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RESEARCH

Can Pheromones Contribute to Phylogenetic Hypotheses? A Case Study of Chrysomelidae

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Abstract

Pheromones mediate species-level communication in the search for mates, nesting, and feeding sites. Although the role of pheromones has long been discussed by various authors, their existence was not proven until the mid-twentieth century when the first sex pheromone was identified. From this finding, much has been speculated about whether this communication mechanism has acted as a regulatory agent in the process of speciation, competition, and sexual selection since it acts as an intraspecific barrier. Chrysomelidae is one of the major Phytophaga lineages, with approximately 40,000 species. Due to this immense diversity the internal relationships remain unstable when analyzed only with morphological data, consequently recent efforts have been directed to molecular analyses to establish clarity for the relationships and found their respective monophyly. Therefore, our goals are twofold 1) to synthesize the current literature on Chrysomelidae sex pheromones and 2) to test whether Chrysomelidae sex pheromones and their chemical structures could be used in phylogenetic analysis for the group. The results show that, although this is the first analysis in Chrysomelidae to use pheromones as a phylogenetic character, much can be observed in agreement with previous analyses, thus confirming that pheromones, when known in their entirety within lineages, can be used as characters in phylogenetic analyses, bringing elucidation to the relationships and evolution of organisms.

Keywords Chemical Ecology · Chemotaxonomy · Chrysomeloidea · Evolution · Sex and Aggregation Pheromones · Bayesian Inference

Introduction

Communication plays a key role in animal behavior. When animals communicate, they transfer information as encoded in a visual, auditive or olfactory signals (Endler 1993; Wyatt 2003). Insects are no different, but their diversity prompts the evolution of several mechanisms that encode information. However, olfactory communication is the most common among insects and it involves the use of chemical compounds to transfer information between individuals (Brezolin et al. 2018). Chemical communication is not something exclusive to insects. Darwin (1871) and many others, viz, Butler (1609) and Fabre (1879–1907) had already addressed that this mechanism is used by a range of organisms, including bacteria, humans, and many others, but it is certain that communication through chemical signals is a predominant feature in insects (Greenfield 2002; Reinhard 2004).

Insects are one of the most diverse animal groups, corresponding to more than half of all known living organisms

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(Cai et al. 2022; Sollai and Solari 2022; Stork 2018; Tihelka et al. 2021). Within Insecta, Coleoptera is the most biodiverse order of the animal kingdom with over 380.000 described species, and an estimated 1.5 million yet undescribed (Cai et al. 2022; Sollai and Solari 2022; Stork 2018). Chrysomelidae and six other beetle families, namely Vesperidae, Oxypeltidae, Disteniidae, Cerambycidae, Orsodacnidae and Megalopodidae, comprise the superfamily Chrysomeloidea. Along with Curculionoidea, these two superfamilies form the clade Phytophaga. This clade is the largest and most diverse lineage of phytophagous beetles, with approximately 125.000 described species. It is the second largest lineage of existing phytophagous animals, while Lepidoptera is the first one (Grimaldi and Engel 2005; Haddad and McKenna 2016; Marvaldi et al. 2009; McKenna et al. 2009, 2015; Robertson et al. 2015).

All chrysomelids are phytophagous and most adults feed on leaves, but adults of some species may feed on pollen. The feeding habits of larvae are more diverse in comparison to adults, being able to feed on roots or leaves, or inside stems and seeds. Many species are considered pests of cultivated plants and can cause direct damage to leaves, roots and stems, compromising the transport of nutrients in the plant. They can also cause indirect damage to plants by acting as vectors in the transmission of viruses (Goméz-Rodríguez et al. 2015; Leschen and Beutel 2014).

Some insects can sequester complex molecules from plants during feeding to produce their pheromones using simple biosynthetic steps such as, reduction, esterification, and epoxidation. There is evidence in the literature that diet has impact on the composition of both cuticle and volatile compounds involved in chemical communication in phytophagous beetles. For example, males of *Hedypathes betulinus* (Klug 1825) (Cerambycidae: Lamiinae) may sequester geranylacetone from green mate leaves during feeding (Andrade et al. 2019) and use it to produce the long-range sex pheromone fuscumol and fuscumol acetate through reduction and esterification steps (Fonseca and Zarbin 2009; Fonseca et al. 2010; Vidal et al. 2010). Impacts of the diet on the cuticular hydrocarbon composition have been reported in Chrysomelidae, females of *Acanthoscelides obtectus* (Say 1831) that have been fed with either beans or chickpeas in laboratory for 50 generations have shown differences in the levels of three cuticular hydrocarbon compounds (pentacosane, 9-methylheptacosane, and triacontane). Males of *A. obtectus* that have been reared on chickpeas for 50 generations in laboratory were able to discriminate between females based on these differences in the cuticle related to diet (Stojković et al. 2014). On the other hand, many other species use *de novo* biosynthesis to produce their pheromones such as using Acetyl-CoA for the biosynthesis of fatty acids or isoprenyl diphosphate for the biosynthesis of terpenes. These two biosynthetic pathways are very common in insects (Jurenka 2004). For example, several Lepidoptera species have pheromones derived from fatty acids (Ando et al. 2004) and several Coleoptera and Hemiptera species have pheromones derived from terpenoids (Jurenka 2004; Zou and Millar 2015).

The Chrysomelidae is the fourth largest family of Coleoptera, with approximately 40.000 described species (Zhang et al. 2022). This family has 12 subfamilies, namely Bruchinae, Cassidinae, Chrysomelinae, Criocerinae, Cryptocephalinae, Donaciinae, Eumolpinae, Galerucinae, Lamprosomatinae, Sagrinae, Spilopyrinae and Synetinae (Leschen and Beutel 2014; Haddad and McKenna 2016).

The 12 subfamilies of Chrysomelidae, were established by morphological analysis (Reid 1995, 2000). The phylogenetic relationships in the group have constantly changed until the advancement of molecular analyses, which provided some stability in the phylogeny of the following three main lineages: clade Chrysomelinae (including the subfamilies, Chrysomelinae and Galerucinae), clade Eumolpinae (including the subfamilies Cassidinae, Cryptocephalinae, Eumolpinae, Lamprosomatinae, Synetinae and Spilopyrinae) and clade Sagrinae (including the subfamilies Bruchinae, Criocerinae, Donaciinae and Sagrinae) (Gómez-Zurita et al. 2008). However, molecular techniques still diverge on establishing relationships between these clades (Fig. 1a, b, c, d) (Haddad and McKenna 2016; Nie et al. 2020b). The topology (clade Sagrinae (clade Chrysomelinae + clade Eumolpinae) is found in the most recent and extensive phylogeny studies (Douglas et al. 2023).

A character is defined as a heritable feature expressed as an independent variable, such as any characteristic of a taxon (Sereno 2007). Any character has phylogenetic potential. Individual characters contribute to evolutionary hypothesis that are expressed, for example, in a matrix. This matrix is used to analyze the phylogenetic relationships between the groups of interest. It is expected that pheromones have phylogenetic potential as a character since they have high specificity and could have evolved as any other trait. In this way, pheromones could be used as a phylogenetic character to solve problems in in the relationships between groups that morphological/molecular analyses were not able to. In addition, pheromones play a fundamental role in mediating insect communication and are widely used in insect pest control tactics (Casari and Ide 2012).

Therefore, our goals are twofold: 1) summarize and synthesize the current literature of pheromones involved in the location and recognition of mates in Chrysomelidae and, 2) analyze the use of Chrysomelidae sex-pheromones in phylogenetic analysis. Since Chrysomelidae is one of the largest beetle families and has a high degree of specificity with its host plants, describing how sex pheromones evolve is of extensive interest to both basic and applied research, such

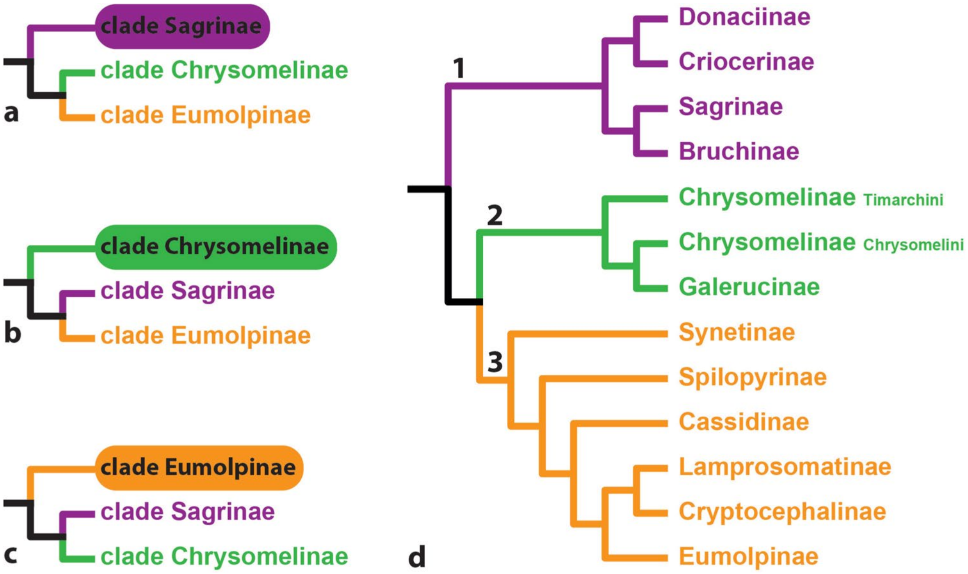


Fig. 1 Phylogenetic relationships of the three main lineages of Chrysomelidae. Methods used to establish relationships between clades are specified in parentheses. **a** Gómez-Zurita et al. 2008 (multilocus ribosomal RNA), Zhang et al. 2018 (nuclear protein-coding), McKenna et al. 2019 (nuclear genes), Cai et al. 2022 (nuclear protein-coding), Douglas et al. 2023 (genome). **b** Nie et al. 2020b (mitogenome), Nie et al. 2020a, b (mitogenome), Zhang et al. 2022 (mitogenome). **c** Timmermans et al. 2015 (mitogenome), Goméz-Rodríguez et al. 2015 (mitogenome). **d** Phylogenetic relationships adapted from Douglas et al. 2023 (three major lineages indicated with numbers 1 clade Sagrinae, 2 clade Chrysomelinae, 3 clade Eumolpinae)

as in the elucidation of the internal relationships between groups and the improvement of current pest control tactics.

Material and Methods

Data Sampling

We performed a systematic search on Chrysomelidae pheromones using the Pherobase©, Web of Science©, and Google Scholar© online platforms. The Pherobase© was used as the main search database, while the Web of Science© and Google Scholar© were used as complementary databases. We reviewed all articles in the "Chrysomelidae" category, as well as in "Bruchidae", present in the Pherobase©. For the Web of Science search, the following parameters were used: ((all = (sex pheromone)) or (all = (Chrysomelidae)) and (all = (pheromone))). The Google Scholar search was performed using the following keywords: Chrysomelidae, pheromone and sex pheromone. A total of 262 articles were analyzed, published between the years of 1965–2023, and 206 taxa were reviewed in this work.

The taxa presented in this review are arranged in alphabetic order descending from family, subfamily, tribe, genus, until species. The subspecies level was included whenever possible. The following online platforms were used to check all species names and their current taxonomic status: The Encyclopedia of Life, The Catalogue of Life©, Inventaire National du Patrimoine Natural, Global Biodiversity Information Facility, Catálogo Taxonômico da Fauna do Brasil (Sistema de Informação sobre a Biodiversidade Brasileira—SiBBr), National Center for Biotechnology Information, and Integrated Taxonomic Information System. Species transferred from the Chrysomelidae to other families are not included in this work to avoid perpetuating taxonomic misunderstanding.

For taxa that share some chemical compounds or blends, additional comments about biology, biogeography, and feeding habits have been added to elucidate the interactions between these species.

Terminals, Characters, and Phylogenetic Analysis

The internal group is composed of thirty-nine recognized species of Chrysomelidae. In addition to Chrysomelidae, we included one species of Anthribidae, two species of Curculionidae, five species of Cerambycidae, and one species of Vesperidae in our phylogenetic analyses that represent the Phytophaga clade. One species of Silvanidae was selected as the outgroup representing the Cucujoidea superfamily (Supplementary Table 1).

The characters were constructed in accordance with the logical structure by following the criterion of character independence and mutually exclusive conditions of their states (Sereno 2007). Characters that could be coded as multi-state such as, biosynthesis pathway, functional groups, saturated compounds, and cyclic compounds, were categorized as present/absent for each possible state after establishing primary homology hypotheses (Tarasov and Solodovnikov 2011; Tarasov and Génier 2015). This kind of arrangement was used because of its efficiency in providing a direct answer to a hypothesis (the character) and an accurate separation of features into subsets of taxa (the present state) demonstrated in previous works (Tarasov and Solodovnikov 2011; Tarasov and Génier 2015). For these characters, this is justified by the difficulty of proposing homologies between such states since the routes required for the transformation of one molecule into another may be numerous and non-homologous as well as unknown. Added to this, we have the fact that each species can present more than one associated compound.

Unambiguous optimization makes it possible to visualize all characters, thus the characters will be presented in a list and will be followed by comments.

We excluded the cuticle compounds of two species of *Chrysochus* and *Phaedon cochleariae* from our analyses due to the high number of compounds identified for cuticle of these species (*i.e.*, 27 compounds identified from the cuticle of *Chrysochus* spp. and 67 compounds identified in the cuticle of *Phaedon cochleariae*) and the lack of data that provides behavioral responses to any of these compounds as a short-range sex- pheromone of these species. We do not encode the functional groups and biosynthesis pathways for *Zabrotes* and *Decellebruchus* due to the absence of data in the literature for these species. Therefore, we only encode the four following characters for *Zabrotes* and *Decellebruchus*: the emitting sex (female), aggregation pheromone (absent), long-range sex-pheromone (present), and short-range sex-pheromone (present) (also known as contact sex-pheromone).

The matrix was build using the NEXUS program version 0.5.0 (Page 2001). For better visualization, the states were coded with a dash (-) when inapplicable and with a question mark (?) when not observed (missing data). However, when such states are analyzed in programs, they end up being interpreted under all possibilities of states present in the character in question (e.g., 0/1).

A supertree was assembled using phylogenetic hypotheses from different taxonomic levels (Phytophaga: (Cai et al. 2022), Chrysomeloidea: (Nie et al. 2020a, b), Chrysomelidae: (Douglas et al. 2023), Bruchinae: (Kergoat et al. 2015), *Acallymma* + *Diabrotica*: (Derunkov et al. 2015), *Leptinotarsa* + *Zygogramma*: (Gómez-Zurita et al. 2008), *Aphthona*: (Konstantinov 1998), *Callosobruchus*: (Tuda et al. 2006), *Diabrotica*: (Eben et al. 2013) and *Galerucella* (Borghuis et al. 2009) to produce a reference topology. We optimized the proposed characters of this reference topology using only the unambiguous changes to describe their evolutionary pathways. Visualization and handling of the resulting cladograms was done in ASADO ver. 1.61 TNT-MRBAYES SLAVER (vl 5.30) (Nixon 2022) and was exported for editing in a specific vectorization program.

For the Bayesian inference, the pheromone dataset was partitioned according to the homoplasy criterion (Rosa et al. 2019). In this criterion, the characters are partitioned according to their homoplasy values, therefore, the characters are organized in partitions corresponding to their values. We measured the homoplasy values using TNT (Goloboff 2008) through an implicit weighing analysis, with the default concavity parameter (k = 3). The values are normalized between 0 and 1, with the lowest value corresponding to no homoplasy, and no values are assigned to non-informative characters (Supplementary 2). In addition, we included the non-informative characters in the partition that corresponds to no homoplasy (homoplasy value = 0.00), as suggested by Gonçalves et al. (2022). The morphological data were modeled according to suggestions by Rosa et al. (2019), as follows: ascertainment bias as variable, branch lengths linked among-partition rate variation, equal rates among-character rate variation, and the branch length prior equal to 10.

The Bayesian inference was carried out in MrBayes 3.2.7 (Ronquist et al. 2012) through the CIPRES Science Gateway portal (Miller et al. 2010). We use two independent runs with four chains each, 2×10^6 generations and 25% of burn-in. Convergence of the chains was checked in MrBayes 3.2.7 and Tracer 1.6 (Rambaut et al. 2013) using as reference ESS (effective sample size) > 200, ASDSF (average standard deviation of split frequencies) ≤ 1 and PSRF (potential scale reduction factor) ~ 1.0. Convergence for topologies was checked through the visualization of the trace plots generated by the function analyze.rwty in the package RWTY (Warren et al. 2017) in the R environment, and according to the analytical references suggested by Wilgenbusch et al. (2004), Nylander et al. (2008), Rambaut et al. (2013) and Warren et al. (2017). The trace plots results are shown in the supplementary 3. For the trees we applied the majority rule consensus with all-compatible groups added (*Contype* = *allcompat*), and the posterior probability was used as branch support.

Results and Discussion

Our literature review found sex pheromone were reported in ten subfamilies belonging to the Chrysomelidae. Six of these subfamilies, namely Bruchinae, Chrysomelinae, Criocerinae, Cryptocephalinae, Eumolpinae and Galerucinae, have either the long- or short-range sex pheromone, or the aggregation pheromone described in the literature (Supplementary Table 1 and Fig. 6). Three subfamilies, namely Cassidinae, Donaciinae and Synetinae, only have reports of interactions mediated by chemical signals or initial investigation on cuticle and tarsal profile (Geiselhardt et al. 2011; Valkama et al. 1997), and for the last subfamilies, Lamprosomatinae, Sagrinae, and Spilopyrinae, any semiochemical-mediated interaction has been found. Currently, these three taxa are comprised by 250, 40 and 39 species, respectively, included species with economic importance and potential use for biological control (Caxambú and Almeida 1999; Chamorro 2014; Jolivet et al. 2014; Lawrence and Lawrence 2014).

Additionally, all the semiochemicals reported for Chrysomelidae, pheromones (**1**–**66**) and kairomones (**67**–**75**), were presented in Figs. 2 and 3.

Overview of Pheromones in Chrysomelidae

Subfamily Bruchinae Latreille, 1802

With approximately 1.650 described species (Morse 2014), individuals allocated to this subfamily are easily recognized by the habit of living inside seeds during their larval stage. Although, there is 36 host plant families recorded as hosts (Johnson 1981, 1989; Johnson et al. 2001; Santos and Ribeiro-Costa 2019), Bruchinae shows a marked preference for Fabaceae (Johnson 1981). The subfamily is distributed throughout the world, except for Antarctica and New Zealand (Kingsolver 2002). Most species are endemic to the Americas and their distribution generally corresponds to the distribution of their host plants. Currently, the subfamily has 69 genera, allocated in six tribes, Amblycerini Bridwell, 1932, Bruchini Latreille, 1802, Eubaptini Bridwell, 1932, Kytorhinini Bridwell, 1932, Pachymerini Bridwell, 1929, and Rhaebini Blanchard, 1845 (Morse 2014; Viana 2016). Bruchini concentrates about 80% of all species in the subfamily, followed by Amblycerini (10%), Pachymerini (9%), and the remaining 1% distributed among the other tribes (Johnson and Romero-Nápoles 2004).

It is worth noting that in this review we are treating Bruchinae as a subfamily belonging to Chrysomelidae (Bocak et al. 2014; Bouchard et al. 2011; Duckett et al. 2004; Farrell 1998; Farrell and Sequeira 2004; Gómez-Zurita et al. 2008; Reid 1995; Reid 2000). Still dealing with the Bruchinae and the names mentioned in Pherobase, we came across in the database with the name *Bruchidius atrolineatus* (Pic 1921), a species that in 2016, was transferred to the genus *Decellebruchus*, and in this review will be treated as *Decellebruchus atrolineatus* (Pic, 1921), following the work of Napóles (2016).

Tribe Amblycerini Bridwell, 1932

Zabrotes Horn, 1885

The *Zabrotes subfasciatus* (Boheman 1833) is a major pest of *Phaseolus vulgaris* L. (Fabaceae), the common bean. Although the genus being native to the Tropical Region, *Z. subfasciatus* has a wide geographic distribution, as it was introduced over the years in Europe, becoming a major pest of Leguminosae (Sari et al. 2003). In relation to the semiochemicals, Pimbert and Pouzat (1988) analyzed, via electroantennogram, the response of males of *Z. subfasciatus* in relation to compounds emitted by females and noted a strong attractiveness, indicating that females emit sexual pheromone that is strongly attractive to males.

Tribe Bruchini Latreille, 1802

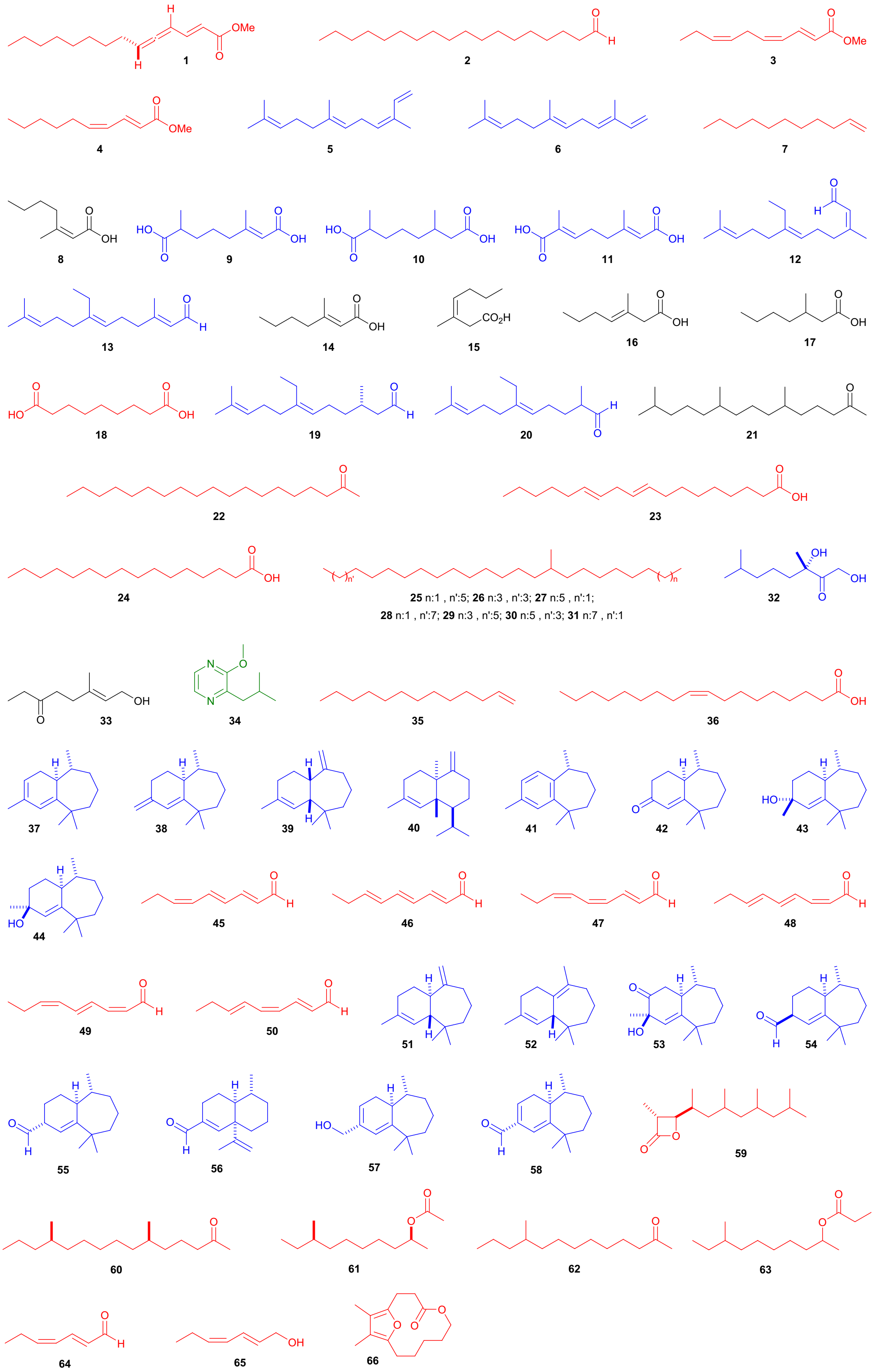
Acanthoscelides Schilsky, 1905

Acanthoscelides is the largest genus of Bruchini, with about 340 valid names and more than 200 to be described (Johnson 1990). This genus is distributed in the new world and has several species of economic importance, as occurs in all Bruchinae groups. However, what stands out is the proportion of the number of known taxa and the amount of work describing pheromones, which is almost non-existent, only one representative, *A. obtectus* (Say, 1831), cosmopolitan species, popularly known as bean weevil and is found infesting *Phaseolus vulgaris* L.

Hope et al. (1967) was the first to suggest the presence of a compound released by males, with a role as a stimulus for copulation. Three year later, Horler (1970) indicate a candidate to sex pheromone in *A. obtectus*, according to the author, the male, few days after emergence produce a substance that attracted the female, being identified as (*E*)-methyl tetradeca-2,4,5-trienoate (**1**). Landor et al. (1971), Kocienski et al. (1977), and Pirkle and Boeder (1978) carried out the synthesis of the pheromone and only in 1981, Mori et al. (1981) synthesized both enantiomers of the dry bean beetle pheromone in high optical purity, confirming the (*R*)-**1** as a natural pheromone.

Vuts et al. (2015a) carried out a series of studies to identify the roles played by the pheromone **1** in the sexual behavior of *A. obtectus* and found that males chose virgin females over other males, and preferred virgin over mated females. They also found that males transfer the pheromone to the females during mating, resulting in mated females being avoided by courting males. Ultimately the authors found, using gas chromatography of hexane extracts, the presence of two male-specific compounds, in addition to pheromone **1**, the octadecanal (**2**), these, in turn, were absent from the behaviorally active female samples, this last compound was mentioned for the first time by Vuts et al. (2015a).

Almost 50 years later Hope's work, the pheromone bouquet of *A. obtectus* is finally published, the (*E*,*R*)-methyl tetradeca-2,4,5-trienoate (**1**), octadecanal (**2**), (2*E*,4*Z*,7*Z*)-methyl deca-2,4,7-trienoate (**3**), (2*E*,4*Z*)-methyl deca-2,4-dienoate (**4**), and the sesquiterpenes (3*Z*,6*E*)- and (3*E*,6*E*)-α-farnesene (**5** and **6**) was identified male-specific volatile component of *A. obtectus* (Vuts et al. 2015b). In the tests realized by the authors, the virgin females were weakly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◂**Fig. 2** Chemical structures of compounds identified as pheromones in Chrysomelidae from *Acanthoscelides obtectus*: **1–6**; *Bruchus rufimanus*: **7**; *Callosobruchus analis*: **8–10**; *C. chinensis*: **9**, **11–13**; *C. maculatus*: **8**, **11**, **14–18**; *C. rhodesianus*: **19–22**; *C. subinnotatus*: **8**, **14**; *Caryedon serratus*: **23**, **24**; *Gastrophysa atrocyanea*: **25–31**; *Leptinotarsa decemlineata*: **32**; *Oulema melanopus*: **33**; *Labidostomis lusitanica*: **34**; *Costalimaita ferruginea*: **35**, **36**; *Altica litigate*: **37**, **38**; *Aphthona czwalinae*, *A. cyparissiae*, and *A. flava*: **37–44**; *Epitrix fuscula*: **37**, **38**, **43–46**; *E. hirtipennis*: **45–50**; *Phyllotreta cruciferae*: **37–42**; *P. pusilla*: **42**, **51–55**; *P. striolata*: **37–42**, **56–58**; *P. vittula*: **37**, **38**, **40–42**, **56**; *Diabrotica. balteata*: **59**; *D. cristata*: **60**; *D. undecimpunctata howardi*: **61**; *D. virgifera virgifera*: **62**; *Diorhabda elongata*: **63**, **64**; *Galerucella calmariensis* and *G. pusilla*: **65**; *Acalymma vittatum*: **66**. Blue: fatty acid/polyketide-derived from acetate pathway pheromones, red: terpenes, green: nitrogenous metabolites and black: biosynthesis not proposed

attracted when pure methyl (*E*,*R*)-methyl tetradeca-2,4,5-trienoate (**1**) was tested alone, meanwhile when a mixture of the six identified compounds was released, they proved to be as active as headspace odors collected from live males (Horler 1970; Vuts et al. 2015b).

Bruchus Linnaeus, 1767

Bruchus rufimanus Boheman, 1833, has been considered a pest in Africa, Asia, North America, and Europe (Bruce et al. 2011). In this species, three classes of semiochemicals regulate the interaction between *B. rufimanus*, its host plant, and the sexual partner (Segers et al. 2021). Kairomones released by *Vicia faba* flowers (Linnaeus 1753) allows adults to find the food source (Bruce et al. 2011), males then produce sex pheromones for attraction and copulation with females (Bruce et al. 2011), and finally, kairomones are released by the pods allowing females to find sites for oviposition (Frérot et al. 2015; Frérot and Leppik 2016).

Bruce et al. (2011), identified nine organic compounds released by flowers and identified that the combination of (*R*)-linalool (**67**), cinnamyl alcohol (**68**), cinnamaldehyde (**69**) are attractive to *B. rufimanus*. In the same study, it was shown that only males release the undecene (**7**), pheromone, which, despite being effective in attracting females under laboratory conditions, when tested in the field, attracted only when together with the kairomones emitted by flowers of *V. faba* (Bruce et al. 2011; Frérot et al. 2015). After copulation in flowers, females lay their eggs in pods, and this behavior is mediated by a combination of (*Z*)-hex-3-en-1-yl acetate (**71**), and more five smaller compounds similar to those found in flowers by Bruce et al. (2011), linalool (**67**), ocimene (**71**), α-humulene (**72**), β-cariofilene (**73**) e limonene (**74**) (Frérot and Leppik 2016).

Callosobruchus Pic, 1902

It is the best-studied genus of this tribe, with five species with some type of chemical compound described in Pherobase. This number is justified by the fact that several species are currently considered of economic importance, causing severe damage to stored grains, especially legumes intended for human consumption. Another peculiar feature is observed in *Callosobruchus*, where two types of pheromones are involved in mating. The first is a sex pheromone released by females, attracting males even at a certain distance, and a second, also a sex pheromone, acting through contact between individuals, that is, at a short distance, and exerting an arousal response only in males, with exposure of the male genital organ, followed by copulation (Shimomura et al. 2010a; Tanaka et al. 1981).

Callosobruchus analis (Fabricius 1781)

Preliminary evidence for a female sex attractant in *C. analis*, was reported by Cork et al. (1991) as being (*Z*)-3-methylhept-2-enoic acid (**8**). According to Tanaka et al. (1981), in this species, two types of pheromones are found during mating, which are subsequently emitted by the female, the first is a sex pheromone that attracts the male at a given distance, and the second is a sex pheromone of contact, released at a short distance and which causes the male to expose his genital organ for copulation.

Using filter paper collection and further analysis using Gas Chromatography-Mass Spectrometry (GC–MS), Shimomura et al. (2010a), were able to identify the following compounds, (*E*)-3,7-dimethyloct-2-enedioic acid (**9**) and 2,6-dimethyloctanedioic acid (**10**), the callosobruchusic acid, which had been previously identified as a contact sex pheromone for *C. maculatus* (Fabricius 1775) and *C. chinensis* (Linnaeus 1758), respectively. Although, unlike the latter two, the two compounds in *C. analis* are stereochemically pure. According to Shimomura et al. (2010a), *C. analis* has highly specific mating behavior, as does *C. rhodesianus* (Pic, 1902), when compared to two other species that live in sympatry, *C. chinensis* and *C. maculatus*. In addition, Yajima et al. (2007) identified (*R*)- and (*S*)-**9** in the natural product at 3:1 ratio and (2*R*,6*S*)-, (2*S*,6*R*)-, (2*S*,6*S*)- and (2*R*,6*R*)-**10** at 43:38:18: trace for *C. chinensis*.

Callosobruchus chinensis Linnaeus, 1758

A first indication that in *Callosobruchus* females are responsible for releasing the sex pheromone was published by Honda and Yamamoto (1976), when studying *C. chinensis*. Later Tanaka et al. (1981; 1982) indicated that Erectin, (2*E*,6*E*)-2,6-dimethylocta-2,6-dienedioic acid (**11**), was produced by both sexes, but only played an excitatory role in males, with exposure of the genitalia and subsequent copulation attempt. In 1990, Ueno et al. identified the kairomone (+)-catechin (**75**) as a stimulant for oviposition, and more than thirty years after the first work, attraction compounds released by females are described by Shimomura et al. (2008), suggesting the following molecules (2*Z*,6*E*)- and (2*E*,6*E*)-7-ethyl-3,11-dimethyldodeca-2,6,10-trienal (**12** and **13**), with the synthesis and field testing of these compounds being later performed by Chiluwal et al. (2017), proving their attractiveness. Shimomura et al. (2016) also indicated

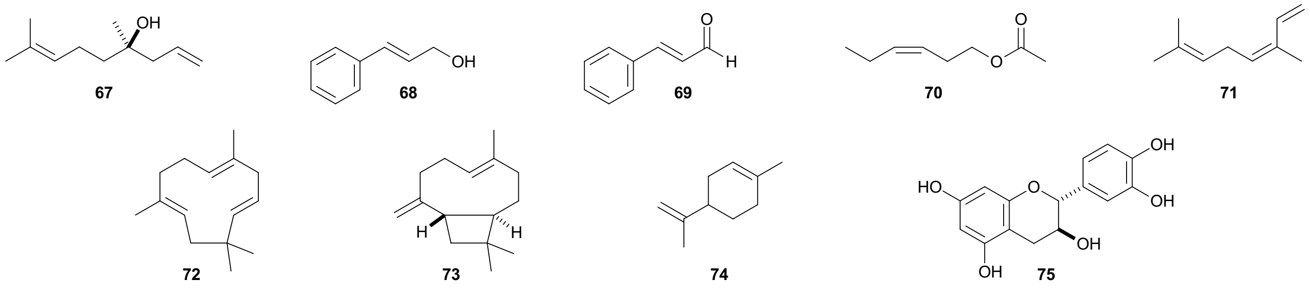

Fig. 3 Chemical structures of substances identified as kairomones for oviposition in *B. rufimanus*: **67**–**74** and *C. chinensis*: **75**

that (*E*)-3,7-dimethyloct-2-enedioic acid (**9**) act as contact pheromone (Shimomura et al. 2016; Tanaka et al. 1981).

Callosobruchus maculatus (Fabricius, 1775)

The cowpea weevil, *C. maculatus*, was studied for the first time by Rup and Sharma (1978), where the authors proposed that the female would be responsible for the release of the sex pheromone. In 1986, Rup developed some bioassays and observed that prior to copulation, the female called the male and directed him to the mating site of interest. Phillips et al. (1996) suggested that five carboxylic acids, released by females, had a synergistic effect on the behavior of males of *C. maculatus*, these are (*Z*)- and (*E*)-3-methylhept-2-enoic acid (**8** and **14**), (*Z*)- and (*E*)-3-methylhept-3-enoic acid (**15** and **16**) and 3-methylhept-2-enoic acid (**17**). Following the author's, tests with single-vial and wind-tunnel demonstrated that all five acids are biologically active for male, but the **15** and **16** are highest attractive, besides stimulating, in addition to flying that was stimulated by the other acids, this two stimulating the approach and contact (Phillips et al. 1996). In addition to the long distance sex pheromone, females of *C. maculatus* also produce a contact sex pheromone, the 2,6-dimethyloctane-1,8-dioc acid (**11**) and nonanedioic acid (**18**) following Nojima et al. (2007).

Callosobruchus rhodesianus (Pic, 1902)

The female sex pheromone of the *C. rhodesianus* was first suggested by Shimomura et al. (2010b), when the authors hypothesized that the 7-ethyl-3,11-dimethyl-6,10-dodecadienal (**19**) would be attractive to males, being the absolute configuration of the natural compound confirmed as (3*S*,6*E*)-**19**. Bioassays using Y-tube olfactometer showed that only the (*S*)-**19** is attractive to males, while the (*R*)-**19** and the racemate are not attractive to the males. In the same year, Shimomura et al. (2010c) suggested another female compound as a pheromone candidate, the (*E*)-6-ethyl-2,10-dimethylundeca-5,9-dienal (**20**). The authors indicated that this compound would possibly work as a minor sex attractant pheromone. The 6,10,14-trimethylpentadecan-2-one (**21**) and nonadecan-2-one (**22**) were identified as the sex contact pheromone, produced by the females (Shimomura et al. 2016).

Callosobruchus subinnotatus (Pic, 1914)

The last species of the genus addressed in this review is *C. subinnotatus*, with only one study related to this species. Shu et al. (1999) proposed that the female produces sex pheromone, attracting males to the emitting source. The authors analyzed the compounds using the Gas Chromatographic and Mass Spectrometric and suggested that the sex pheromone consisted of two short-chain fatty acids, the (*Z*)- and (*E*)-3-methylhept-2-enoic acid (**8** and **14**), being the composition of these molecules confirmed by electrophysiological and behavioral bioassays, where they were used synthetic compounds.

Despite the *C. rhodesianus* and *C. maculatus* have overlapping host plant, *Vigna unguiculata* (Linnaeus) Walp., the natural distribution (prior to anthropogenic dispersal) and pheromones are distinct (Tuda et al. 2006), resulting in the hindrance of cross copulation in these two species. For the other *Callosobruchus* species, namely *C. analis*, *C. chinensis*, and *C. subinnotatus*, as much as they share one compound, the other compounds that form the blend in these species are distinct (Table I), as are their respective host plants.

Decellebruchus Borowiec, 1987

Sex pheromones were first reported by Nammour et al. (1988), where females of *D. atrolineatus* (Pic, 1921) were identified as responsible for the release of the sex pheromone. Later experiments confirmed the attractiveness of males to compounds released by females (Pouzat and Nammour 1989) and the location of possible glands involved in the release of this pheromone (Biemont et al. 1992). It is worth noting that none of the works mentioned proposed the structure of the sex pheromone.

Tribe Pachymerini Bridwell, 1929

Caryedon Schoenherr, 1823

The genus has only one species represented, *Caryedon serratus* (Olivier 1790). Following the pattern of other species, *C. serratus* is also considered of economic importance, since it attacks *Arachis hypogaea* (Linnaeus, 1753) (Fabaceae). Furthermore, after a series of investigations of attractiveness, using five hexadecanoic acid ester derivatives, the authors found that, the males are significantly attracted to benzoyl hexadecanoate. By investigating other platforms and repositories, it was possible to locate other works addressing the use of chemical communication in *C. serratus*.

Chaibou et al. (1993) indicated the presence of pheromone released by females during scotophase, this being attractive to males, but no structure was suggested. Panday et al. (2011) in order to establish an attractiveness for males and females, as a counterpoint to the use of insecticides, performed an attractiveness test with extracts of pods and kernels in different solvents, being possible to observe a greater attractiveness of both sexes for the methanol extract of shelled groundnut. Based on this result, the authors analyzed it in the Gas Chromatograph-Mass Spectrometry and found the presence of octadeca-9,12-dienoic acid (**23**) and palmitic acid (**24**), as major constituents, may be responsible for the attractiveness. Some years later, Jyothi et al. (2014), attested to the presence of a sex pheromone released by females and an aggregation pheromone, the latter released by males. For this, the authors used a Y-tube olfactometer for the bioassays and investigated the responses of males and females in relation to their conspecific headspace extracts and groundnut seed extracts. Through the results obtained, the authors hypothesized that females would be responsible for the release of sex pheromones, and males for the aggregation pheromone. Beyond that, both sexes responded considerably to groundnut seed extracts, with females having a superior response to males, 76.1% to 67.6%, respectively, these results agree with those obtained previously by Panday et al. (2011) and Chaibou et al. (1993).

Subfamily Cassidinae Gyllenhal, 1813

The Cassidinae is the second largest subfamily of Chrysomelidae (Fukumori et al. 2022), with approximately 6.000 species described with worldwide distribution, nevertheless most species of this subfamily are found in the Neotropical region (Chaboo 2007). Despite the diversity of this group, there is only one record of cuticle chemical compounds identified in this subfamily and one study of female contact sex pheromone (Geiselhardt et al. 2011; Kawazu et al. 2011).

Tribe Cassidini Gyllenhal, 1813

Cassida Linnaeus, 1758

Geiselhardt et al. (2011) investigated the chemical composition of tarsi and elytra SPME samples of *Cassida viridis* Linnaeus, 1758 and 34 other Coleoptera species, that have convergently developed widened tarsi for substrate adhesion. Their results indicate that there are no substantial differences in the chemical composition of tarsal and elytral samples in all species studied. All chemical components identified in this study are characteristic for insect cuticular lipids, such as saturated, unsaturated, and methyl-branched hydrocarbons (Geiselhardt et al. 2011). Therefore, no pheromones have been described to date in this subfamily.

Tribe Cryptonychini Chapuis, 1875

Brontispa Sharp, 1904

The *Brontispa longissima* (Gestro 1885), popularly known as coconut hispine beetle, is a serious pest of *Cocos nucifera* L., and other several ornamental palms (Liebregts and Chapman 2004, Nakamura, Konishi and Takasu 2006). In 2011, Kawazu et al. investigated the existence of the females contact sex pheromone. The results indicated the presence of a sex pheromone in *B. longissima* and suggested that these compounds consist of one or more less-polar compounds, like saturated hydrocarbons.

Subfamily Chrysomelinae Latreille, 1802

This subfamily is the fifth largest in Chrysomelidae, with about 3.000 species (Reid 2006), allocated in 132 genera and 2 tribes, Chrysomelini and Timarchini (Riley et al. 2002). However, on the Pherobase platform, more than 50 articles are found for the subfamily, a higher amount compared to Galerucinae. This number is also justified by the pest status of some taxa, especially regarding commodities, such as *Solanum tuberosum* (Linnaeus, 1753).

The advantage of this interest, which is too focused on some groups, as is the case of Chrysomelinae, is the possibility of discovering a range of interactions mediated by semiochemicals, as is the case of secretions for the protection of immature forms described for *Linaeidea* and *Chrysophtharta* (Moore 1967; Sugawara et al. 1979), sequestration and use of cantharidin in a mimetic way, through predation of individuals of the Meloidae family (Islami and Nikbakhtzadeh 2009), identification of glands involved in the release of chemical compounds in *Leptinotarsa* (Daloze et al. 1986), *Chrysolina* (Laurent et al. 2003) and *Chrysomela* (Wallace and Blum 1969), defensive compounds, of the monoterpene type, used as markers of choice by the predator, in the plant-herbivore-predator interaction (Sears et al. 2001), tarsal and elytral cuticular compounds, the latter being involved in sex-specific recognition in *Gastrophysa* (Sugeno et al. 2006; Geiselhardt et al. 2011) and *Phaedon* (Geiselhardt et al. 2009).

The largest number of interactions described, however, was due to the sequestration of chemical compounds from the host plants, present in *Oreina* (Ehmke et al. 1999; Pasteels et al. 1988), *Platyphora* (Pasteels et al. 2001) and *Phratora* (Pasteels et al. 1983), Kairomones in *Gastrolina* (Matsuda 1978), *Gastrophysa* (Matsuda and Matsumoto 1975; Matsuda 1976), *Leptinotarsa* (Visser et al. 1979), *Phaedon*

(Nielsen 1978; Tanton 1965) and *Phratora* (Peacock et al. 2001), and defensive compounds released by larvae and adults of *Calligrapha* (Timmermans et al. 1992), *Chrysolina* (Pasteels et al. 1979), *Chrysomela* (Blum et al. 1972; Hollande 1909; Matsuda and Sugawara 1980; Schütz et al. 1997; Termonia and Pasteels 1999), *Gastrophysa* (Pauls et al. 2016; Sugawara et al. 1979), *Gonioctena* (Dettner and Schwinger 1987), *Plagiodera* (Meinwald et al. 1977) and *Phratora* (Pauls et al. 2016).

Tribe Chrysomelini Latreille, 1802

Gastrophysa Chevrolat, 1836

Popularly known as the japanese green duck leaf beetle, the *Gastrophysa atrocyanea* Motschulsky, 1860, uses a blend of contact pheromone encountered in the female body as the attraction to copula, 9-methylheptacosane (**25**), 11-methylheptacosane (**26**), 13-methylheptacosane (**27**), 9-methylnonacosane (**28**), 11-methylnonacosane (**29**), 13-methylnonacosane (**30**), 15-methylnonacosane (**31**) (Sugeno et al. 2006).

Leptinotarsa Chevrolat, 1837

The *Leptinotarsa decemlineata* Say, 1824, is considered a pest in Solanaceae plantations, such as eggplant, tomato, pepper, tobacco, but mainly potato (Kuhar et al. 2006), has description in the literature. According to Oliver et al. (2002), the aggregation pheromone (*S*)-3,7-dimetil-2-oxo-6-octene-1,3-diol (**32**), is released only by males, but recognized by both sexes (Dickens et al. 2002). Cuticular hydrocarbons are also known to *L. decemlineata*, being the profile of males and females different from each other, being able to play a role of recognition between the sexes (Dubis et al. 1987), in addition to a series of studies that prove insect-plant interaction mediated by kairomones (Bolter et al. 1997; DeWilde et al. 1969; McIndoo 1926; Dickens 1999, 2000; Schanz 1953; Schütz et al. 1997).

Phaedon Dahl, 1828

The *Phaedon cochleariae* (Fabricius 1792), commonly called mustard beetle, also use the contact pheromone, being 65 compounds identified by Geiselhardt et al. (2009), for both females and males, and this was used for the male to discriminate and chose the female for copulation, since the compounds differ in quantity between the sexes.

Tribe Doryphorini Motschulsky, 1860

Zygogramma Chevrolat, 1836

The *Zygogramma bicolorata* (Pallister 1953) is mainly used as a control agent for *Parthenium*, a plant considered toxic to animals, including humans. Qadir et al. (2021) analyzed the cuticular profile of females and males and reported the presence of the chain-length which ranged from C14 to C36. In the study, no sex-specific differences were observed in the CHC profiles, but they did show a difference quantitatively. The authors also observed that the abdominal extracts of the females attracted the males, resulting in their aggregation behavior on the paper disks. The hypothesis raised in the paper then, is that females release short-range sex pheromones to attract males (Qadir et al. 2021).

Subfamily Criocerinae Latreille, 1807

This subfamily has 1500 living species allocated in 3 tribes and 20 genus (Bukejs and Schmitt 2016). Despite it has a cosmopolitan distribution, the vast majority of the species are found in the Subtropical and Tropical regions. Of the three tribes, only Lemiini is represented, which is the largest tribe with eleven genera, including here the two largest genera, *Lema*, *sensu lato*, which comprises about 60% of all known species in the subfamily, and *Oulema*, with 128 species (Vencl and Leschen 2014). Although most species of the subfamily, both in the larval and adult stages, attack the leaf surface, some species may attack ovules or other parts of flowers, and as stem-borers and gall-forming. Some species have become pests of commercial products, such as asparagus, lilies, potatoes, rice, and other grains (Vencl and Leschen 2014).

Tribe Lemiini Heinze, 1962

Oulema Des Gozis, 1886

This genus has a single description of aggregation pheromone, and for a species that is considered an important pest of wheat, barley, and oats, *Oulema melanopus* (Linnaeus, 1758). The pheromone, (*E*)-8-hydroxy-6-methyloct-6-en-3-one (**33**), was first suggested by Cossé et al. (2002), and according to the authors it is released by males but is attractive to both sexes. The following year, Rao et al. (2003), confirmed the pheromone and attested to its attractiveness in the field.

Subfamily Cryptocephalinae Gyllenhal, 1813

With 5.300 species distributed worldwide, Cryptocephalinae has its richness concentrated in the tropical and subtropical regions. Two tribes, Chlamisini Gressitt, 1946 and Clytrini Lacordaire, 1848, have cuticular profiles described each with a genus, *Neochlamisus* Karren, 1972 and *Lachnaea*, respectively (Geiselhardt et al. 2011; Rutledge et al. 2014). In addition to these two, the genus *Labidostomis*, belonging to the Clytrini, is represented by a single known aggregation pheromone (López et al. 2022).

Tribe Clytrini Lacordaire, 1848

Labidostomis lusitanica (Germar, 1824)

The *L. lusitanica* is a polyphagous species, consuming a variety of plant genera, such as *Populus*, *Polygonum*, *Quercus*, *Rumex*, and *Salix*, and is considered a pest of species of economic importance pistachio nuts, *Pistacia vera* (Anacardiaceae), feeding voraciously on pistachio crops, being capable of defoliate the youngest plants within hours (Gómez et al. 2021). Due to this economic appeal, López et al. (2022) initiated studies to understand the interactions of this species mediated by chemical compounds. It was possible to observe that in the field, males and females aggregate on pistachio trees, and in the laboratory, it was proven that the male emits a compound that causes this behavior, the 2-isobutyl-3-methoxypyrazine (**34**). In olfactometer tests, both sexes responded to the pheromone (López et al. 2022).

Subfamily Eumolpinae Thomson, 1859

With a cosmopolitan distribution, the subfamily has about 500 genera and more than 7.000 species, with the distribution of these individuals, concentrated mainly in the tropics The adults feed on the outer part of the leaves, mostly dicotyledon, some of which are toxic, while the larvae feed on underground roots, but there are some species that feed on monocotyledon and gymnosperms (Jolivet et al. 2014).

Tribe Eumolpini Hope, 1840

Chrysochus Chevrolat, 1836

The *Chrysochus cobaltinus* LeConte, 1857 utilizes cuticular hydrocarbon profiles in its close-range sex communication, here the cuticular compounds found in the female's body, are responsible for stimulating the males to copulate (Peterson et al. 2007). In addition to discovering that the CHCs compounds mediate communication between males and females of the species, the authors tried to understand whether these hydrocarbon profiles would be efficient, to the point of preventing two closely related species that share the same biogeographic region from mating (Supplementary Table 1).

Therefore, they carried out a series of experiments with the two species that form a hybrid zone in Washington State (WA) (U.S.A.), *Chrysochus cobaltinus* and *Chrysochus auratus* (Fabricius, 1775), where conspecific dead females have been offered to males with their cuticles intact, removed and painted with hexane, and with male and female cuticular extract of both species (conspecific and heterospecific). Based on the results, where males responded positively to the unmanipulated conspecific female cadavers to the detriment of all other treatments, it was possible to demonstrate that the hydrocarbon profiles playing an important role with respect to the evolution of reproductive isolation (Howard et al. 2003; Peterson et al. 2007). In the bioassays conducted years earlier, it was possible to observe that males from the hybrid zone tend to be more selective than males from outside these zones, just as females are more distinguishable (Peterson et al. 2005), suggesting that this set of reproductive traits are continuously reinforcing sexual isolation through natural selection, thus preventing hybridization (Dobzhansky 1940).

Despite being in a hybrid zone, these two *Chrysochus* species have different feeding habits, *Chrysochus auratus* has a restrictive diet, feeding exclusively on *Apocynum cannabinum* and *A. androsaemifolium* (Apocynaceae) (Dobler and Farrell 1999; Dussourd and Eisner 1987; Williams 1992), while *C. cobaltinus* has a broader diet, feeding on *Asclepias speciosa* and *A. eriocarpa* (Asclepiadaceae) in addition of the two species of *Apocynum* (Dickinson 1995; Dobler and Farrell 1999). Therefore, the feeding habit together with species- and sex-specific recognition through CHCs profile, contribute to the reproductive isolation of these two species that are in a hybrid zone.

Costalimaita Bechyně, 1954

Data on *Costalimaita ferruginea* (Fabricius 1801) were found in two unpublished theses, (R Molinário de Souza, PhD Thesis, Federal University of Viçosa, 2013) and (ME Vieira Xavier, PhD thesis, Federal University of Alagoas, 2019). Both report aggregation behavior in freshly fed *Eucalyptus* leaves. Despite this, the authors found different results regarding other compounds related to the species, so for the analyses only the data from Xavier (2019) was considered, because it is a more complete work, in our point of view. The compound heptadecane was specific in samples from *C. ferruginea* females. The compounds tetradecene (**35**) and (*Z*)-9-octadecenoic acid (**36**), were specific to males.

Subfamily Galerucinae Latreille, 1802

The 14.500 currently known species are allocated in 1.100 genus and two tribes, distributed worldwide (Nadein and Bezděk 2014; Nie et al. 2018; Douglas et al. 2023). Adults consume the outer part of leaves, pollen and nectar from female flowers, and the larvae are fruit and leaf miners, and may also feed on the outer part of roots, buboes, and leaves (Nadein and Bezděk 2014).

Tribe Alticini Newman, 1835

This tribe contains approximately 10.000 species allocated in 601 genera (Douglas et al. 2023), and the biodiversity of this taxon is concentrated mainly in the tropics of the southern hemisphere (Nadein and Bezděk 2014). Eleven genera allocated to Alticini have some type of chemical compound described in the literature, ranging from flavonoids (Matsuda 1978), emission of volatiles associated with host plants (Kumano-Nomura and Yamaoka 2009), sesquiterpenes released by males (Bartelt et al. 2001), defensive squirts (Evans et al. 2000), alkaloid sequestration (Dobler et al. 2000), even aggregation pheromones (Beran et al. 2011, 2016; Zilkowski et al. 2006).

Altica Geoffroy, 1762

Altica fragariae (Nakane, 1955) and *Altica viridicyanea* (Baly, 1874)

In order to understand the roles of the CHC's profiles in two sympatric species, Xue et al. (2016) have developed some mating bioassays, with females and males of the *A. fragariae* and *A. viridicyanea*. The result showed that both males preferred a conspecific female instead of the female of the sister species, and they preferred the females with the CHCs intact, indicating that the CHCs play a crucial role in the process of the male detecting the conspecific female for mating, discrimination between related species, age and to distinguish the sexual mature female from immature one (Xue et al. 2016, 2018).

Altica litigata Fall, 1910

Known to cause damage to plants in the Lythraceae and Onagraceae families, *Altica litigata*, has had its pheromones investigated (Carruthers et al. 2011) and two molecules have been proposed, (6*R*7*S*)-himachala-9,11-diene (**37**) and (6R,7S)-2,2,6-trimethyl-10-methylene-bicyclo[5.4.0]-undec-1,11-ene (**38**), both of which are emitted by males of this species.

Aphtona Chevrolat in Dejean, 1836

Bartelt et al. (2001), investigated the pheromones of some species of *Aphthona* Chevrolat, 1836, namely, *A. czwalinae* Weise 1888, *A. cyparissiae* (Koch 1803), and *A. flava* Guillebeau, 1894. These species are known to consume leafy spurge, *Euphorbia esula* Linnaeus, 1753, species belonging to the Euphorbiaceae family. The results showed that the possible pheromones of the studied species of *Aphthona* were a himachalane-type terpenes, being two new enantiomers hydrocarbons (6*R*,7*S*)-himachala-9,11-diene (**37**) and (6*R*,(6*R*,7*S*)-2,2,6-trimethyl-10-methylene-bicyclo[5.4.0]-undec-1,11-ene (**38**), trans-α-himachalene (**39**), γ-cadinene (**40**) and (*R*)-*ar*-himachalene (**41**), one norsesquiterpene ketone (1*S*,2*R*)-2,6,6-trimethylbicyclo[5.4.0]undec-7-en-9-one (**42**) and two alcohols, (3*R*,9*R*,9a*S*)- and (3*S*,9*R*,9a*S*)-3,5,5,9-tetramethyl-2,3,5,6,7,8,9,9a-octahydro-1*H*-benzo[7]annulen-3-ol (**43** and **44**), found in the three species studed (Bartelt et al. 2001).

According to Gassmann et al. (1996) these species have an overlapping distribution in Eastern Europe and share the same host plants, however there are two distinct groupings. *A. cyparissiae* and *A. flava* are brownish species and are preferentially distributed in open and dry areas, while *A. czwalinae* are black and are found preferentially in closed and humid areas. In his taxonomic revision, Konstatinov (1998), establishes taxonomic groups that reflect these ecological differences, in addition to other morphological ones, being the *cyparissiae* group for the species *A. cyparissiae* and *A. flava* and the *hammarstroemi* group for *A. czwalinae*. Such conditions together, and possibly behavioral aspects, with the differences found by Bartelt et al. 2001 for the blends of each species prevent cross-attraction between them.

Epitrix Foudras in Mulsant, 1859

Epitrix fuscula Crotch, 1873, had its compounds elucidated by Zilkowski et al. (2006). They proposed six specific male compounds, the two most abundant were (2*E*,4*E*,6*Z*)- and (2*E*,4*E*,6*E*)-nona-2,4,6-trienal (**45** and **46**). The other four minor compounds are himachalane-type sesquiterpenes, two of them are hydrocarbons, (6*R*,7*S*)-himachala-9,11-diene (**37**) and (6*R*,7*S*)-2,2,6-trimethyl-10-methylene-bicyclo[5.4.0]-undec-1,11-ene (**38**), and the other two are alcohols, (3*R*,9*R*,9a*S*)- and (3*S*,9*R*,9a*S*)-3,5,5,9-tetramethyl-2,3,5,6,7,8,9,9a-octahydro-1*H*-benzo[7]annulen-3-ol (**43** and **44**). Two years late, Zilkowski et al. (2008) indicated that *Epitrix hirtipennis* (Melsheimer 1847) also emits a blend of 2,4,6-nonatrienals, namely (2*E*,4*E*,6*Z*)-, (2*E*,4*E*,6*E*)-, (2*E*,4*Z*,6*Z*)-, (2*Z*,4*E*,6*E*)-, (2*Z*,4*E*,6*Z*)- and (2*E*,4*Z*,6*E*)- nona-2,4,6-trienall (**45**–**50**).

Longitarsus Berthold, 1827

The *Longitarsus jacobaeae* (Waterhouse 1858) was studied by Zhang and McEvoy (1994). It was possible to observe in the laboratory and field bioassays that male individuals were attracted when filter paper or tansy ragwort leaves, *Senecio jacobaea* Linnaeus, 1753, were offered right after the females were exposed, indicating that these would be responsible for the attraction of the opposite sex. No pheromone or structure was suggested by the authors, only the indication that the female would be responsible for the emission and that this would be a possible aggregation pheromone.

Phyllotreta Chevrolat in Dejean, 1836

Phyllotreta cruciferae (Goeze, 1777)

The first works indicating that the male crucifer flea beetle, *P. cruciferae*, released aggregation pheromones, this being capable to attracts both sexes when the males are feeding on host plant, were carried out by Peng and Weiss (1992) and Peng et al. (1999), through bioassays carried out in the laboratory and in the field. Only two year later, Bartelt et al. (2001) proposed six male-specific sesquiterpenes as candidates for aggregation pheromone of *P. cruciferae*.

Posteriorly the syntheses of some himachalene-type sesquiterpenes are proposed by the Muto et al. (2004) and Mori (2005). Soroka et al. (2005) performed a series of field experiments with males and female of *P. cruciferae*. They observed that individuals were attracted by the pheromone compound and allyl isothiocyanate, the latter coming from *Brassica napus* Linnaeus, the host plant of the beetles. The authors noticed a considerable increase in attractiveness when they offered the pheromone mixture and allyl isothiocyanate together.

Tóth et al. (2011) realized similar field test, using pure enantiomers of *P. cruciferae* pheromone components (6*R*,7*S*)-himachala-9,11-diene (**37**), (6*R*,7*S*)-2,2,6-trimethyl-10-methylene-bicyclo[5.4.0]-undec-1,11-ene (**38**), (+)-α-himachalene (**39**), γ-cadinene (**40**) and (*R*)-*ar*-himachalene (**41**), (1*S*,2*R*)-2,6,6-trimethylbicyclo[5.4.0]undec-7-en-9-one (**42**), in combination with isothiocyanate, and obtained results similar to those found by Soroka et al. (2005). The authors observed that the compound (6*R*,7*S*)-himachala-9,11-diene (**37**) alone was as attractive as the mixture, indicating that this is the main compound of the pheromone of *P. cruciferae* (Tóth et al. 2005).

Phyllotreta pusilla Horn, 1889

The *P. pusilla*, another crop pest, has the male aggregation pheromone described, when Bartelt et al. (2001) proposed six new sesquiterpenes for the *Phyllotreta* genus, being five for the *P. pusilla*, (1*S*,2*R*)-2,6,6-trimethylbicyclo[5.4.0]undec-7-en-9-one (**42**), (3*S*,9*R*,9a*S*)- and (3*R*,9*R*,9a*S*)-5,5,9-trimethyl-2,3,5,6,7,8,9,9a-octahydro-1*H*-benzo[7]annulene-3-carbaldehyde (**51** and **52**), (4a*S*,5*R*,8a*S*)-5-methyl-8a-(prop-1- en-2-yl)-3,4,4a,5,6,7,8,8a-octahydronaphthalene-2-carbaldehyde (**53**), (9*R*,9a*S*)-5,5,9-trimethyl-5,6,7,8,9,9a-hexahydro-1*H*-benzo[7]annulen-3-yl]methanol (**54**) and (9*R*,9a*S*)-5,5,9-trimethyl-5,6,7,8,9,9a-hexahydro-1*H*-benzo[7]annulene-3-carbaldehyde (**55**).

Phyllotreta striolata (Fabricius, 1803)

This species is considered an important pest of Brassicaceae in North America, as well in Southeast Asia. Beran et al. (2011), using the Taiwanese *P. striolata* population, found that the males emitted volatiles by feeding and these volatiles can attract males and females in the field. Therefore, the authors analyzed the compounds and found that six sesquiterpenes were emitted by feeding males, (6*R*,7*S*)-himachala-9,11-diene (**37**), (+)-α-himachalene (**39**), γ-cadinene (**40**) (*R*)-*ar*-himachalene (**41**), trans-α-himachalene (**56**), and β-himachalene (**57**), being the sesquiterpene **37** was active male-specific compound. Field tests were developed for verified the of the compound of both host plants and males. Based on the results, where the synthetic pheromone required the concomitant presence of the host plant's volatile, allyl isothiocyanate, to be attractive, the authors hypothesized that the adults respond to the pheromone only when the specific host volatiles are present (Beran et al. 2011).

In this same year, Bartelt et al. (2001) studied the American *P. striolata* population, and founded more three specific-males compounds, an sesquiterpenoid ((3*S*,9*R*,9a*S*)-3-hydroxy-3,5,5,9-tetramethyl-5,6,7,8,9,9ahexahydro-1*H*-benzo[7]annulen-2(3*H*)-one (**58**), being the major compound, (6*R*,7*S*)-2,2,6-trimethyl-10-methylene-bicyclo[5.4.0]-undec-1,11-ene (**38**) and (1*S*,2*R*)-2,6,6-trimethylbicyclo[5.4.0]undec-7-en-9-one (**42**), both detected as minor compound. Following these results, Beran et al. (2016) reanalyze the compounds emitted by the Taiwanese population of *P. striolata* and indicate that the blends of male sesquiterpenoids are qualitatively different between the Taiwanese and American populations.

Beran et al. (2016) identified an evolutionarily new family of terpene synthesis genes in *P. striolata*, one of which is directly involved in the biosynthesis of the male aggregation pheromone. Still in this work (Beran et al. 2016), the authors, through a phylogenetic analysis of the genes, suggest that the trans isoprenyl diphosphate synthase gene family was present in the ancestor of Galerucinae, having this functionally diversified.

Phyllotreta vittula (Redtenbacher, 1849)

Tóth et al. (2011), indicated that *P. vittula* and *P. cruciferae* (European population) had similarity regarding pheromones, as *P. vittula* responded to the majority compound emitted from the male of *P. criciferae*, the (6*R*,7*S*)-2,2,6-trimethyl-10-methylene-bicyclo[5.4.0]-undec-1,11-ene (**38**). It is worth mentioning that, in the test field, *P. cruciferae* prefers the major compound, plus the 3-butenyl isothiocyanate, the host plant compounds, whereas *P. vittula* prefers the major compound in conjunction with allyl isothiocyanate, also the host plant compounds. The another's compounds found in the *P. vittula* extracts are (6*R*,7*S*)-himachala-9,11-diene (**37**), γ-cadinene (**40**) (*R*)-ar-himachalene (**41**), (1*S*,2*R*)-2,6,6-trimethylbicyclo[5.4.0]undec-7-en-9-one (**42**) and trans-α-himachalene (**56**), being the bouquet an aggregation pheromone.

Tribe Galerucini Latreille, 1802

This tribe counts with 4.500 species allocated in 499 genus (Douglas et al. 2023). There are a diversity of chemical interactions described for Galerucini, elytral cuticular hydrocarbons and tarsal secretions (Geiselhardt et al. 2011), anthraquinones deposited together with eggs to prevent predation, which is carried out mainly by ants (Hilker and Schulz 1991; Hilker et al. 1992) and floral volatiles to attract pollinators (Andrews et al. 2007), and aggregation pheromone in *Diorhabda elongata* (Brullé 1832), *Galerucella calmariensis* (Linnaeus, 1767) and *Galerucella pusilla* (Duftschmid 1825) (Bartelt et al. 2006; Cossé et al. 2005).

Acalymma Barber, 1947

Popularly known as striped cucumber beetle, the *Acalymma vittatum* (Fabricius, 1775) is the cause of great economic losses in cucumber and melon cultivars. Given its economic appeal, Morris et al. (2005) investigated the pheromone of this species, and an β-lactone, vittatalactone, was suggested as a compound emitted by the male, activating aggregation behavior in females. The structure was determined to be vittatalactone, (3*R*,4*R*)-3-methyl-4-(1,3,5,7-tetramethylloctyl) oxetan-2-one (**59**), using GC–MS combined with microderivatization techniques, and NMR (Morris et al. 2005).

Diabrotica Chevrolat, 1836

Among all the genera allocated in Galerucinae, *Diabrotica* draws attention for the number of studies, more than 30. The justification is given by the number of species that are considered of economic importance, as is the case of *Diabrotica virgifera* LeConte, 1868, which in its larval stage is considered the main pest of corn in the USA (Eben 2022). If we compare with the current number of species allocated to *Diabrotica*, around 400 (Derunkov and Konstantinov 2013; Eben 2022), the number of taxa with pest status becomes negligible, but the fact is that the genus now has greater attention for preying on items that are considered commodities, especially in countries that are large producers, such as the USA, the main corn exporter with a record crop valued at US$ 18.7 billion in 2021 (U.S. Department of Agriculture n.d).

Diabrotica balteata LeConte, 1865

In 1987, the sex pheromone released by females of *D. balteata*, was identified as 6,12-dimethylpentadecan-2-one (**60**) (Chuman et al. 1987). Field trials with traps were performed by McLaughlin et al. (1991), and the results indicated that the bioactive form of this sex pheromone is (*R*,*R*)- 6,12-dimethylpentadecan-2-one.

Diabrotica cristata (Harris, 1836)

The synthetic pheromone compound from *D. virgifera virgifera* proved to be attractive to *D. virgifera zeae* Krysan & Smith, 1980 and *D. porracea* Harold, 1875, both belonging to the *virgifera* species group, with stereoisomerism of this compound causing the specific response among the taxa in the cluster (Guss et al. 1983a, 1984). *D. cristata*, also belonging to this group, is an exception, with males being attracted to the compound (2*S*,8*R*)-8-methyldecan-2-yl acetate (**61**) (Guss et al. 1983a).

Diabrotica undecimpunctata howardi Barber, 1947

Sex pheromones released by females were described for *D. undecimpunctata howardi* Barber, 1947, and the synthetic compound 10-methyltridecan-2-one (**62**) is attractive to males of *D. undecimpunctata undecimpunctata* Mannerheim, 1843 and *D. undecimpunctata duodecimnotata* (Guss et al. 1983b).

In addition to sex pheromone-mediated interactions, *Diabrotica* spp. also has kairomones as mediators (Ventura et al. 2000; Marques et al. 2009). Metcalf et al. (1980) demonstrated that some bitter substances, characteristic of the Cucurbitaceae, act as kairomones in relation to some species of *Diabrotica*. These toxic substances, which emerged as repellents against herbivory, became phagostimulants, indicating a coevolutionary association between Cucurbitaceae and *Diabrotica*, which, according to the authors, has been regulated by a single group of terpenoids, the cucurbitacins, acting on host selection, and by a series of volatile phenylpropanoids that stimulate pollen collection, thus fertilizing cucurbits (Metcalf et al. 1980; Metcalf 1994).

Diabrotica virgifera virgifera LeConte, 1868

Despite having been indicated by Ball and Chaudhury (1973) and Guss (1976), the first sex pheromone for *Diabrotica* was only described in 1982, with the female of *D. virgifera virgifera*, responsible for the release of the propionate compound of 8-methyldecan-2-yl propanoate (**63**) (1982).

Diorhabda Weise, 1883

The mediterranean tamarisk beetle *Diorhabda elongata*, is used as biological control the saltcedar, *Tamarix* spp., species that is exotic and invasive in the US, causing annual losses of about $285,000,000 (Zavaleta 2000). Cossé et al. (2005) investigated the possible pheromones through the analysis of the volatiles collected from the males and females. The authors founded that the males produced two compounds, (2*E*,4*Z*)-hepta-2,4-dienal (**64**) and (2*E*,4*Z*)-hepta-2,4-dien-1-ol (**65**), that elicited antennae of males and females. In field tests, the compound **65** was more attractive than the mixture of both compounds, in a 1:1 ratio, with males and females attracted in a similar proportion, confirming the authors' hypothesis that these would be aggregation pheromone (Cossé et al. 2005).

Galerucella Crotch, 1873

Galerucella calmariensis (Linnaeus, 1767), *G. pusilla* (Duftschmidt 1825) and *G. tenella* (Linnaeus, 1971)

Galerucella calmariensis, *Galerucella pusilla* and *Galerucella tenella* occur throughout Europe (except the very north) and their geographic distribution seem to follow their exclusive/primary host plants (Blossey 1995; Fors et al. 2015; Manguin et al. 1993). *Galerucella calmariensis* and *G. pusilla* are monophagous species that feed exclusively on *Lythrum salicaria* Linnaeus, 1753, (Lythraceae) while *G. tenella* is a polyphagous species that primarily feeds on *Filipendula ulmaria* and other Rosaceae species (Borghuis et al. 2009; Fors et al. 2015). The occurrence of *G. calmariensis* and *G. pusilla* species overlap in location, ecological niche, and time of year in the native Europe (Manguin et al. 1993). It is not clear in the literature how much overlap in geographical distribution exists between *G.* calmariensis/*G. pusilla* and *G. tenella* in their native range, but these three species seem to have been collected in areas of Sweden where their primary/exclusive host-plant species are present within close distance (Fors et al. 2015). *Galerucella calmariensis* and *G. tenella* were introduced into the United States in the early 1990`s as biological control agents for the invasive *L. salicaria* (Hight et al. 1995).

There are reports in the literature that *G. calmariensis*, *G. pusilla* and *G. tenella* produce the same compound as aggregation pheromone. Bartelt et al. (2006) studied volatiles compounds of *Galerucella calmariensis* and *Galerucella pusilla*, and found out that males of these two species produce the dimethylfuran lactone, 12,13-dimethyl-5,14-dioxabicyclo[9.2.1]-tetradeca-1(13),11-dien-4-one (**66**), as aggregation pheromone. This compound from natural and synthetic sources elicited responses on females and males of the two species in both laboratory and field settings (Bartelt et al. 2006, 2008). On a later study, Fors et al. (2015) investigated the production of and response to the dimethylfuran lactone in five species of *Galerucella*, including *G. tenella*, *G. calmariensis* and *G. pussila*. They also detected the lactone **66** in volatile collections of male *G. tenella*. The behavioural attraction of male and female *G. tenella* to the synthetic lactone 65 were confirmed with olfactometer assays in the laboratory (Fors et al. 2015). Although these three species produce and respond to the same pheromone compound and have similar geographical distributions, cross-attraction between *G. tenella* and *G. calmariensis*/*G. pusilla* is unlikely due to differences in ecological niche. In fact, the attraction of *G. pusilla* and *G. tenella* to the lactone 65 is synergized by their respective host-plant odours in laboratory settings (*i.e.*, there is a synergistic effect between the lactone 65 and *L. salicaria* odour in the attraction of *G. pusilla* and *F. ulmaria* odour in the attraction of *G. tenella*) (Fors et al. 2015). The reproductive isolation between *G. calmariensis* and *G. tenella* may be at least partially maintained by differences in several morphological characters between these two species, such as colour, size, and male genitalia (Manguin et al. 1993).

Pheromone production in *G. calmariensis* seems to be related to feeding on *L. salicaria*. Bartelt et al. (2008) investigated this relationship between pheromone production in *G. calmariensis* and host plant feeding by transferring pheromone producing males feeding on *L. salicaria* to roses and willows as an alternative food source in the laboratory. They observed that pheromone emission ceased when beetles were transferred to the alternative hosts. In addition, beetle survival rate was lower when feeding on the alternative hosts in comparison to *L. salicaria.* Pheromone emission returned to typical levels a week after survivor beetles feeding on rose and willow were transferred back to *L. salicaria* (Bartelt et al. 2008). This is an indication that pheromone production in *G. calmariensis*, *G. pusilla* and *G. tenella* could be related to the sequestration and metabolization of compounds from the primary/exclusive host plant since these three species produce and respond to the same pheromone compound and they have similar molecular characteristics (Borghuis et al. 2009; Hambäck et al. 2013).

Pyrrhalta Joannis 1865

Pyrrhalta aenescens Fairmaire, 1878 and *Pyrrhalta maculicollis* (Motschulsky, 1853)

Widely distributed in eastern Asia, both species are considered a serious pest of elm trees. Although they are very similar with respect to morphology, genitalia, and molecular studies have been able to distinguish them (Nie et al. 2012). Zhang et al (2014) investigated mate recognition via cuticular hydrocarbons in order to understand how the isolation of these two sympatric species occurs. Mating experiments revealed that is a strong sexual isolation between them, where males preferred the conspecific females with intact CHCs and conspecific CHCs reapplied after the process of removal, and heterospecific females when they have been treated with the CHCs of the conspecific females. Furthermore, chemical analyses have shown that the hydrocarbon profiles vary between the two species, *P. aenescens* profile consisted of mono-methyl-branched alkanes between C22 and C29, while *P. maculicollis* dimethyl-branched alkanes between C29 e C35 (Zhang et al. 2014).

The Neglected Taxa

The following subfamilies have some kind of investigation regarding chemical compounds but not a description of pheromones. Some of these neglected taxa make up a large majority of Chrysomelidae species, such as Cassidinae, so future research regarding pheromones of these lineages is necessary for understanding the evolution of compounds within the family.

The Cassidinae is the second largest subfamily of Chrysomelidae (Fukumori et al. 2022), with approximately 6.000 species described with worldwide distribution, nevertheless most species of this subfamily are found in the Neotropical region (Chaboo 2007). Despite the diversity of this group, there is only one record of cuticle chemical compounds identified in this subfamily. Geiselhardt et al. (2011) investigated the chemical composition of tarsi and elytra SPME samples of *Cassida viridis* Linnaeus, 1758 and 34 other Coleoptera species, that have convergently developed widened tarsi for substrate adhesion. Their results indicate that there are no substantial differences in the chemical composition of tarsal and elytral samples in all species studied. All chemical components identified in this study are characteristic for insect cuticular lipids, such as saturated, unsaturated, and methyl-branched hydrocarbons (Geiselhardt et al. 2011). Therefore, no pheromones have been described to date in this subfamily.

The Criocerinae has two genera in which interactions mediated by chemical cues have been described, namely *Lema* and *Oulema*. Plant–insect chemical mediated interactions involving the single species of the genus *Lema*, namely *L. unicolor* Clark, 1866, have been suggested by Pedersen et al. (2013) as it was observed visiting flowers of the orchid *Luisia curtissi* Seidenf, 1997 in northern Thailand. However, no pheromones have been identified for *L. unicolor*. In the other hand, *Oulema* has the aggregation pheromone produced by male *Oulema melanopus* (L.) identified by Cossé et al. (2002), and its activity has been confirmed in both laboratory and field settings (Cossé et al. 2002; Rao et al. 2003).

The *Donacia brevicornis* Ahrens, 1810 and *D. marginata* Hoppe, 1795, both species pertaining to the subfamily Donaciinae Kirby, 1837, are studied by Geiselhardt et al. (2011). As a result, there is a chemical congruence between elytral and tarsal cuticular lipids for a whole grouping of species that have enlarged tarsi and specialized attachment structures. However, this pattern did not hold in a phylogenetic context suggesting that this congruence is not conserved within Donaciini. A similar result was obtained by Martin and Drijfhout (2009), when investigating the similarity of cuticular hydrocarbons in Formicidae, in the light of a hypothetical phylogenetic relationships.

The Synetinae, has only two genera, *Syneta* Dejean, 1835, and *Thricolema* Crotch, 1874, the first with eleven species and the second with only one. *Syneta* has a Holarctic distribution, while *Thricolema* occurs in California and Oregon (Silfverberg 2010). About chemical communication, the only mention to the subfamily is by Valkama et al. (1997), which describe the attractiveness of the *Ips typographus* (Curculionidae, Scolytinae) pheromone trap, Ipslure® (2-methyl-3-buten-2-ol, cis-verbenol and ipsdienol). As a result, 40. 884 individuals belonging to 53 species and 18 families were captured, including *Syneta betulae* (Fabricius, 1792), with five individuals captured.

Pheromones Through the Lineages of Chrysomelidae

Based on the knowledge we have so far about Chrysomelidae, it is possible to affirm that both females and males are responsible for the emission of pheromones (Supplementary Table 1), but when we analyze them in relation to their respective functions, the aggregation pheromones are mostly related to males, with a single exception *Longitarsus jacobeae* (Alticini), while the contact and sexual pheromones are mostly found in females, except for a single lineage of Bruchinae composed of *Acanthoscelides obtectus* and *Bruchus rufimanus* (Bruchinae), both emit sexual pheromones (Supplementary Table 1 and Fig. 6). In the outgroup this pattern is only repeated in *Hedypathes betulinus* (Cerambycidae: Lamiinae).

Exploring the chemical structures of the pheromones, we found that alcohol and ester are exclusive to males. The most representative functional group in the pheromones of Chrysomelidae were the carboxylic acids with ten compounds (**8–11**, **14–18**, **23**, **24**) and three of them were a diacids (**9–11**), used by *Callosobruchus analis*, *C. chinensis*, *C. maculatus*, *C. subinnotatus* and *Caryedon serratus*. These unusual compounds as pheromones are polar with lower volatility than similar compounds containing other functional groups like alcohols, esters, and aldehydes. These pheromones are probably left on the trail to direct individuals of the opposite sex to the meet. Fatty acid/polyketide-derived from acetate pathway and terpenes were also present in the pheromones including an allene (**1**) from *Acanthoscelides obtectus*, homosesquiterpene, (2*E*)- and (2*Z*)-homofarnesals (**11** and **12**), from *Callosobruchus rhodesianus* and a norsesquiterpenes, (1*S*,2*R*)-2,6,6-trimethylbicyclo[5.4.0]undec-7-en-9-one (**42**), from *Aphthona cyparissiae*, *A. czwalinae*, *A. flava*, *Phyllotreta* cruciferae, *P. pusilla*, *P. striolata* and *P. vittula*.

Galerucini is the second major group, after Bruchini, where the females are responsible for the production of sexual pheromones, with four species allocated only in *Diabrotica* (Supplementary Table 1). Interestingly, all the four species of *Diabrotica* presented a high similarity in the pheromones, being two methyl-branched ketones (**59** and **61**) in *D. balteata* and *D. undecimpunctata howardi*, and two esters from the reduction of the methyl-branched ketones to secondary alcohols (**60** and **62**) in *D. cristata* and *D. elongata*. This distinction in functional groups corroborates two distinct lineages present in the genus, poliphagous species from fucata group with *D. balteata* and *D. undecimpuctata* and oligophagous from virgifera group with *D. cristata* and *D. virgifera virgifera* (Eben and Espinosa de Los Monteros 2013).

In the Alticini we noticed the opposite, males are the sex predominantly responsible for the emission, with nine species allocated in the *Aphthona*, *Epitrix* and *Phyllotreta*. Interestingly, the male-specific pheromones reported for the species were cyclic terpenes, himachalane-type sesquiterpenes and γ-cadinene (**37–44**, **51–58**) present in *E. fuscula*, *P. striolata*, *P. cruciferae*, *A. czwalinae*, *A. cyparissiae*, and *A. flava*. These compounds are different in the unsaturation position and the presence of oxygenated groups but come from the same biosynthetic pathway.

Terminals, Characters, and Phylogenetic Analysis

Beyond the study of pheromones for pest application, we use these compounds as characters in a phylogenetic hypothesis, to try to understand how the evolution of these groups occurs. Most commonly found in the literature are phylogenetic trees using morphology, molecular data, or a combination of both to elucidate internal relationships and understand the evolution of taxons. Recently the use of pheromones in phylogenetic analysis has been raised, especially in Lepidoptera, where the study of semiochemicals is more advanced, but for the Chrysomelidae, this is the first investigation.

A phylogenetic tree is a diagram-like representation that deals with the relationships of evolutionary descent among populations, species, or higher taxa (Wiley and Lieberman 2011). In this representation, the lines represent species over time and the joining of these lines, nodes, the moments of speciation, i.e., the moment when a parent species splits into two or more daughter species, or cladogenesis from a common ancestor (Wiley and Lieberman 2011). Other elements that can be added to this representation are the characters, which can be of different origins (morphological, molecular, ecological), and their conditions in each taxon indicating how the descent of such characteristics occurs (Hinchliff et al. 2015). Thus, a tree, a phylogenetic hypothesis, can then be proposed through analysis with the purpose of knowing the evolutionary history of a taxon and thus produce classifications that reflect such relationships within this group (Huson and Bryant 2006). Another result to be analyzed may be its predictive potential, since it is possible to assume the condition of a taxon according to the evolution of the group in which it is found or is evolutionarily related (Bush 2001). However, for this, one should aim for a greater representativeness of the taxa in question.

A complete table of the species and characteristics related to pheromones is provided in the supplementary material (Supplementary 2). The comparison of the taxa conditions enabled the construction of a matrix (Supplementary 3) with 68 characters that follow. The characters are discussed according to the optimizations made in the reference topology (Fig. 5).

We emphasize that the investigation of morphological characters related to the production of pheromones such as the positioning of the glands was not possible. The presence of these characters would substantially modify the coding structure since they would make some characters dependent on them while others would appear as inapplicable.

List of Characters

1. Male pheromone emitter: (0) absent; (1) present. The data examined indicate that males may or may not produce pheromones while females seem to obligately produce sexual contact pheromones (see character 5). Thus, the presence of pheromone production by males does not exclude pheromone production by the female (next character). Such a character has 12 steps, that is, 12 changes throughout evolution, being the highest number of steps among all characters.
2. Female pheromone emitter: (0) absent or unchecked; (1) present.
3. Aggregation pheromone: (0) absent or unchecked; (1) present. Males mostly produce aggregation pheromones, the exceptions here being only *Bruchus* and *Acanthoscelides* from Bruchinae as well as *Hedypathes* (Cerambycidae) in the outgroup.
4. Sexual pheromone: (0) absent or unchecked; (1) present. Females mostly produce sex pheromones, the exceptions here being only *Longitarsus* de Alticini.
5. Pheromone, sexual, contact: (0) absent or unchecked; (1) present. It is noteworthy that the species of *Callosobruchus* and *Myllocerinus* (Sun et al. 2017) also produce distance sex pheromone (character 6). Which makes us hypothesize that possibly all females produce at least sexual contact pheromones. A significant portion of the species present questions for this character since there are no tests for this purpose.
6. Pheromone, sexual, distance: (0) absent or unchecked; (1) present. For males, sex pheromones are presented exclusively as distance pheromones, unlike females who produce distance and/or contact sex pheromones according to their molecular weight. However, investigations in this regard deserve to be carried out.
7. Pheromone, biosynthesis, acetate: (0) absent; (1) present. The three distinct biosynthesis found, acetate, terpene (character 21) and nitrogenous metabolites (character 28) are not mutually exclusive since each taxon can produce compounds from different routes.
8. Pheromone, biosynthesis, acetate, type: (0) acyclic; (1) cyclic. Although there is the possibility of more than one type occurring in the set of compounds of a species, we did not find such a condition.
9. Pheromone, biosynthesis, acetate, methyl-branched: (0) absent; (1) present.
10. Pheromone, biosynthesis, acetate, starter unit, acetyl: (0) absent; (1) present.
11. Pheromone, biosynthesis, acetate, starter unit, propionyl: (0) absent; (1) present.
12. Pheromone, biosynthesis, acetate, extender units, 2: (0) absent; (1) present. Produced only by male *Diorhabda* of Galerucini.

13. Pheromone, biosynthesis, acetate, extender units, 3: (0) absent; (1) present.
14. Pheromone, biosynthesis, acetate, extender units, 4: (0) absent; (1) present. Produced only by male *Acallymma* of Galerucini and *Acanthoscelides* of Bruchinae.
15. Pheromone, biosynthesis, acetate, extender units, 5: (0) absent; (1) present. Produced only by male *Bruchus* of Bruchinae as well as *Oryzaephilus* (Silvanidae) of the outgroup (Pierce et al. 1985).
16. Pheromone, biosynthesis, acetate, extender units, 6: (0) absent; (1) present. Produced only by male *Diorhabda* of Galerucini, *Epitrix* of Alticini and *Bruchus* of Bruchinae.
17. Pheromone, biosynthesis, acetate, extender units, 7: (0) absent; (1) present. Produced only by male *Caryedon* of Bruchinae as well as *Myllocerinus* (Curculionidae) in the outgroup.
18. Pheromone, biosynthesis, acetate, extender units, 8: (0) absent; (1) present.
19. Pheromone, biosynthesis, acetate, extender units, 9: (0) absent; (1) present. Produced only by female *Gastrophysa* of Chrysomelinae and *Callosobruchus rhodesianus* of Bruchinae.
20. Pheromone, biosynthesis, acetate, extender units, 13: (0) absent; (1) present. Produced only by female *Tetropium* (Cerambycidae) in the outgroup (Silk et al. 2007; Silk et al. 2011).
21. Pheromone, biosynthesis, terpene: (0) absent; (1) present.
22. Pheromone, biosynthesis, terpene, type: (0) acyclic; (1) cyclic.
23. Pheromone, biosynthesis, terpene, monoterpene: (0) absent; (1) present. Produced only by male *Leptinotarsa* of Chrysomelinae.
24. Pheromone, biosynthesis, terpene, triterpene: (0) absent; (1) present. Produced only by male *Araecerus* (Anthribidae) in the outgroup (Yang et al. 2017).
25. Pheromone, biosynthesis, terpene, sesquiterpene: (0) absent; (1) present.
26. Pheromone, biosynthesis, terpene, norsesquiterpene: (0) absent; (1) present. Produced only by male *Aphtona* and *Phyllotreta* of Alticini as well as *Tetropium* and *Hedypathes* (Cerambycidae) in the outgroup.
27. Pheromone, biosynthesis, terpene, homosesquiterpene: (0) absent; (1) present. Produced only by female *Callosobruchus chinensis* and *C. rhodesianus* of Bruchinae.
28. Pheromone, biosynthesis, nitrogenous metabolites: (0) absent; (1) present.
29. Pheromone, functional group, alcohol: (0) absent; (1) present. The alcohol functional group was verified only in males.
30. Pheromone, functional group, alcohol, primary: (0) absent; (1) present.
31. Pheromone, functional group, alcohol, secondary: (0) absent; (1) present.
32. Pheromone, functional group, alcohol, tertiary: (0) absent; (1) present.
33. Pheromone, functional group, alcohol, allylic: (0) absent; (1) present.
34. Pheromone, functional group, aldehyde: (0) absent; (1) present.
35. Pheromone, functional group, amide: (0) absent; (1) present. The amide functional group was verified only in females and until now only in *Migdolus* (Vesperidae) in the outgroup (Leal et al. 1994).
36. Pheromone, functional group, amine: (0) absent; (1) present. The amine functional group was verified only in males and until now only in Cryptocephalinae.
37. Pheromone, functional group, carboxylic acid: (0) absent; (1) present.
38. Pheromone, functional group, ester: (0) absent; (1) present.
39. Pheromone, functional group, ester, primary: (0) absent; (1) present.
40. Pheromone, functional group, ester, secondary: (0) absent; (1) present.
41. Pheromone, functional group, ester, methyl-ester: (0) absent; (1) present.
42. Pheromone, functional group, eter: (0) absent; (1) present. The eter functional group was verified only in males and until now only in Cryptocephalinae.
43. Pheromone, functional group, hydrocarbon: (0) absent; (1) present.
44. Pheromone, functional group, ketone: (0) absent; (1) present.
45. Pheromone, saturated: (0)absent; (1) present.
46. Pheromone, unsaturated: (0) absent; (1) present.
47. Pheromone, unsaturated, monoene: (0) absent; (1) present.
48. Pheromone, unsaturated, diene: (0) absent; (1) present.
49. Pheromone, unsaturated, triene: (0) absent; (1) present.
50. Pheromone, unsaturated, tetraene: (0) absent; (1) present.
51. Pheromone, unsaturated, hexaene: (0) absent; (1) present.
52. Pheromone 8: (0) absent; (1) present.
53. Pheromone 9: (0) absent; (1) present.
54. Pheromone 11: (0) absent; (1) present.
55. Pheromone 14: (0) absent; (1) present.
56. Pheromone 37: (0) absent; (1) present.
57. Pheromone 38: (0) absent; (1) present.
58. Pheromone 39: (0) absent; (1) present.
59. Pheromone 40: (0) absent; (1) present.
60. Pheromone 41: (0) absent; (1) present.

61. Pheromone 42: (0) absent; (1) present.
62. Pheromone 43: (0) absent; (1) present.
63. Pheromone 44: (0) absent; (1) present.
64. Pheromone 45: (0) absent; (1) present.
65. Pheromone 46: (0) absent; (1) present.
66. Pheromone 56: (0) absent; (1) present.
67. Pheromone 66: (0) absent; (1) present.
68. Pheromone 77: (0) absent; (1) present.

Implication of Pheromones in Phylogenetic Hypotheses

The Bayesian inference analyses with the pheromone dataset did not present difficulties in the mixing of the chains and convergence for the topologies. The two runs were successful in exploring the sample space, presenting ASDSF values below 0.001, ESS values greater than 1000 and PSRF equal to 1.0 for all parameters, without exceptions (Supplementary 3). The partitioning of the morphological data under the homoplasy criterion resulted in a scheme of nine partitions, with homoplasy values varying between 0 and 0.70, plus non-informative characters (Supplementary 2). 25% (17) of the characters had zero homoplasy and approximately 14.7% (10) of the characters were non-informative.

The Fig. 4 shows a majority rule tree resulting from the Bayesian analysis using the pheromone dataset, with posterior probability as branch support. Although the recovered topology does not reflect widely known phylogenetic relationships (Nie et al. 2020a, b; Douglas et al. 2023), analyzes of the pheromone dataset shed new light on our understanding of clade recognition in Chrysomelidae. First, the topology does not support the monophyly of Chrysomelidae and also for the known arrangement of the subfamilies (Fig. 4). For genera with more than one species, *Galerucella* (Galerucinae, Galerucini), *Aphthona* and *Epitrix* (Galerucinae, Alticini) and *Chrysochus* (Eumolpinae) were recovered as monophyletic. *Phyllotreta*, are paraphyletic in relation to *Aphthona* while all other genera are polyphyletic.

Such a result may also be related to factors such as the low sampling in relation to the richness and diversity of the family's eating habits, since the information is concentrated on groups of economic interest. Added to this, such works, for the most part, are incomplete in relation to the complexity that the chemical communication of the taxon in question may become. The revisitation and completeness of this information for the taxa reviewed here is of paramount importance even before the inclusion of new taxa. In this way, we would have a matrix with a smaller number of missing data, making this information base more robust. As an example of this data incompleteness, two of the main stored grain pests, *Bruchus pisorum* and *Decellebruchus atrolineatus* (=*Bruchidius atrolineatus*) (Rees 2007), do not have their chemical compounds identified.

Despite the divergences still present in current phylogenetic hypothesis (Zhang et al. 2022), we assume for the purposes of discussion the clade Sagrinae as a sister lineage to the others (clade Sagrinae (clade Chrysomelinae + clade Eumolpinae)). When analyzing proposed characters on the pre-established topology for the family, considering the positioning of lineages that have no associated pheromones (Chrysomelinae-Timarchini, Donaciinae, Lamprosomatinae, Sagrinae, Spilopyrinae and Synetinae), we obtain a cladogram with 263 steps, consistency index of 25 and retention index of 53 (Fig. 5). In this analysis Chrysomelidae does not show any homoplasy or synapomorphy due to pheromone characters. However, this feature should be better investigated in a comparative way with other families of Phytophaga such as the positioning of the producing glands and derived characters such as sexual behavior.

At the level of the three main clades, we have two homoplasies that supports the clade Eumolpinae and Chrysomelinae (absence of sexual pheromone of distance, 6:0; presence of methyl-branched in acetate biosynthesis, 9:1). First condition with reversal in *Diabrotica*. In Sagrinae clade also presented on *Bruchus rufimanus* and *Acanthoscelides obtectus* as well as *Malodon*, *Tetropium* and *Hedypathes* (Cerambycidae) in the outgroup. Second condition with reversal in *Diorhabda elongata* and *Epitrix*. In Sagrinae clade also presented on *Callosobruchus subnnotatus*, *C. maculatus* and *C. analis* as well as *Araecerus* (Anthribidae) in the outgroup.

Synapomorphies are observed at some levels such as the tribe Alticini (pheromone **37**, 56:1; pheromone **38**, 57:1 both with reversion in *Phyllotreta pusilla* and *Epitrix hirtipennis* and inapplicability in *Longitarsus jacobaeae*), genera group as *Epitrix*, *Longitarsus* and *Aphtona* (tertiary alcohol, 32:1 with inapplicability in *Epitrix hirtipennis* and *Longitarsus jacobaeae*) and the genera *Epitrix* (pheromone **45**, 64:1; pheromone **46**, 65:1) and *Galerucella* (pheromone **66**, 67:1) (Fig. 5). In de outgroup the pheromone **77**, 68:1 is a synapomorphy that supports the two subfamilies (Spondylidinae and Lamiinae) of Cerambycidae (Fig. 5).

Considering this trend of clusters when analyzing only the pheromone characters, we can deduce that such relationships have the potential to be better clarified if these characters are used to complement morphological, molecular, and ecological characters (Fig. 6).

Conclusion

Chrysomelidae, as well as other phytophagous groups, has been shown to be an excellent model for studying insect-plant interactions. Regarding pheromones, it is evident that the majority described so far in the literature are aggregation pheromones. Nevertheless, the knowledge is very low, regarding pheromones in Chrysomelidae when compared to

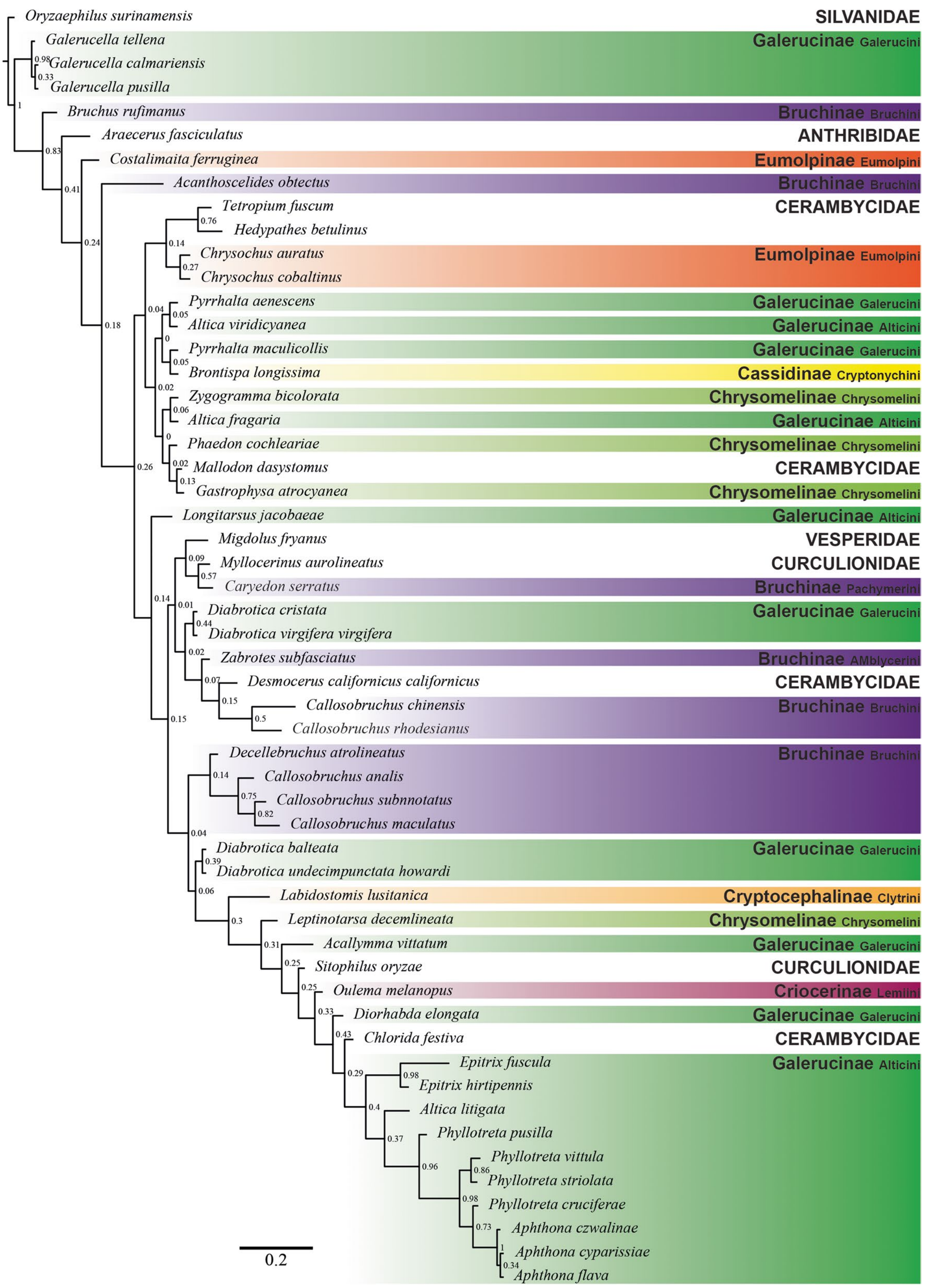

Fig. 4 Phylogenetic relationship among Chrysomelidae based in the pheromone dataset. Tree resulting from a Bayesian analysis with 68 characters split into eight partitions under homoplasy criterion. Consensus tree with all compatible groups added and posterior probability as support branch. Classification proposed by Bouchard et al. (2011) on the right

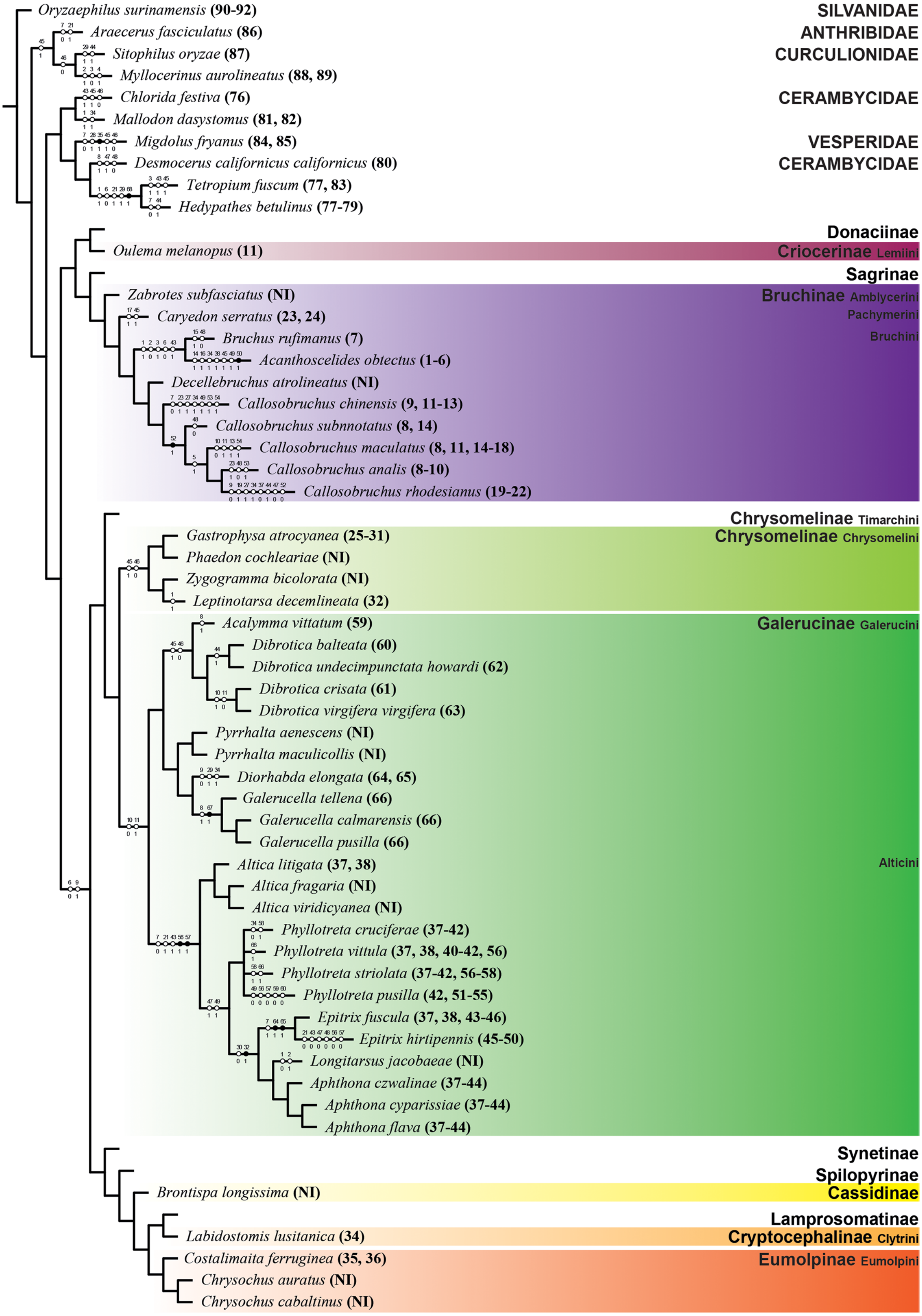

Fig. 5 Phylogenetic relationship among Chrysomelidae based in a supertree (see material and methods for details). Unambiguous state changes under parsimony criteria are represented by filled circles for reversible or non-reversible synapomorphic transformations and by empty circles for homoplastic transformations. Classification proposed by Bouchard et al. (2011) on the right. numbers in parentheses correspond to the pheromone numbers in table 1 and PI: Present and not identified

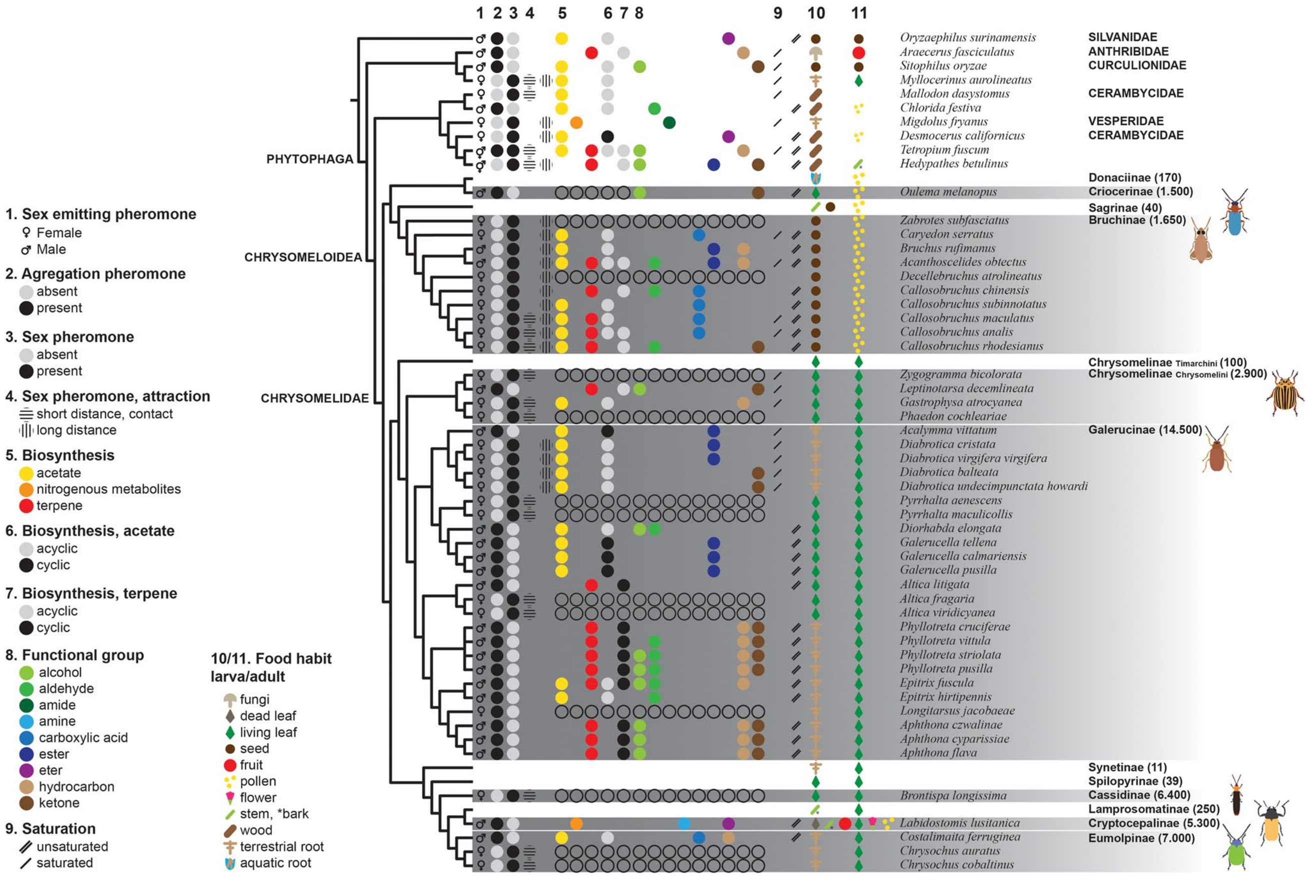

Fig. 6 Synthesis of the data matrix composed of pheromonal characters for Chrysomelidae. Values in parentheses relative to the diversity of the taxon according to Leschen and Beutel 2014. Classification according to Bouchard et al. (2011) on the right

the nearly 40,000 species described for this family, we credit this fact to the little knowledge regarding natural history for a considerable portion of individuals, small size of individuals compared to other groups belonging to Cerambycidae and Curculionidae, for example, making it difficult to collect volatiles and carry out the experiments, and finally, the interest directed towards the groups that cause damage to grains intended for human consumption, given the economic appeal, massive investment and the expressive number of individuals found in the field, thus facilitating the development of experiments.

Pheromones have proven to be strong candidates as characters for use in phylogenetic analysis, being used most successfully in Lepidoptera, a group that has been and is extensively studied and has a vast knowledge regarding pheromones and other types of communication mediated by chemical molecules. The opposite is observed in Chrysomelidae, where we found a derisory number of papers dealing with pheromones in several subfamilies, such as Cassidinae, Criocerinae and Eumolpinae, and in other subfamilies such as Synetinae, Spilopyrinae, Donaciinae and Sagrinae there is no information, resulting in a low sampling of taxa for analysis. Another problem that was observed is the lack of uniformity in the investigations, where one species has data on cuticle, aerations, bioassays, and others only an arena test, resulting in an analysis with missing data for several important taxa, as is the case of *Zabrotes subfasciatus*.

Therefore, we strongly suggest that other research groups start working with other lineages that are outside our biogeographic occurrence, such as Palophaginae and Zeugophorinae (subfamilies of Megalopodidae), Philinae and Vesperinae (subfamilies of Vesperidae), Orsodacnidae, Dorcasominae and Spondylidinae (subfamilies of Cerambycidae), Cassidinae, Criocerinae, Donaciinae, Eumolpinae, Sagrinae, Spilopyrinae, and Synetinae (subfamilies of Chrysomelidae), and finally Disteniidae and Oxypeltidae, both belonging to Phytophaga clade. These future studies should be as exploratory as possible by investigating the volatile and cuticular compounds in a transparent way, highlighting possible absences as informative conditions for character coding. This will contribute to future and more robust analyses, not only in Chrysomelidae, but in Phytophaga as a whole.

Although this is the first analysis in Chrysomelidae to use pheromones as a phylogenetic character, much can be observed in agreement with previous phylogenetic analyses (morphological and molecular), thus confirming that pheromones can be used as characters in phylogenetic analyses in conjunction with morphological, ecological, and molecular data, bringing elucidation to the relationships and evolution of organisms in all taxonomic levels. It is certain that, as more pheromones are described, especially from the two scarcer lineages, we will be able to use the chemical characters with more congruence since we will have a larger and more robust elucidative sample.

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Author Contributions Aluska Tavares dos Santos: Conceptualization, Data Curation, Investigation, Methodology, Visualization, Writing—Original Draft, Writing—Review & Editing. João Pedro Albuquerque de Souza: Investigation, Methodology, Visualization, Writing—Review & Editing. Isaac Reis Jorge: Formal analysis, Investigation, Methodology, Visualization, Writing—Review & Editing. Samara M. M. Andrade: Investigation, Visualization, Writing—Review & Editing. Mauricio Oswaldo Moura: Formal analysis, Visualization, Writing—Review & Editing. Brunno Bueno Rosa: Formal analysis, Methodology, Visualization, Writing—review & Editing. Paulo Henrique Gorgatti Zarbin: Supervision, Visualization, Writing—Review & Editing.

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Declarations

Competing Interests The authors declare no conflict of interest.

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