However, in *Osmoderma eremita* (Cetoniinae, Scarabaeidae), it is males that attract females by means of a sex pheromone, similar to, for example, the bruchid *Acanthoscelides obtectus* (Chrysomelidae) (Horler 1970). Male-derived aggregation pheromones are widespread in weevils (Curculionidae) and bark beetles (Scolytidae) (Wertheim et al. 2005), but they also are known in scarabs in the Dynastinae (Scarabaeidae). All identified scarabaeoid pheromones are air-borne substances serving as long-range sex signals, although *Oplostomus haroldi* (Cetoniinae, Scarabaeidae) uses a non-volatile compound as a sex signal, that acts upon contact. Such contact sex pheromones also are known in longhorn beetles (Cerambycidae) (Allison et al. 2004).

The plethora of allelochemicals that scarabaeoid beetles exploit to find suitable food or egg-laying substrates reflects well the ecological diversity of the superfamily. These kairomones often act together with pheromones (see Reddy and Guerrero 2004) to synergize behavior (e.g., attraction), as reported for *Melolontha* scarabs (Scarabaeidae) (Reinecke et al. 2002). Examples of such interactions between intra- and inter-specific communication channels can also be found in *Phyllotreta* flea beetles (Chrysomelidae) (Tóth et al. 2012) and bark beetles (Gitau et al. 2013). Exploitation of this synergistic interplay between pheromones and plant-derived kairomones has led to successful semiochemical-based pest management programs. For the most effective detection, monitoring, and mass-trapping of *Popillia japonica* (Ladd et al. 1981) and *Anomala rufocuprea* (Imai et al. 1997) (Rutelinae, Scarabaeidae), plant kairomone-based lures are utilized in combination with their respective sex pheromones, with the ratio of female *A. rufocuprea* of total catches being significantly higher in traps baited with the combined lures. This may be of high practical value, as the removal of females may have direct effects on the size of future population densities (mass trapping). In addition, it may serve as a more precise means of detection by monitoring the sex that lays the eggs, allowing more accurate prediction of the time of emergence of larvae (Wall 1989). Aggregation pheromones in the Dynastinae are highly attractive to conspecifics of both sexes, and currently are applied in bucket traps for monitoring and mass trapping of *Oryctes rhinoceros* (Hallet et al. 1995) and *Scapanes australis* (Rochat et al. 2002).

In contrast to pheromones and kairomones, allomones used for defense against predators are rarely reported among the Scarabaeoidea, even though they are quite common among other coleopteran groups, e.g., the Staphylinidae, Meloidae, and Tenebrionidae (Dettner 1987).

## Future Perspectives

Future research on the chemical ecology of scarabaeoid beetles requires further studies on the identification and field application of pheromones and plant-derived allelochemicals to detect native crop pests and invasive species, monitor their spatial and temporal distribution, and the mass-trapping of selected species. New research directions will emerge for both above- and belowground interactions, including population control of scarabaeoid beetles with natural enemies via plant induced signaling in response to herbivore damage (Pickett et al. 2012), or through application of pathogens (fungi, nematodes), in attract-and-infect approaches (Koller et al. 2005). Detailed studies on pheromone systems, using scarabaeoid beetles as model organisms, will also allow us to gain a better understanding of more fundamental aspects of intraspecific chemical communication (see Ishida and Leal 2008; Nikonov and Leal 2002). Also, chemically mediated interactions of the Scarabaeoidea with their host plants will shed light on the driving forces of plant/herbivore evolution. In addition, further investigations into the relationships between scarabaeoid beetles and their symbionts will promote advancements, not only in the field of chemical ecology, but also in the research of natural products, which could lead to the discovery of novel drugs for medical care.

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