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Parasitoid Beetles of the Families Rhipiceridae and Ripiphoridae (Coleoptera): Biology, Ecology, and Evolutionary Insights

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Abstract: Parasitoid beetles of the families Rhipiceridae and Ripiphoridae represent rare examples of parasitic adaptation within the order Coleoptera. Their life cycles are highly specialized, involving planidial larvae capable of locating and parasitizing cicadas, bees, and wasps. This study provides a comprehensive synthesis of the biological and ecological characteristics of these families, highlighting their morphology, host–parasitoid interactions, and evolutionary significance. Data were collected from scientific databases, including Scielo, PubMed, BioOne, Google Scholar, and ResearchGate, with emphasis on original and review articles published. The Rhipiceridae are primarily associated with cicadas, exhibiting an endoparasitic cycle in which larvae penetrate underground nymphs, while the Ripiphoridae display broader host diversity, including hymenopterans and wood-boring beetles. Results indicate that both families exhibit hypermetamorphosis and morphological adaptations, such as planidial larvae that facilitate host invasion. Their ecological roles include regulation of host populations and indirect effects on pollination dynamics. Although knowledge of immature stages and molecular phylogeny remains limited, recent advances in taxonomy and genetics have expanded their biogeography and life history. These beetles demonstrate striking examples of convergent evolution between Coleoptera and Hymenoptera, reinforcing their importance in studies of parasitism, biodiversity, and ecosystem regulation.

Keywords: Biocontrol, Ectoparasitoid, Endoparasitoid, Hymenoptera, Wasp.

RESEARCH PAPER

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1. INTRODUCTION

The beetle families Rhipiceridae and Ripiphoridae represent remarkable cases of parasitoid lifestyles within Coleoptera, an order that is otherwise dominated by phytophagous, predatory, or saprophagous lineages. Parasitoidism is rare among beetles, and its occurrence in these groups illustrates an advanced degree of evolutionary specialization. By exploiting other insects as hosts, these beetles reveal the ecological plasticity and adaptability that characterize Coleoptera as one of the most diverse animal orders (Lawrence and Newton, 1995a; Triplehorn and Johnson, 2005).

In the case of the Rhipiceridae, commonly referred to as "cicada beetles," the parasitoid cycle is closely associated with cicadas. Their eggs hatch into highly mobile first-instar larvae, known as planidia, which actively search for underground cicada nymphs. Once contact is established, the larva penetrates the host's body and develops internally as an endoparasitoid, feeding on hemolymph and internal tissues until pupation. Adults are rarely encountered in nature, often attracted to lights at night, while the biology of immature stages remains poorly understood, especially in tropical regions where diversity may be higher (Crowson, 1981; Costa *et al.,* 2009)

The Ripiphoridae, also called "wedge-shaped beetles," display even greater ecological and behavioral diversity in their parasitoid strategies. Many species attack hymenopterans, particularly solitary bees and wasps, though some lineages parasitize cockroaches. Similar to rhipicerids, ripiphorids produce planidial larvae capable of attaching to adult hosts during foraging or flight. For example, in bee-associated species, the planidia cling to the female bee's body and are carried passively into the nest. Once inside, they transfer to the developing bee larva or provisions, initiating a parasitoid relationship that eventually leads to host death. Such strategies create intricate ecological interactions, as ripiphorids can influence pollinator populations and indirectly affect pollination dynamics in ecosystems (Engel, 2005).

Both families share the evolutionary innovation of planidial larvae, a unique adaptation that facilitates host location and invasion. This trait is considered one of the most advanced forms of larval mobility in parasitoid beetles and allows these species to overcome the behavioral and ecological defenses of their hosts (Although parasitoidism is more widespread and diverse among Hymenoptera, the independent evolution of similar strategies in Coleoptera highlights the convergent paths of natural selection (Nikitsky, 1998a; Nikitsky, 1998b; Kathirithamby, 2017). From an ecological perspective, Rhipiceridae and Ripiphoridae play important roles in regulating insect populations. Rhipicerids act as natural regulators of cicada populations, which can reach high densities and affect vegetation. Ripiphorids, in turn, interact directly with bee and wasp communities, potentially altering pollinator population structures and the ecological networks in which they participate. These parasitoid interactions illustrate how even small and poorly studied beetle families can exert disproportionate ecological impacts (Costa *et al.,* 2009; Kathirithamby, 2017).

Despite their significance, knowledge about the biology, ecology, and diversity of these families remains scarce. Many aspects of their life cycles are still poorly documented, particularly in the tropics. New species continue to be described, underscoring the need for integrative studies that combine taxonomy, molecular biology, and ecology. Thus, the parasitoid beetles of Rhipiceridae and Ripiphoridae are not only entomological curiosities but also key elements in understanding the evolution of parasitism and its broader implications for biodiversity (Engel, 2005; Pinto, 2009).

Parasitism represents one of the most complex and specialized ecological strategies in insects. While it is widespread and highly diversified among Hymenoptera, its occurrence in Coleoptera is restricted to a few lineages. The families Rhipiceridae and Ripiphoridae are among the rare examples of beetles that evolved into parasitoid lifestyles. Both rely on highly mobile planidial larvae, which allow them to locate or attach to suitable hosts. Despite their rarity, these beetles demonstrate remarkable evolutionary convergence with wasps and provide valuable insights into host exploitation, adaptation, and insect biodiversity (Crowson, 1981; Kathirithamby, 2017; Sukirno, 2017).

This manuscript aims to synthesize and analyze the current knowledge on the biology, ecology, and evolutionary adaptations of parasitoid beetles belonging to the families Rhipiceridae and Ripiphoridae (Coleoptera), with emphasis on their life cycles, host–parasitoid interactions, larval strategies, and ecological roles.

2.0 METHODS

This study was based on a comprehensive narrative review of the entomological literature focusing on parasitoid beetles of the families Rhipiceridae and Ripiphoridae. To address the limited and scattered nature of available information, we integrated data from taxonomic descriptions, ecological studies, and evolutionary analyses rather than following a strict systematic review protocol. Relevant publications were retrieved from multiple scientific databases and repositories, including ZooBank, BioOne, PubMed, Web of Science, and Scopus, as well as from classical monographs and regional faunal catalogues. Searches were conducted using combinations of keywords related to the target taxa and their biology, such as Rhipiceridae, Ripiphoridae, parasitoid Coleoptera, planidial larvae, and host–parasitoid interactions.

Because biological information on these beetle families is scarce, no temporal limits were applied, allowing the inclusion of both early descriptive studies and recent ecological or molecular research. Sources were considered relevant when they provided information on life-history traits, larval behavior, host associations, or ecological roles, whereas records restricted to distributional data were not included. The selected information was synthesized qualitatively and organized into thematic sections addressing host–parasitoid relationships, planidial larval strategies, adult morphology and reproductive behavior, and broader ecological and evolutionary implications. This approach allowed the integration of fragmented observations into a coherent overview of the biology of these parasitoid beetle families.

3.0 RESULTS AND DISCUSSIONS

Results indicate that Rhipiceridae exhibit endoparasitic development primarily in cicadas, while Ripiphoridae display broader host ranges, attacking Hymenoptera and other insects. Both families undergo hypermetamorphosis, a process involving distinct larval morphologies and behaviors across instars. These findings emphasize the adaptive convergence of parasitoid strategies and their role in maintaining ecological balance. Thus, this study contributes to expanding knowledge of the biological and evolutionary traits of these unique Coleopteran families (Table 1).

Table 1: Parasitoids in these families play critical roles in regulating host populations, often acting as natural biocontrol agents. By parasitizing beetles and other insects, they contribute to ecological balance within their habitats. Their presence also reflects biodiversity indicators sensitive to environmental change

Family	Host Group	Ecological Role	Distribution	Habitat Type	Significance
Rhipiceridae	Cicadas (nymphs)	Controls cicada populations, reduces outbreaks	Americas, Africa, Oceania	Subterranean, near cicada habitats	Indicator of soil biodiversity and host abundance
Ripiphoridae	Bees, wasps, and roaches	Alters pollinator networks, regulates nesting species	Europe, Asia, North Africa	Floral environments and bee nests	Influences pollination dynamics and community structure
Rhipiceridae	Cicada nymphs	Endoparasitoid development	South America	Subterranean soils	Regulation of cicada populations
Ripiphoridae	Solitary bees	Larval parasitism	Europe	Floral habitats	Influence on pollinator communities
Ripiphoridae	Wasps	Brood parasitism	Mediterranean region	Dry habitats	Trophic interaction
Rhipiceridae	Cicadas	Hypermetamorphosis life cycle	North America	Forest soils	Evolutionary specialization
Ripiphoridae	Bees	Phoretic larval behavior	Asia	Flowering ecosystems	Host dispersal strategy
Ripiphoridae	Wood-boring beetles	Larval parasitism	Asia	Forest ecosystems	Community regulation
Rhipiceridae	Cicada nymphs	Endoparasitoid stage	Africa	Soil habitats	Host population control
Ripiphoridae	Wasps	Nest parasitism	North Africa	Shrublands	Biodiversity interaction
Ripiphoridae	Bees	Parasitoid development	Eurasia	Meadows	Pollinator interaction
Rhipiceridae	Cicadas	Internal larval development	Oceania	Subterranean habitats	Ecological balance

Larval examination revealed a consistent parasitic pattern: females deposit eggs near cicada habitats, and the planidial larvae actively locate nymphal hosts underground. Once inside, larvae develop as internal parasitoids, completing their development before cicada emergence. In *S. niger*, larvae exhibit advanced morphological specialization for subterranean movement. Mature larvae recovered from cicada pupae showed sclerotized terminal segments and reduced appendages, confirming their adaptation to parasitism.

The developmental stages of rhipicerid parasitoids associated with cicada nymphs are illustrated in Figure 1. The diagram highlights the larval morphology with reduced legs, the pupal stage developing underground, and the parasitic interaction with the host.

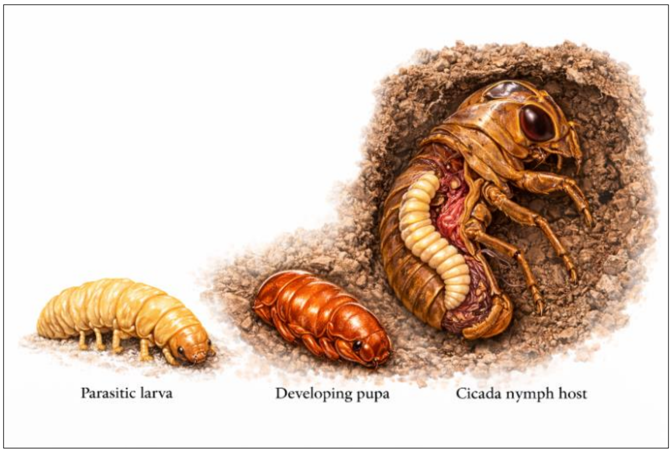

Figure 1: Developmental stages of a parasitoid beetle associated with cicada nymphs (Coleoptera: Rhipiceridae). The illustration shows the robust larva with reduced legs, the pupa developing in the subterranean environment, and the parasitic interaction with the cicada nymph host. These features highlight the morphological adaptations typical of endoparasitoid development in rhipicerid beetles

A generalized life cycle of parasitoid beetles from the families Ripiphoridae and Rhipiceridae is presented in Figure 2, illustrating the sequence from egg deposition to adult emergence.

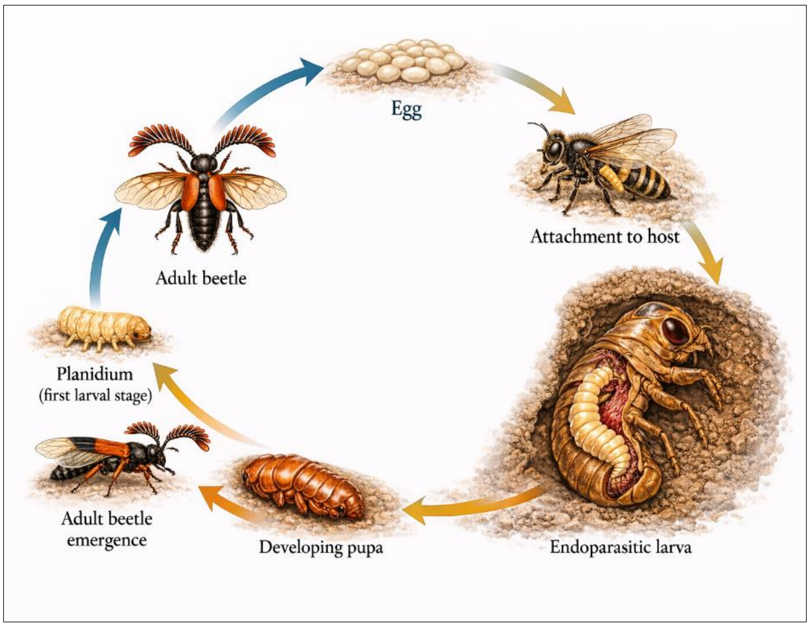

Figure 2: Generalized parasitoid life cycle of beetles from the families Ripiphoridae and Rhipiceridae (Coleoptera). The diagram illustrates the sequence from egg deposition to the mobile planidium larva, host attachment and entry, endoparasitic larval development, pupation, and adult emergence. This scheme highlights the complete metamorphosis and the host-dependent parasitic strategy characteristic of these beetle families

3.1. FAMILY RHIPICERIDAE

The Rhipiceridae are a family of beetles poorly known in European and North African fauna due to their rarity. They do not exist in the Iberian fauna. Only one Rhipiceridae larva is known as a highly specialized ectoparasite. Of still debated phylogeny, they are today considered together with the Dascillidae Guérin-Méneville, 1843 as the only two families that make up the superfamily (Elzinga, 1977; Alonso Zarazaga, 1981; Lawrence, 1995a; Lawrence, 1995b). The family Rhipiceridae is composed of five genera: *Arrhaphipterus* Kraatz, 1862 (the only one present in the western Palaearctic), *Chameorhipis* Latreille, 1834 (tropical, subtropical, and southern Africa), *Polymerius* Philippi, 1871 (Chile), *Rhipicera* Latreille, 1817 (Australia, New Caledonia and South America) and *Sandalus* Knoch, 1801(Figure 3) (North America, South America, eastern and southern Africa, Asia (Lawrence and Newton,1995b).

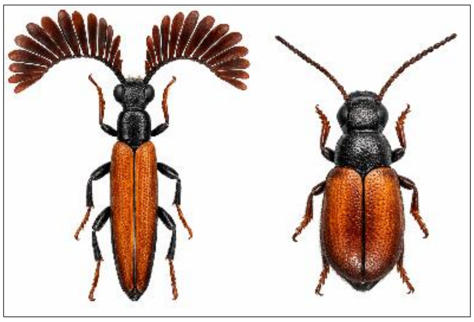

Figure 3: illustrates sexual dimorphism in *Sandalus niger* Knoch, 1801 (Rhipiceridae), showing the male with large flabellate antennae and a slender body, and the female with a compact body and simple antennae. The image highlights the morphological differences related to mating behavior and sensory adaptation. This figure emphasizes the pronounced sexual dimorphism typical of the family

In Rhipiceridae, females lay eggs in soil habitats where cicadas occur. After hatching, planidia actively search for cicada nymphs underground. Upon finding a host, they penetrate the cuticle and establish themselves as internal parasitoids. Development is completed within the host, which ultimately dies before the adult beetle emerges (Lawrence and Newton,1995b). *Sandalus niger* Knoch, 1801, it is a cicada parasite beetle, meaning that both adults and larvae feed on types of cicadas. Males' and females' appearances. Males are light brown with red, feathery antennae, while females look like common black beetles. They are generally inactive beetles that remain motionless and do not fly unless on blind dates (Figure 4) (Crowson,1971; Elzinga, 1977; Zarazaga, 1981; López-Colón, 2001).

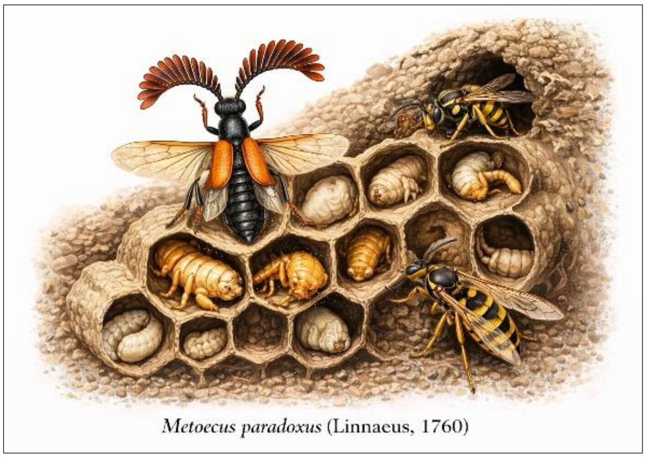

Figure 4: *Sandalus niger* Knoch, 1801 (Coleoptera: Rhipiceridae), adult habitus in dorsal view showing the characteristic morphology of the species. Adapted from Lawrence (1995a, 1995b) and Lawrence *et al*., (2010); illustration by Hastings

Colors: Brown and Black: Habitat: Maple trees. Adult food sources: Plant sap, nectar, fruit, and small insects. Larval food sources: Fluids from cicada nymphs. Bite: Sting. Non-toxic and usually poses no threat to human health. No need to worry too much. Phytophagous: Feeds on plants and usually does not cause a major problem. However, if you notice that the numbers are increasing, you need to take it seriously (Crowson, 1971; Elzinga, 1977; Zarazaga, 1981; López-Colón, 2001).

Eggs are typically laid in the soil near host plants. Since larvae live inside wood, they can be found by examining dead or decaying trees, particularly those with soft or rotten wood. Inspect for boreholes or sawdust around the base of the tree that may indicate their presence. Pupa involves carefully opening up decaying wood where the larvae are known to reside. *Sandalus niger* pupates inside the wood before emerging as adults. Adult *S. niger* adults often emerge from their pupal cases to feed on tree sap and can be found on or around trees that exhibit sap flow or wounds. Observing such trees, especially at dusk or during warm nights, can increase the likelihood of encountering them (Figure 5) (Elzinga, 1977; Zarazaga,1981; López-Colón, 2001).

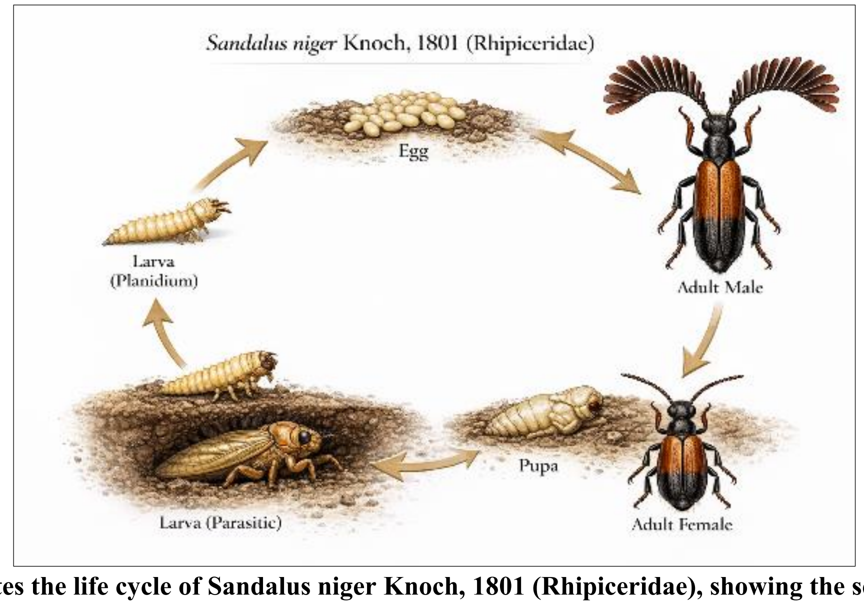

Figure 5: Illustrates the life cycle of Sandalus niger Knoch, 1801 (Rhipiceridae), showing the sequence from egg, larva, and pupa to adult male and female stages. The diagram highlights the parasitoid development associated with cicada nymphs. This visual representation emphasizes the species' metamorphosis and sexual dimorphism

After hatching, the larvae attach themselves to and feed on the roots. As they mature, these larvae remain underground. Searching for these larvae requires careful digging around host plants to unearth them. Pupae also form in the soil, requiring digging near larval feeding areas, but tend to be deeper compared to larvae. The adult *S. niger* emerges from the pupae and is commonly found on or near the same host plants, but above ground. They can be observed by carefully observing plant leaves and stems during their active periods. Found in North America. Predators: Birds, reptiles, rodents, small mammals (Elzinga, 1977; Arnett *et al.,* 2002; Ruiz *et al.,* 2016; Sakenin *et al.,* 2018; Ghahari *et al.,* 2021).

Unique feature: *S. niger* has unique larvae that live inside cicada nymphs, absorbing nutrients without killing the host until they emerge. Hot, dry weather conditions are most favorable for locating *S. niger*, as they promote the activity of many insects, including those of the order Coleoptera *Arrhaphipterus* Kraatz, 1862, includes half a dozen species that colonize southern Europe, *Anatolia olivetorum* Kraatz, 1859, from Greece, northern Africa (Algeria and Morocco), *Anatolia phlomidis* (Daniel, 1900), Syria and Asia Minor, Kurdistan and Transcaucasia (Lawrence and Newton, 1995a). A single species in the Maghreb countries: *Arrhaphipterus larclausei* Reitter, 1894. *Arrhaphipterus larclausei* Reitter, 1894 (López-Colón, 2001).

3.2. FAMILY RIPIPHORIDAE

The Ripiphoridae family is a small beetle family comprising about 450 species worldwide. The Ripiphoridae family comprises 38 genera and over 400 species, distributed across five continents (Lawrence *et al.,* 2010). Images have a heterogeneous morphology and are therefore difficult to characterize as a family (Falin, 2002). Males are characterized by the shape of antennae that are flabelled or biflabelled, except for those belonging to the Asian tribe Eorhipidiini Iablokoff-Khnzorian, 1986 (subfamily Ripidiinae) that have filiform. The females are similar to males and are differentiated by the distinct shape of the antennae, except those from the Ripidiini tribe Gerstaecker, 1855 (subfamily Ripidiinae), which are larviformes (Figure 6) (Lawrence and Newton, 1995b; Beltrán and Beltrán, 2001; Arnett *et al*., 2002; Batelka, 2007; Barreda, 2015).

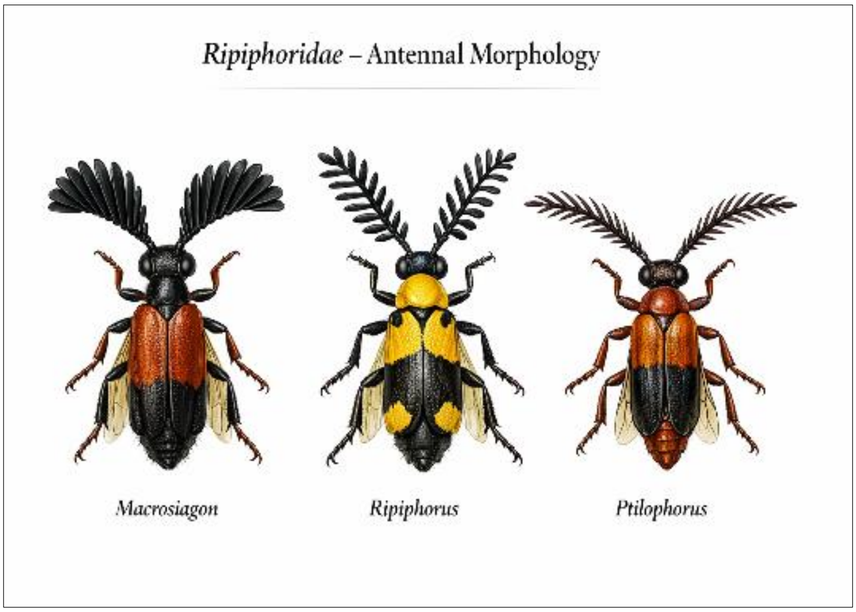

Figure 6: *Macrosiagon, Ripiphorus* Bosc, and *Ptilophorus* Dejean, 1834. The figure shows the segmentation and lamellar structure of the antennae, which serve as key diagnostic features for male identification. This image emphasizes the sensory adaptations associated with mate detection and species differentiation within the family

Ramsey *et al*., (2007) demonstrated that the flabellate antennae of male *Rhipicera* function as efficient molecular capture structures, increasing the surface area and airflow interaction, which likely enhances pheromone detection during mate searching. However, to get an idea of the European representation, also very limited, and compare it with the peninsular one, just comment that in the British Isles, there is only one, *Metoecus paradoxus* (Linnaeus, 1761), parasitic of wasps, which also lives in Spain; in northern Europe, three, in Poland, five, and in central Europe, another five, all of them also in Spain except *Pelecotoma fennica* (Paykull, 1799) and *Ripidius pectinicornis* Thunberg, 1806. On the other hand, in Morocco, there are only five species, making the Iberian fauna, within its limitations, the richest in Europe and the entire Mediterranean basin combined (Figure 7) (Arnett *et al*., 2002; Ruiz, 2007; Batelka, 2009; Batelka and Hájek, 2009; Ruiz, 2010; Owens *et al.*, 2014; Barreda, 2015).

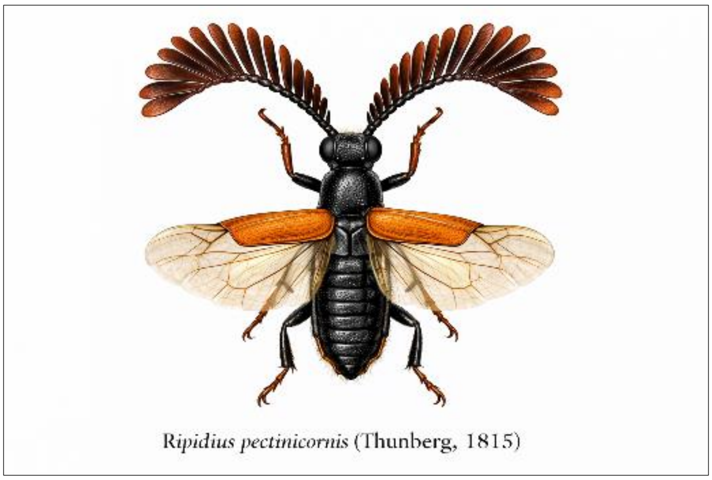

Figure 7: Adult specimen of *Ripidius pectinicornis* (Thunberg, 1815) (Coleoptera: Ripiphoridae) in dorsal view. The illustration highlights the characteristic morphology of the species, including the reduced elytra, membranous hind wings, and the distinctive flabellate antennae typical of males in the family Ripiphoridae. These structures represent important diagnostic traits used in the identification of ripiphorid beetles

The species that attack wasps and bees generally lay eggs in flowers, from which small larvae hatch almost immediately, and one of them lands, at which point they take the opportunity to cling to the visitor to move to the host's nest. The larva then enters the body of the Hymenoptera larva and waits until it enters the pupa stage to begin consuming it and completing its development at the cost of the host's life. It appears in very varied habitats, probably because it is more closely linked to the species it parasitizes than to the environment in which it is found. The Ripiphoridae is a very unusual family of beetles, as they are parasitoid beetles of certain wasps and bees, cockroaches, or other wood-boring beetles (Figure 8) (Ruiz, 2010; Owens *et al.,* 2014).

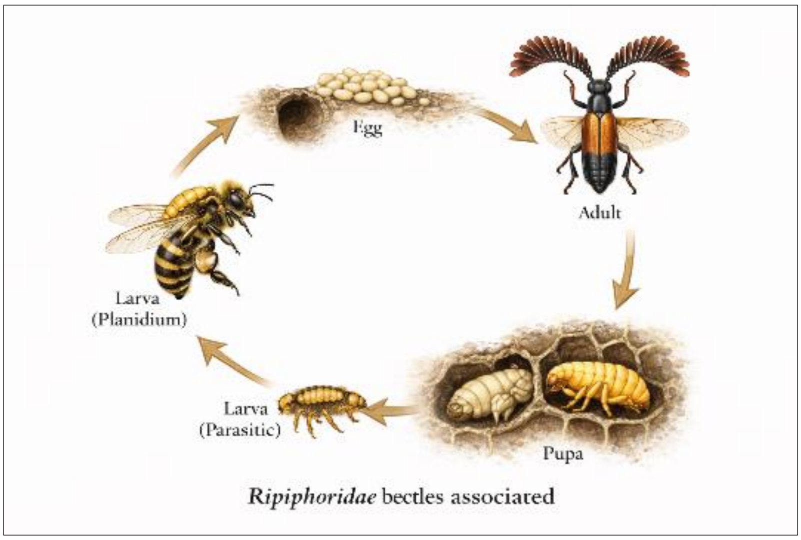

Figure 8: Illustrates the life cycle of Ripiphoridae beetles associated with bees, progressing through egg, larva, pupa, and adult stages. The diagram shows the parasitoid larva (planidium) attaching to a bee, developing within its larva, and pupating inside the nest cell. This figure highlights the unique parasitic adaptation and complete metamorphosis characteristic of the family

The larvae go through a first phase called planidium, in which they have the necessary mobility to search for a host, which is very different from the other phases of development. In Rhipiceridae, females lay eggs in soil habitats where cicadas occur. After hatching, planidia actively search for cicada nymphs underground. Upon finding a host, they penetrate the cuticle and establish themselves as internal parasitoids. Development is completed within the host, which ultimately dies before the adult beetle emerges (Batelka, 2009; Ruiz, 2010; Owens *et al.,* 2014)

The species that attack wasps and bees generally lay eggs in flowers, from which small larvae hatch almost immediately, waiting for one of them to land. At this point, they take the opportunity to cling to the visitor to move to the host's nest. The larva then enters the body of the Hymenoptera larva and waits until it enters the pupa stage to begin consuming it and completing its development at the cost of the host's life (Arnett *et al*., 2002; Batelka, 2009; Barreda, 2015). Worldwide and throughout much of NA (Holanda), more diverse towards the south; in our area, *Ripiphorus* and *Macrosiagon* are widespread, and *Pelecotoma* sp. throughout NE (Niger). Parasitize bees/wasps (Ripiphorinae), wood-boring beetle larvae Pelecotominae, and cockroaches (Ripidiinae) (Figure 9) (Tomlin and Miller, 1989; Batelka and Hoehn, 2007; Bouchard *et al.,* 2011; Rittner and Dafny, 2018).

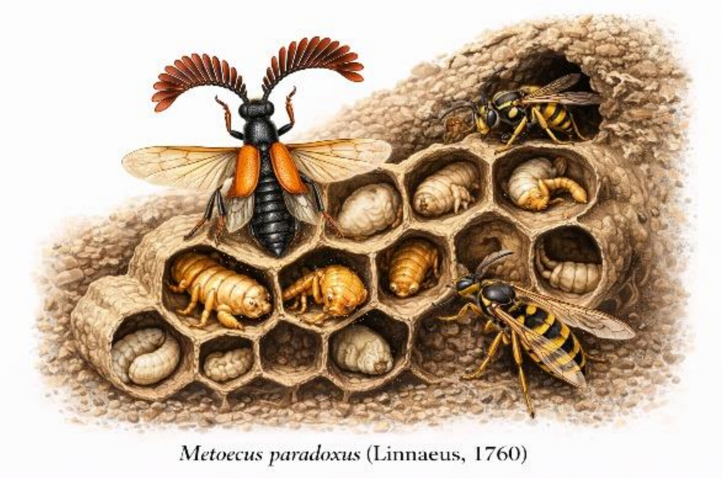

Figure 9: *Sandalus niger* Knoch, 1801 (Coleoptera: Rhipiceridae). Adult specimen in dorsal view illustrating the characteristic body morphology of the species. Adapted from Lawrence (1995a), Lawrence (1995b), and Lawrence *et al.,* (2010); illustration by Hastings

The beetle is between 6 and 10 millimeters long in the male and 10 and 13 millimeters in the female. In Dark brown or greyish color, with a fine, dense, and short, light pubescence that covers it practically in its entirety, giving it a velvety appearance. Brown tones can be lighter or darker, uniform or with lighter colored elytra. The male's antennae draw attention, with the nine distal ears presenting an anterior extension that unfolds in a fan shape, making it resemble a deer's antler (Batelka and Hoehn, 2000; Ruiz, 2007; Batelka and Hájek, 2009; Ruiz, 2010). The first of these extensions in the third section of the base is 5 to 6 times shorter than the next. The pronotum widens behind and ends with a pronounced angle on each side; It is 1.4 times wider than it is long, and its lateral edge is slightly concave (Figure 10) (University of Wisconsin, 2012; Batelka *et al.,* 2022).

Figure 10: Adult specimen of *Ptilophorus dufourii* (Latreille, 1817) (Coleoptera: Ripiphoridae) in dorsal view, highlighting the general body morphology, including the elongated body, flabellate antennae, and the distinctive coloration pattern of the elytra characteristic of the species

The species seems to be linked to arid lands with little vegetation cover, but other areas are recorded in areas with trees: pine forests, pine-kermes oak forests, and holm oak forests, so a gap in the knowledge of the habits of this species is evident. With a spring-like appearance and diurnal habits, the males fly low above the ground. It has been cited as a pollinator in a Spanish orchid that also lives in the Southeast Regional Park: *Ophrys lutea* Cav., 1793 (Orchidaceae), the "yellow bee". Wide distribution that colonizes southern and central Europe, and northern Africa (Maghreb); to the southeast, it reaches Turkey, Israel, Jordan, Iran, and to the east, southern Russia, Armenia, and the Caucasus. In Spain, it is known from all of Catalonia and Aragon, La Rioja, Castilla, León, Murcia, the Valencian Community, Madrid, Castilla-La Mancha, Extremadura, and Andalusia. It also lives in Portugal and Spain (Figure 11) (Ruiz, 2007; Batelka and Hájek, 2009; Ruiz, 2010; Barreda, 2015; Batelka *et al.,* 2022).

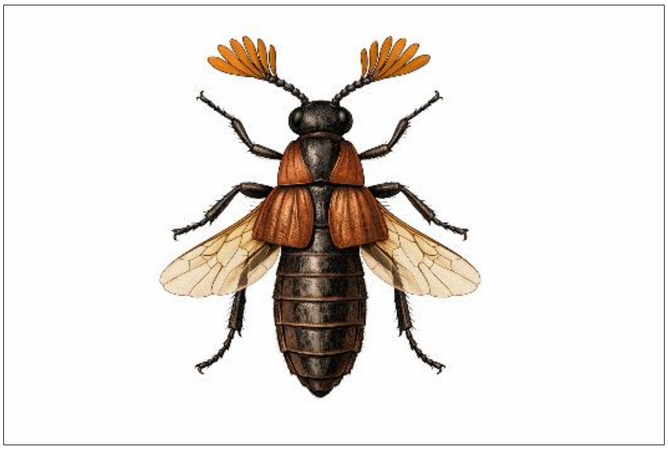

Figure 11: Adult specimen of *Ripiphorus fasciatus* (Say, 1824) (Coleoptera: Ripiphoridae) showing the general body morphology from a dorsal view. The illustration highlights the characteristic wedge-shaped body, reduced elytra, membranous hind wings, and the distinctive flabellate antennae typical of males in the family Ripiphoridae

It is a highly unusual lifestyle for a beetle; most practitioners are flies or wasps. Their hosts are ground-nesting bee larvae, with each beetle species targeting certain bee genera. Hosts of *Ripiphorus fasciatus* (Say, 1824), include several species of burrowing bees and sweat bees. Females oviposit on flowers as soon as the buds begin to open. They can lay five to fifteen eggs in a single flower. Females of *Ripiphorus smithii* Snellen, 1896, have produced up to 850 eggs (Batelka and Hájek, 2009). Flowers open eggs to hatch once pollinators begin visiting, and planidium/stage beetle larvae stand upright on flowers to intercept their ancestral hosts. Larvae are somewhat armored, and although some have claws or suckers on their feet that allow them to latch onto visiting bees and ride with them to their underground nests, they have their jaws to grab a bee (Figure 12) (Peck and Thomas, 1998; Gordh and Headrick, 2003; Majka *et al.,* 2006; Batelka *et al.,* 2022).

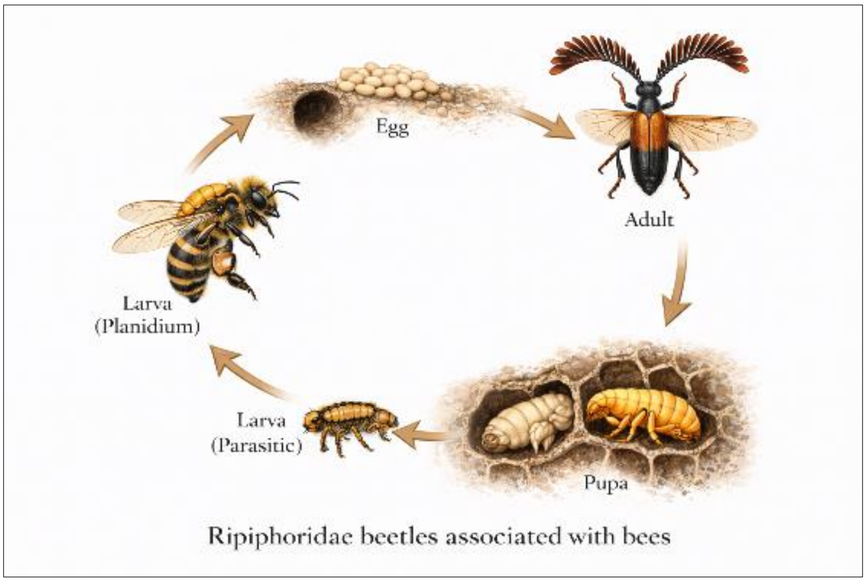

Figure 12: illustrates the life cycle of Ripiphoridae beetles associated with bees, progressing through egg, larva, pupa, and adult stages. The diagram shows the parasitoid larva (planidium) attaching to a bee, developing within its larva, and pupating inside the nest cell. This figure highlights the unique parasitic adaptation and complete metamorphosis characteristic of the family

The larvae enter one of the bee's egg chambers and wait until the bee has finished storing pollen and nectar for its young. She lays an egg and closes the chamber, sealing the Ripiphoridae larva. When the bee larvae hatch, the triungulin penetrates the host and feeds on its endoparasitoid. The *Ripiphorus* Bosc, 1791, larva is still in its first instar but begins to do real damage the following spring as the bee prepares to pupate. It leaves the host's body and starts feeding from the outside as an ectoparasitoid, molting five times, and then turns into a pupa within the cell when the bee is consumed. She emerges as an adult and leaves the bee tunnel (Owens *et al.,* 2014; Iskandarova *et al.,* 2024).

1.0 *Macrosiagon ferruginea* (Fabricius, 1775)

The examined specimens present tarsomeres banded with black and orange-yellow, as seems to be usual in European and African populations, unlike those in Asia and Arabia that present a completely black chromatic pattern on their tarsals, a character without taxonomic value *M. ferruginea* has a wide distribution in the Western World, which extends across southern Europe, Asia including Japan, North Africa, and sub-Saharan Africa (which beaches South Africa), reaching India in the eastern region (Sáez-Bolaño and López-Colón, 2006; Batelka, 2007a; Batelka and Hoehn, 2007b; Ruiz, 2007).

The samples studied were found on inflorescences of *Mentha* sp. (Family Lamiaceae), in the light of a small alcornocal *Quercus suber* L., ascribed to the association *Myrto communis-Quercetum suberis* Barbero, Quézel & Rivas Mart. 198, which alternates with xeric serial vegetation typical of the stages of plant degradation and forest formation. In its preimaginal stages, *M. ferruginea* parasitized solitary birds of the subfamily Eumeninae (Hymenoptera: Vespidae), with its development in *Euodynerus variegatus* (Fabricius, 1793). In this sense, it is worth noting that along with the specimens reviewed, numerous Eumeninae Hymenoptera were observed in inflorescences of *Mentha* sp. (Figure 13) (Falin *et al.,* 2000; Batelka, 2007; Ruiz, 2007; Batelka and Hájek, 2009).

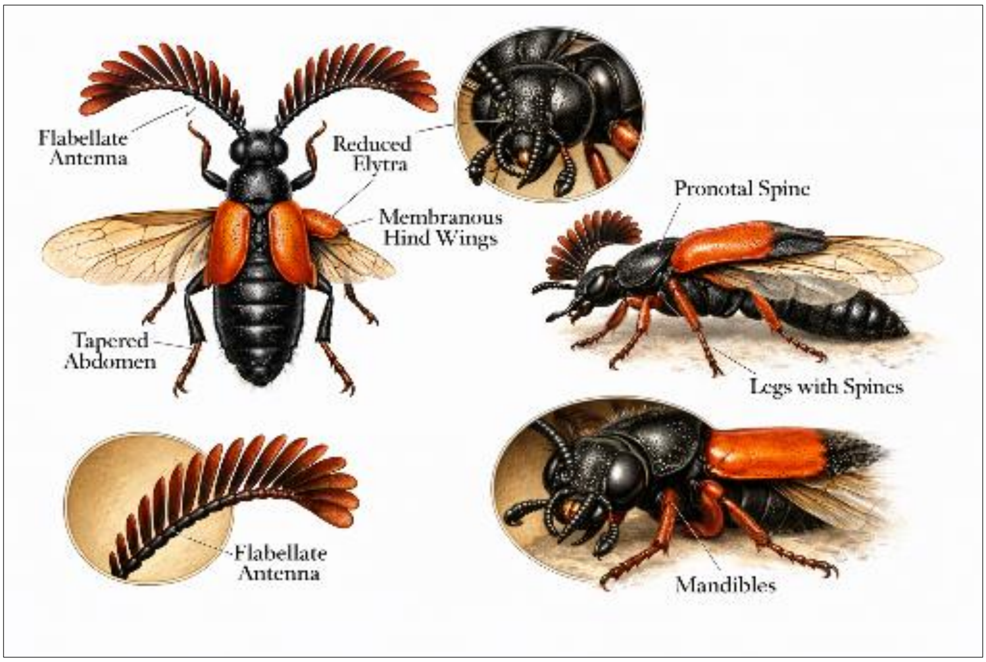

Figure 13: Detailed morphology of *Macrosiagon ferruginea* (Fabricius, 1775) (Coleoptera: Ripiphoridae). Dorsal and lateral views with detail of antenna and head structures. Diagnostic morphological characters typical of the genus *Macrosiagon* are indicated

2.0. *Ripiphorus Subdipterus* Bosc d'Antic, 1792

It is the only representative of the genus *Ripiphorus* Bosc, 1792, present in Europe. This species is characterized by having very short elytra. The head and prothorax are black, the testicles are yellow, and the abdomen has a variable color, from yellow to black, passing through intermediate tones. The antennas are also very variable in color, with the same tones as the abdomen. Yellow paws with dark femurs. Head with abundant and cut pubescence. Size variable between 5 and 10 mm (Figure 14) (López-Colón, 2000; Beltrán and Beltrán, 2001; Seral and Beltrán, 2008).

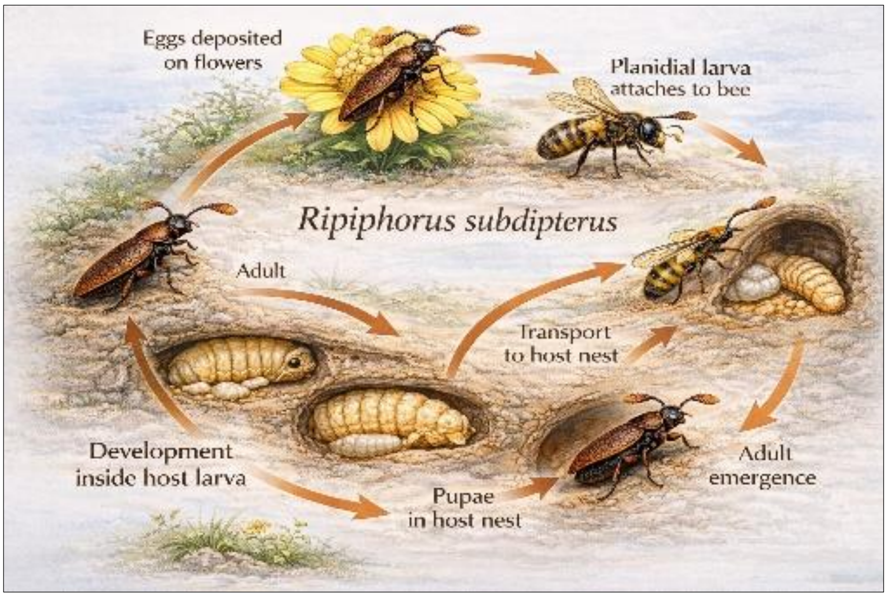

Figure 14: Life cycle of *Ripiphorus subdipterus* Bosc d'Antic, 1792, (Coleoptera: Ripiphoridae), a parasitoid beetle associated with bee hosts. Eggs are deposited on flowers, where the planidial larva attaches to a visiting bee and is transported to the host nest. Larval development occurs inside the host larva, followed by pupation and adult emergence

It is located in southern Europe, Turkey, Syria, part of the Middle East, the Caucasus, and the southern zone of the former Soviet Union. In the Iberian Peninsula, most of the records are located in the northeast zone, east and center, often by isolated specimens, and the rest in the south. Cuni on August 11, 2007, flying over inflorescences of *Eryngium* sp. (Apiaceae). Which represents the first record of the species for the province of Cuenca. Ripiphorus is rarely found in nature because its immature stages occur mainly within the larvae of their hosts, and its adult free-living stage is very short, 1-2 days. Its secret life cycle makes it very difficult to assess its economic and ecological impact. Additional research is necessary to determine the abundance and effects of Ripiphorus species (Figures 15-16) (López-Colón, 2000; Beltrán and Beltrán, 2001; Ruiz, 2007; Seral and Beltrán, 2008; Ruiz, 2010; Owens *et al.,* 2014).

Figure 15: Parasitoid–host interactions in beetles of the families Rhipiceridae and Ripiphoridae (Coleoptera). (A) A larva of Rhipiceridae parasitizing a cicada nymph in a subterranean environment. (B) A larva of Ripiphoridae developing within a bee brood cell, associated with a bee host. The figure illustrates the contrasting host associations and developmental environments characteristic of these two parasitoid beetle families

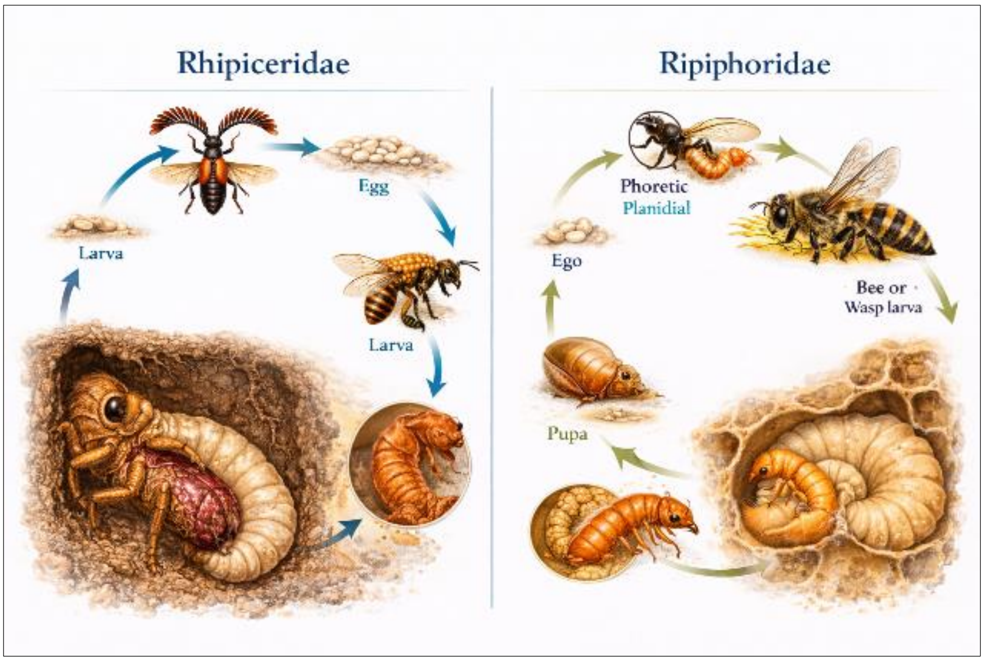

Figura 16: Comparative life cycles of parasitoid beetles from the families *Rhipiceridae* and *Ripiphoridae* (Coleoptera). Rhipiceridae parasitize cicada nymphs in subterranean environments, whereas Ripiphoridae parasitize bees or wasps through phoretic planidial larvae. The diagram highlights differences in host association and developmental strategies between the two families

The interaction between rhipicerids and cicadas is straightforward: the beetle larva kills its host, thereby acting as a population regulator. In ripiphorids, however, interactions are more complex. By parasitizing bees and wasps, they can indirectly affect pollination networks and the reproductive success of plants. Some species exhibit host specificity, while others are generalists, attacking multiple host taxa. This flexibility demonstrates their ecological role in shaping community dynamics (Table 2) (Pinto, 2009).

Table 2: Parasitoids from Rhipiceridae and Ripiphoridae exhibit complex life cycles characterized by hypermetamorphosis, with active triungulin larvae and later inactive stages. Their development is closely linked to specific hosts, often involving concealed phases within the host environment. These adaptations ensure survival, dispersal, and synchronization with host availability

Feature	**Rhipiceridae (Cicada Beetles)**	**Ripiphoridae (Wedge-Shaped Beetles)**
Egg deposition	Soil near cicada habitats	Vegetation near flowers frequented by bees
First instar	Planidial, actively searching in soil	Planidial, phoretic, attaches to adults
Host entry	Penetrates the cicada nymph underground	Carried to nest via adult host
Development	Internal parasitoid kills cicada nymph	Consumes larva or provisions in the brood cell
Adult emergence	From soil, nocturnal, short-lived	From nests, diurnal in many species
Feature	Rhipiceridae (Cicada Beetles)	Ripiphoridae (Wedge-Shaped Beetles)
Egg deposition	Soil near cicada habitats	Vegetation near flowers frequented by bees
First instar	Planidial, actively searching in soil	Planidial, phoretic, attaches to adults
Host entry	Penetrates the cicada nymph underground	Carried to nest via adult host

Chemical communication plays an important role in host–parasitoid interactions and reproductive behavior in many insects. Although the chemical ecology of parasitoid beetles is still poorly studied, available evidence indicates that members of the families Rhipiceridae and Ripiphoridae are associated with specific chemical substances or chemical strategies. In Ripiphoridae, chemical integration into host nests has been clearly demonstrated. The species *Metoecus paradoxus* (Linnaeus, 1761) (Coleoptera: Ripiphoridae), a social parasite of vespid wasps, exhibits a Cuticular Hydrocarbon (CHC) profile closely resembling that of its host, *Vespula vulgaris* (Linnaeus, 1758) (Hymenoptera: Vespidae). This chemical resemblance reduces host aggression and facilitates survival within the wasp nest. The shared compounds include linear alkanes, methyl-branched alkanes, and alkenes, which are key components of nestmate recognition systems in social Hymenoptera (Table 3) (Ranse *et al.,* 2007; Barbero *et al.,* 2009).

Table 3: Chemical substances associated with Rhipiceridae and Ripiphoridae. This table summarizes the types of chemical substances reported or inferred for these parasitoid beetle families, their chemical nature, and their proposed biological functions in host–parasitoid interactions and reproductive behavior

Family	Species / Genus	Type of substance	Chemical nature	Biological function	Reference
Ripiphoridae	*Metoecus paradoxus* (Linnaeus, 1761)	Cuticular hydrocarbons (CHCs)	Linear alkanes, methyl-alkanes, alkenes	Chemical mimicry and integration into wasp nests	Barbero *et al.,* 2009
Rhipiceridae	*Rhipicera* spp.	Volatile odor cues (putative pheromones)	Not chemically identified	Mate location and long-range olfactory detection	Ramsey *et al.,* 2007
Rhipiceridae	Cicada nymphs	Endoparasitoid development	South America	Subterranean soils	Regulation of cicada populations
Ripiphoridae	Solitary bees	Larval parasitism	Europe	Floral habitats	Influence on pollinator communities
Ripiphoridae	Wasps	Brood parasitism	Mediterranean region	Dry habitats	Trophic interaction
Rhipiceridae	Cicadas	Hypermetamorphosis life cycle	North America	Forest soils	Evolutionary specialization
Ripiphoridae	Bees	Phoretic larval behavior	Asia	Flowering ecosystems	Host dispersal strategy
Ripiphoridae	Wood-boring beetles	Larval parasitism	Asia	Forest ecosystems	Community regulation
Rhipiceridae	Cicada nymphs	Endoparasitoid stage	Africa	Soil habitats	Host population control
Ripiphoridae	Wasps	Nest parasitism	North Africa	Shrublands	Biodiversity interaction
Ripiphoridae	Bees	Parasitoid development	Eurasia	Meadows	Pollinator interaction
Rhipiceridae	Cicadas	Internal larval development	Oceania	Subterranean habitats	Ecological balance

In contrast, for Rhipiceridae, direct identification of specific chemical compounds remains limited. However, males of the genus *Rhipicera* possess highly specialized flabellate antennae that are structurally adapted for capturing airborne molecules. Morphological and functional studies suggest that these antennal structures enhance the detection of female-associated odors, likely pheromonal in nature, although the chemical identity of these substances has not yet been characterized. Together, these findings indicate that Ripiphoridae rely on chemically mediated host integration through cuticular hydrocarbons, whereas Rhipiceridae likely depend on olfactory cues related to mate location. The scarcity of identified compounds highlights a major knowledge gap and emphasizes the need for future studies combining chemical analyses with behavioral and ecological approaches (Ranse *et al.,* 2007; Barbero *et al.,* 2009).

The independent emergence of parasitoids in both families illustrates convergent evolution. Hymenoptera and Coleoptera diverged over 250 million years ago, yet both developed parasitoid lineages. The functional parallels, such as planidial larvae, host manipulation, and synchronization with host life cycles, demonstrate similar selective pressures driving similar solutions. This makes rhipicerids and ripiphorids prime examples for studying host-parasitoid coevolution and insect diversification. Ecological roles and host (Pinto 2009; Barreda 2015; Kumar *et al.,* 2021).

Both families exhibit morphological and behavioral traits that evolved independently yet share striking similarities. The presence of highly mobile planidial larvae, synchronized host emergence, and specialized mouthparts suggests convergent evolution toward parasitic life cycles. Fossil evidence suggests that parasitic behavior among beetles dates back to the Cretaceous period, revealing the deep evolutionary roots of host exploitation in the Coleoptera. Molecular phylogenetic studies using mitochondrial genomes confirmed the monophyly of Ripiphoridae and its close relationship with Rhipiceridae, despite their independent evolutionary origins (Figure 17) (Pinto 2009; Barreda 2015; Kumar *et al.,* 2021).

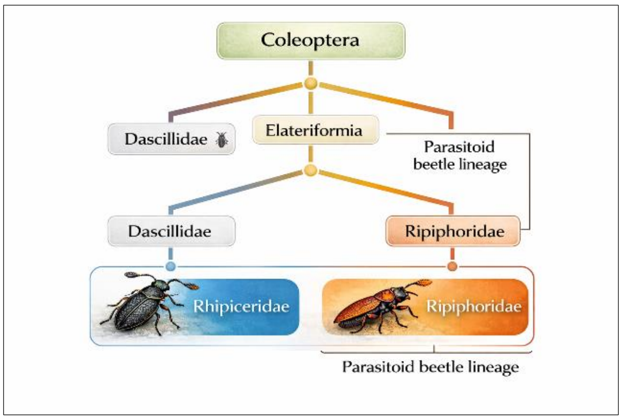

Figure 17: Presents a simplified phylogenetic tree showing the evolutionary relationships among beetle families within the order Coleoptera. The diagram highlights the close relationship between Rhipiceridae and Ripiphoridae, with Dascillidae represented as a related lineage. This figure summarizes the evolutionary context and taxonomic placement of both parasitoid families

Ecologically, Rhipiceridae contribute to controlling cicada populations, whereas Ripiphoridae influence pollinator dynamics, indirectly affecting plant reproduction. Together, they demonstrate the profound impact of parasitoid beetles on ecosystem equilibrium and biodiversity maintenance. The biological and ecological patterns observed in Rhipiceridae and Ripiphoridae highlight an exceptional example of convergent evolution in parasitic beetles. Although both families belong to distinct lineages within Coleoptera, their life cycles reveal similar adaptive strategies for efficiently exploiting hosts. These parallels, including the evolution of planidial larvae, endoparasitic development, and synchronized emergence with host species, demonstrate repeated evolutionary solutions to similar ecological pressures (Petrovic *et al.,* 2020; Hassan *et al.,* 2021; Almeida and Rodrigues, 2022).

In Rhipiceridae, the parasitism of cicada nymphs represents one of the most specialized forms of endoparasitism among beetles. The life cycle of *S. niger* from egg deposition in the soil to larval penetration of the cicada host illustrates precise temporal and behavioral synchronization with its host's life history. The morphological simplification of the larval appendages, the development of a sclerotized terminal abdomen, and the capacity to survive within the host's body reflect adaptations that maximize survival and minimize detection (Tomlin and Miller, 1989; Nikitsky, 1998a; Kathirithamby, 2017).

Conversely, Ripiphoridae show broader ecological versatility and more complex behavioral strategies. Their life cycles involve hypermetamorphosis, a phenomenon also seen in Strepsiptera and certain Hymenoptera, suggesting that this adaptation evolved multiple times among insect parasitoids. The triungulin larva, characterized by its mobility and phoretic behavior, enables efficient host transfer and colonization. Such mobility is critical for parasitism of solitary bees and wasps, which nest in concealed locations (Tomlin and Miller, 1989; Nikitsky, 1998b; Kathirithamby, 2017).

The dual ecological role of Ripiphoridae, both parasitoids and incidental pollinators, adds another dimension to their biological importance. Adults of *P. dufourii* and *M. ferruginea* frequently visit flowers, contributing to pollen transfer even as their larvae parasitize Hymenoptera. This paradoxical relationship illustrates how parasitism and mutualism can coexist within the same lineage, depending on life stage and ecological context. From an evolutionary perspective, fossil and molecular evidence indicate that both families diverged early in Coleopteran history but developed parasitic strategies independently. Genetic studies using mitochondrial genomes reveal homologous regulatory pathways associated with larval mobility and host detection, supporting the hypothesis of functional convergence rather than shared ancestry (Table 4) (Kumar *et al.,* 2021; Wu *et al.,* 2023; Nikishin, 2025).

Table 4: Taxonomy and phylogenetic relationships remain unresolved for several genera; host ranges and degrees of host specificity are poorly documented. Early larval biology and hypermetamorphosis are rarely observed; life-history parameters (fecundity, mortality, diapause) lack standardized estimates

Family	Knowledge gap	Research priority
Rhipiceridae	Immature stages are poorly known	Larval descriptions, life cycle studies
Rhipiceridae	Phylogenetic relationships uncertain	Molecular phylogenetics
Ripiphoridae	Host specificity unclear	Ecological network analysis
Ripiphoridae	Effects on pollinator populations	Long-term population monitoring
Rhipiceridae	Host identification poorly documented	Host association studies and field surveys
Ripiphoridae	Early larval biology is rarely observed	Experimental studies on planidial behavior

Family	Knowledge gap	Research priority
Ripiphoridae	Limited molecular data available	Genomic and phylogenomic analyses
Rhipiceridae	Geographical distribution incompletely known	Biogeographic surveys and taxonomic revisions
Ripiphoridae	Impact on pollinator communities is poorly quantified	Population ecology and conservation studies

The ecological implications of these beetles extend beyond individual host relationships. Rhipiceridae act as natural regulators of cicada populations, preventing outbreaks that can damage vegetation. Meanwhile, Ripiphoridae influence pollinator networks by altering the population structure of bees and wasps, indirectly affecting plant reproductive success. Their presence, therefore, can serve as an indicator of ecosystem health and the balance of biodiversity. Despite these insights, major knowledge gaps persist. Data on immature stages, host specificity, and population dynamics remain limited, particularly in tropical regions where diversity is highest. Integrative studies combining morphology, molecular phylogenetics, and ecological modeling are urgently needed to clarify host associations and evolutionary pathways. Expanding sampling efforts and employing advanced genomic and imaging techniques will be critical to fill these gaps and refine the taxonomy of these enigmatic beetle families (Tomlin and Miller, 1989; Nikitsky, 1998a; Kathirithamby, 2017; Petrovic *et al.,* 2020; Hassan *et al.,* 2021; Almeida and Rodrigues, 2022).

Despite their importance, both families remain poorly studied. In Rhipiceridae, the biology of immature stages is almost completely unknown, and molecular data are scarce. In Ripiphoridae, host specificity, ecological impacts on pollinator networks, and phylogenetic relationships remain unclear. Modern techniques such as DNA barcoding, molecular phylogenies, and ecological modeling are urgently needed to clarify these aspects. Such research could also reveal undescribed biodiversity, particularly in the tropics (Figure 18) (Costa *et al.,* 2009; Pinto, 2009).

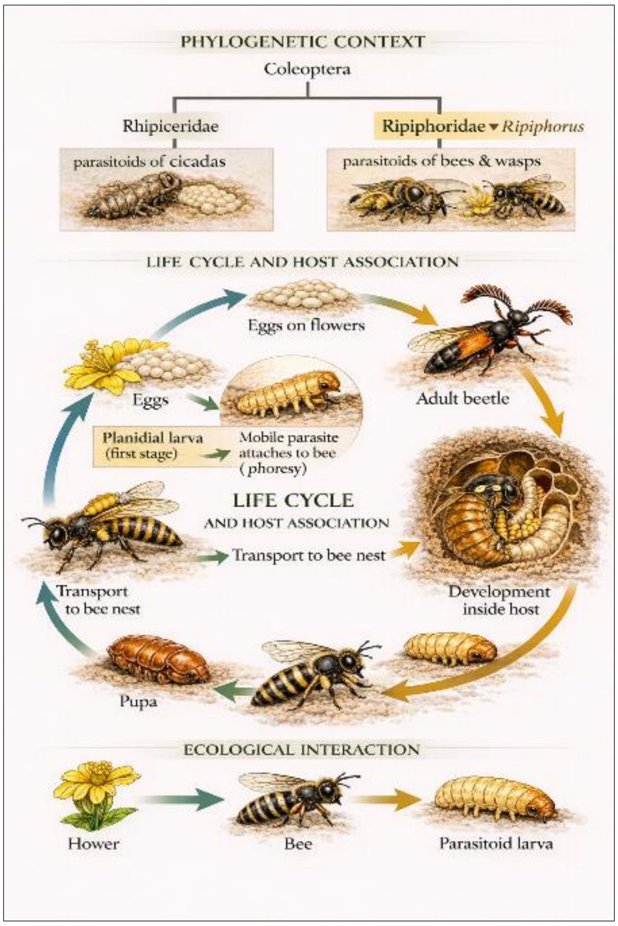

Figure 18: Conceptual overview of the biology and evolutionary context of Ripiphoridae beetles, highlighting *Ripiphorus subdipterus*. The diagram summarizes the parasitoid life cycle, including egg deposition on flowers, planidial larval attachment to bee hosts, development within the host nest, and adult emergence, together with the phylogenetic placement of Ripiphoridae within Coleoptera

4.0. CONCLUSION

This review highlights the remarkable biological diversity and evolutionary convergence of the Rhipiceridae and Ripiphoridae (Coleoptera). Although both families are rare and poorly represented in collections, they demonstrate extraordinary adaptations to parasitism, including hypermetamorphosis, host synchronization, and morphological specialization for host invasion. Rhipiceridae species, such as *S. niger* and *A. larclausei*, act as endoparasitoids of cicadas, functioning as natural biocontrol agents within their ecosystems. Ripiphoridae, including *R. fasciatus*, *P. dufourii*, and *M. ferruginea*, display more complex ecological interactions by parasitizing bees and wasps while participating in pollination networks.

The comparative evidence suggests that parasitism within Coleoptera has evolved multiple times under similar ecological pressures, demonstrating a profound case of evolutionary convergence between unrelated lineages. Their study not only enriches our understanding of insect evolution but also underscores the intricate connections between parasitism, biodiversity, and ecosystem function. Future research integrating molecular biology, behavioral ecology, and environmental monitoring will be essential to deepen knowledge about these families.

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