

Research article

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The mimicry complex of the acrobat ant *Crematogaster scutellaris* in Tunisia: *Colobopsis imitans* and *Mimocoris rugicollis* (Hymenoptera: Formicidae; Heteroptera: Miridae)

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Abstract

The ant *Crematogaster scutellaris*, distributed across the western Mediterranean region and east to the west Balkans, is a visual mimicry model for various other organisms, including different other species of ants. It is an ecologically and behaviorally dominant species, foraging through large permanent trails that workers pugnaciously defend by biting and spraying a toxic secretion. Here we report on two interesting novelties discovered by monitoring *Cr. scutellaris* foraging trails in Tunisia: first, we present the first records of the mimicking ant *Colobopsis imitans* in the country, filling a distribution gap and confirming a previous biogeographic hypothesis; second, we identified the mirid *Mimocoris rugicollis*, whose brachypterous females are known as myrmecomorphs, as a mimic of *Cr. scutellaris*. Both *Co. imitans* and *M. rugicollis* were observed following or stationing near *Cr. scutellaris* trails, often in the presence of another mimicking ant, *Camponotus lateralis*. Still little is known about the ecology and behavior of most *Cr. scutellaris* mimics, with some species still undescribed. Further research is needed to investigate the evolutionary pressures shaping this adaptation.

Key words: Batesian mimicry, Formicidae, Miridae, Maghreb.

Ants have a pervasive ecological impact in terrestrial habitats, which also takes effect in the evolutionary pressure they apply to the trophic networks they are part of, leading to a wide range of evolutionary adaptations in other organisms (Parker & Kronauer 2020). Ant communities tend to have a hierarchical structure, and behaviorally and ecologically dominant species exert a disproportionately stronger impact on other organisms due to their numerosity, aggressiveness, and territoriality (Hölldobler & Wilson 1990; Lach et al. 2010). As such, they often become a model in complex visual mimicry systems that may involve a variety of other organisms: recurrent myrmecomorphs include spiders, beetles, and true bugs, but also subordinate ant species with small colonies and lesser defensive abilities; most behave as Batesian mimics with a few aggressive mimicry examples also reported and Müllerian mimicry normally considered unlikely (Schifani et al. 2022a).

Known ant-mimicking ants are located sparsely across the phylogeny of Formicidae (Emery 1886; Forel 1886; Santschi 1919; Gobin et al. 1998; Merrill & Elgar 2000; Ito et al. 2004; Ward 2009; Gallego-Ropero & Feitosa 2014; Powell et al. 2014; Pekár et al. 2017; Rasoamanana et al. 2017; Seifert 2019; Schifani et al. 2022a; Pérez-Delgado & Wagner 2024). However, there is a recurrent evolution of mimicking relationships involving dominant myrmicine ants of the genus *Crematogaster* as models, and formicine ants from the genera *Camponotus* and *Colobopsis* (of the Camponotini tribe) as mimics (Ito et al. 2004; Schifani et al. 2022a; Pérez-Delgado & Wagner 2024). In these cases, interactions between mimics and their models are also often characterized by trail-sharing or trail-following: model species tend to form permanent, well-defended foraging trails that the mimics exploit to hide or find resources with or without the consent of the model workers (Emery 1886;

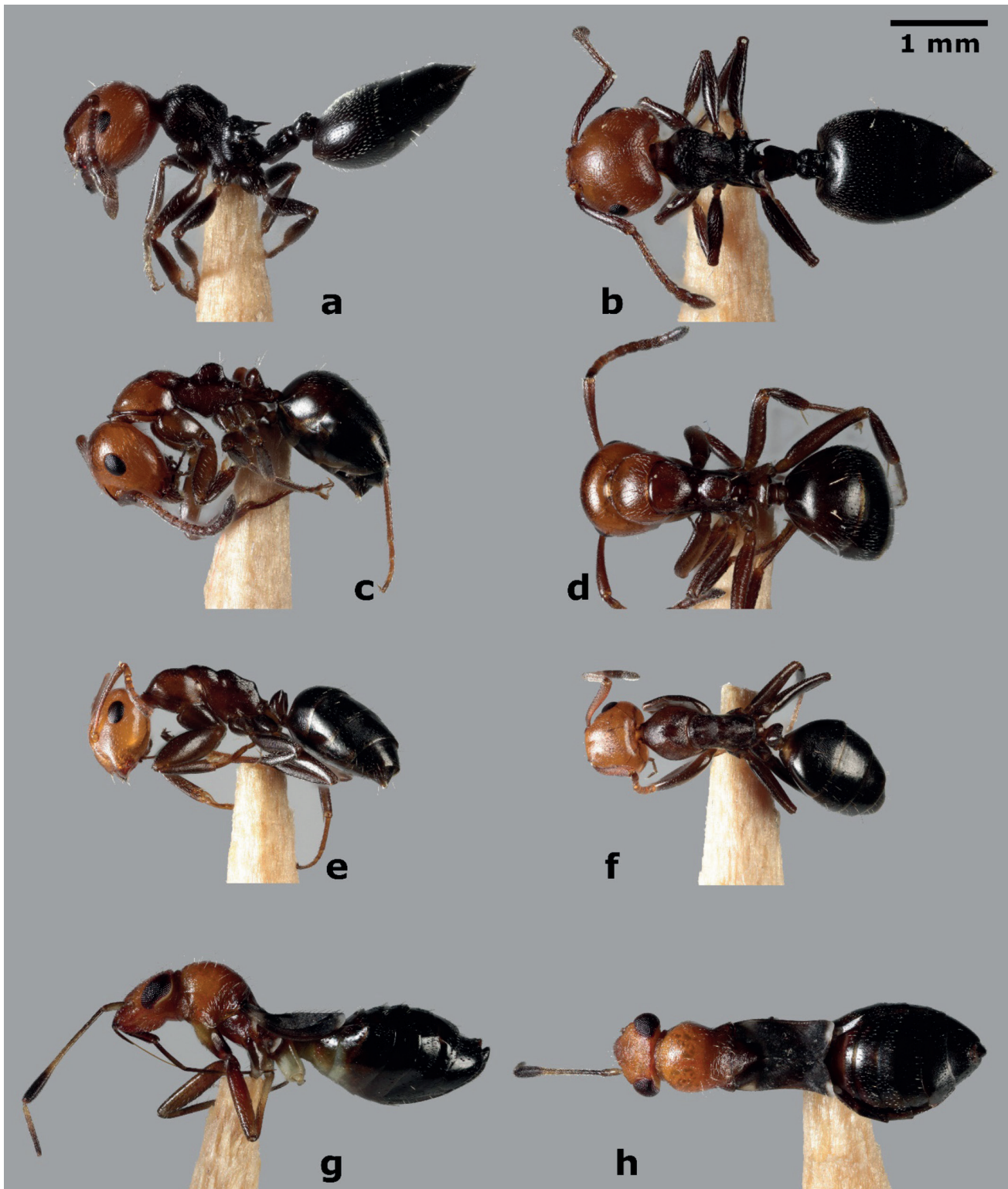


Fig. 1 – A worker of the dominant ant *Crematogaster scutellaris* (a, b) and its three mimics collected on a corn oak (*Quercus suber*) at Cap Serrat, Tunisia: workers of the ants *Camponotus lateralis* (c, d) and *Colobopsis imitans* (e, f), and the adult female of the mirid bug *Mimocoris rugicollis* (g, h).

Santschi 1919; Gobin et al. 1998; Ito et al. 2004; Menzel et al. 2010; Powell et al. 2014; Schifani et al. 2022a; Pérez-Delgado & Wagner 2024). In the western Palearctic, the *Crematogaster scutellaris* (Olivier, 1792) group is

the model for ant species combining visual mimicry with trail-following in at least three cases: *Camponotus lateralis* (Olivier, 1792), which is a mimic of *Cr. scutellaris*, *Cr. schmidti* (Mayr, 1853), and *Cr. ionia* (Forel, 1911);



Fig. 2 – Verified distribution records of *Colobopsis imitans*. Circles indicate literature data (Schifani et al. 2022), while triangles indicate new points reported in this study. Map from Stadia Maps – stadiamaps.com and Stamen Design – stamen.com.

Camponotus guanchus Santschi, 1908, which is a mimic of *Cr. alluaudi* Emery, 1893; *Colobopsis imitans* Schifani, Giannetti, Csósz, Castellucci, Luchetti, Castracani, Spotti, Mori & Grasso, 2022, which is a mimic of *Cr. scutellaris* (Menzel et al. 2010; Seifert 2019; Schifani et al. 2022a; Pérez-Delgado & Wagner 2024). *Co. imitans* is the recently described sister species of *Co. truncata* (Spinola, 1808), which instead has a mimicry relationship whose model is the dolichoderine ant *Dolichoderus quadripunctatus* (Linnaeus, 1771). It is also possible that *Ca. ruber* Emery, 1925 (closely related to *Ca. guanchus*), so far not observed to perform trail-following, is another mimic of *Cr. scutellaris*, while the non-mimic *Ca. cf. piceus* (Leach, 1825) has been observed to follow *Cr. scutellaris* trails occasionally (Schifani et al. 2022a; Pérez-Delgado & Wagner 2024). *Crematogaster scutellaris* itself is also a visual mimicry model for many non-ant organisms, including spiders and solitary wasps; however, many of these are poorly known, some could be undescribed species and these relationships have never been explored in detail (Schifani et al. 2022a).

By observing mimics associated with *Cr. scutellaris* trails in Tunisia, we discovered two interesting novelties, which are here described in detail: the first record of *Co. imitans* in the country and the first report of the mirid bug *Mimocoris rugicollis* (Costa, 1853) as an ant mimic specifically associated with *Cr. scutellaris*.

Collection of mimics of *Cr. scutellaris* took place by carrying out opportunistic observations of *Cr. scutellaris* trails on trees and hand-collecting specimens during a field expedition in the Tunisian regions of Bizerte, Béja, and Jendouba (28.IV-03.V.2024). All samples were stored in 96% EtOH in the authors' collections. Specimens were identified under a stereoscopic microscope based on Carapezza (1997), Seifert (2019), and Schifani et al. (2022a). Images were taken using a Canon MP-E 65mm f/2.8 1–5x macro lens and the software Helicon Focus.

Colobopsis imitans was collected in Cap Serrat (Bizerte, 37.206650, 9.232127, 3 m asl, on *Quercus suber* L. trees near coastal dunes and a temporary freshwater pond, 29.IV.2024) and in Ain Draham (Jendouba, 36.728755, 8.678518, 760 m asl, on *Q. suber* trees in a mixed oak forest with *Q. canariensis* Wild., 01.V.2024), in both cases along *Cr. scutellaris* trails (Fig. 1,2). Adult females of *M. rugicollis* were collected in the same first site of Cap Serrat, two individuals being spotted on the same tree and near the same *Cr. scutellaris* trail as *Co. imitans* (Fig. 1). In both sites, we also collected *Ca. lateralis* on the same trees, while the non-mimic *Ca. cf. spissinodis* Forel, 1909 was observed to follow *Cr. scutellaris* trails in Cap Serrat.

The Tunisian ant fauna, as well as the diversity of ant-associated organisms in the country still deserve great faunistic and taxonomic efforts. The Maghreb region in North Africa hosts a remarkable proportion of rare ant species within the global diversity hotspot represented by the Mediterranean (Kass et al. 2022), yet many of them await a modern taxonomic revision and distribution data are still more limited as compared to other Mediterranean regions (Guénard et al. 2017). The discovery of *Colobopsis imitans* in Tunisia confirms the biogeographic hypothesis by Schifani et al. (2022a) who predicted it to occur continuously from Sicily west to Algeria, Morocco, and southern Iberia, but without being able to study Tunisian specimens. *Colobopsis truncata* had been previously reported in Tunisia by Forel (1890) and Santschi (1929), but these records should most likely be attributed to *Co. imitans* instead (Schifani et al. 2022a). The biogeographically closest area where *Co. truncata* is found is represented by Sardinia and no sympatric occurrence of the two species has yet been discovered in the eastern range (Schifani et al. 2022a). During our surveys, we have also collected *Ca. ruber*, but it was not observed in association with *Cr. scutellaris* trails.

Mimocoris rugicollis was first recorded in Tunisia by Carapezza (1997). Despite being considered an ant mimic, before the present report of *Cr. scutellaris*, no model ant species had been clearly identified. Only Horvath (1923), who described the Corsican *M. formosus* Horvath, 1923 (later recognized as a junior synonym of *M. rugicollis*) said females were collected with the ant *Aphaenogaster spinosa* Emery, 1878. We cannot rule out a degree of behavioral plasticity in *M. rugicollis* and an association with multiple ants: *Aphaenogaster sardoa* group species (mostly similar and widespread in the Mediterranean – Schifani et al. 2022b) do not climb trees nor form foraging trails and may occur in habitats without trees or bushes where *Cr. scutellaris* cannot. However, *A. spinosa*, like almost all species of the group, is entirely black, while instead *Mimocoris formosus* was described as bicolored, black with a reddish head, consistent with our finding of a visual resemblance of *Cr. scutellaris* (Horvath 1923). The wide diversity of *Cr. scutellaris* mimics is remarkable and still awaits further exploration. Schifani et al. (2022a) discovered putative cases of mimicry in *Gelis* sp. (Hymenoptera, Ichneumonidae), *Leptorchestes* sp. (Araneae, Salticidae), and *Phrurolithus* sp. (Araneae, Phrurolithidae) – some of them possibly representing undescribed species. *Mimocoris rugicollis* represents the first Hemipteran mimic of *Cr. scutellaris* to be discovered and belongs to the Miridae subfamily Philinae that hosts several ant mimics across the world (e.g., Carvalho & Gross 1982; McIver & Stonedahl 1987). In this species, ant mimicry seems to represent a defensive mechanism exclusive of adult females, which are brachypterous in contrast to the macropterous males fully capable of flying. A similar case has recently been uncovered, with two Canarian endemic mirid bugs of the genus *Perenotus* being identified as mimics of *Cr. alluaudi* (Pérez-Delgado & Wagner 2024).

Over the last few years, *Cr. scutellaris* has attracted a growing attention due to its impactful ecological role in agricultural and forest habitats (e.g., Castracani et al. 2017; Giannetti et al. 2019; 2021; 2022; Frizzi et al. 2020; Schifani et al. 2023a,b,c; Smargiassi et al. 2023). However, for all the mimics associated with it and its trails (whose pheromone has been recently characterized by Scarano et al. 2024), there is still a substantial absence of field data or experimental evidence indicating which ones are the predatory taxa against which mimicry may play an important role and which ones are ecologically important enough to have exerted a significant evolutionary pressure for the success of these adaptations (Schifani et al. 2022a).

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