Is mimicry a diversification-driver in ants? Biogeography, ecology, ethology, genetics and morphology define a second West-Palaearctic Colobopsis species (Hymenoptera: Formicidae)

Mimicry as a diversification driver in ants? Biogeography, ecology, ethology, genetics, and morphology define a second West-Palearctic *Colobopsis* species (Hymenoptera: Formicidae)

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ABSTRACT

The West-Palearctic *Colobopsis* ant populations have long been considered a single species (*Colobopsis truncata*). We studied the diversity of this species by employing a multidisciplinary approach and combining data from our surveys, museum and private collections, and citizen science platforms. As a result, we have revealed the existence of a second species, which we describe as *Colobopsis imitans* sp. nov., distributed allopatrically from *C. truncata* and living in the Maghreb, Sicily and Southern Iberia. While the pigmentation of *C. truncata* is reminiscent of *Dolichoderus quadripunctatus*, that of *C. imitans* sp. nov. is very similar to *Crematogaster scutellaris*, with which *C. imitans* sp. nov. lives in close spatial association, and whose foraging trails it habitually follows, similarly to *Camponotus lateralis* and other ant-mimicking ants. The isolation between *C. imitans* sp. nov. and *C. truncata* seems to have occured relatively recently because of the significant, yet not extreme morphometric differentiation, and to mtDNA polyphyly. Both *C. imitans* sp. nov. and *C. truncata* appear to employ mimicry of an unpalatable or aggressive ant species as an important defensive strategy; this 'choice' of a different model species is motivated by biogeographic reasons and appears to act as a critical evolutionary driver of their diversification.

ADDITIONAL KEYWORDS: ADAPTATION – BATESIAN MIMICRY – COI MTDNA – DISCRIMINANT-FUNCTION ANALYSIS – MEDITERRANEAN – MULTIVARIATE STATISTICS – NORTH AFRICA – SIBLING SPECIES – SPECIATION.

INTRODUCTION

Ants (Insecta: Formicidae) are a hyperdiverse group of organisms which counts about 13,860 species (Bolton, 2021) and is extraordinarily successful in most terrestrial ecosystems (Hölldobler & Wilson, 1990; Gibb *et al.*, 2017; Seifert, 2017). Such high diversification stems from several evolutionary strategies and lifestyles, and enables even hundreds of different ant species to coexist in the same habitat (Hölldobler & Wilson, 1990; 2008). However, only one or very few dominant species generally characterize even the most species-rich ant communities: these species form very populous colonies, with large, often permanent foraging trails, and they defend territories that may extend over hectares (Hölldobler & Wilson, 1990; Andersen, 1995; 1997; Grasso *et al.*, 1998; 1999; 2005; Arnan *et al.*, 2018). These ants are exposed to higher predation risk compared the ones whose workers forage solitarily or in small groups, and are accordingly equipped with effective defensive mechanisms (Buschinger & Maschwitz, 1984; Hölldobler & Wilson, 1990; Dornhaus & Powell, 2010; Seifert, 2018). Most ant species live in small colonies and forage solitarily or in small groups, only occasionally form trails, and develop evasive anti-predatory strategies (e.g. Hölldobler & Wilson, 1990; Tautz et *al.*, 1994; Andersen, 1995; Dornhaus & Powell, 2010; Helms *et al.*, 2014; Larabee & Suarez, 2015; Seifert, 2018; Grasso *et al.*, 2020). Of the species that live in small colonies, the only ones armed with dangerous defences are some predatory ants which retain the primitive feature of a powerful functional stinger to hunt (Buschinger & Maschwitz, 1984; Hölldobler & Wilson, 1990; Dornhaus & Powell, 2010).

Well-armed ant species, in particular the ones that build large colonies, are a very good model for several mimicking organisms, mostly arthropods. Some of these mimics are myrmecophilous organisms: commonly ant predators or parasites, they have adapted to live within or close to ant colonies by relying on chemical or acoustic mimicry (e.g. Geiselhardt *et al.*, 2007; Barbero *et al.*, 2009; Cushing, 2012; Parker & Grimaldi, 2014; Parker, 2016; Scarparo *et al.*, 2019). On the other hand, myrmecomorph species resemble their ant model thanks to morphological and/or behavioural adaptations (e.g. Komatsu 1961; Jackson & Drummond, 1974; Oliveira & Sazima, 1984; Oliveira 1988; Cobben, 1986; McIver, 1987; McIver & Stonedahl, 1993; Trjapitzin & Trjapitzin, 1995; Cassis & Wall, 2010; Chandler, 2010; Durkee *et al.*, 2011; Huang *et al.*, 2011; Cushing, 2012; Pekár, 2014; Corcobado *et al.*, 2016; Pekár *et al.*, 2017; Harvey *et al.*, 2018; de L. Nascimento & Perger, 2018; Gnezdilov, 2019). The main aim of myrmecomorphism is predation avoidance: compared to the mimics, models usually possess superior defensive mechanisms and are also more numerous. As such, they are usually interpreted as Batesian mimics (e.g. Jackson & Drummond, 1974; McIver, 1987; Durkee *et al.*, 2011; Huang *et al.*, 2011; Cushing, 2012; Harvey *et al.*, 2018), whose evolution can be favoured by model abundance (Kikuchi & Pfenning, 2010).

Many ant mimics are ants themselves. Some are parasites (e.g. inquilines) that act similarly to myrmecophilous organisms (Buschinger, 2009), relying on chemical adaptations to interact with the host species. However, there are some free-living ant species that act as mimics of more aggressive or dominant ant species and are therefore interpreted as Batesian mimics. Nonetheless, solid empirical evidence to reject the alternative hypothesis of Müllerian mimicry (see Müller, 1879; Pasteur, 1982; Ritland, 1991) is rarely available (Ito *et al*., 2004; Wagner, 2014). In these species, chromatic mimicry is the prevalent mechanism, while behavioural or morphological adaptations are more rarely documented (Emery, 1886; Forel, 1886; Santschi, 1919; Gobin *et al.*, 1998; Merril & 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, 2019a). In addition, recurrent behaviour among mimicking ant species is interspecific trail-following, which consists in the mimics regularly infiltrating into the foraging trails of the model and may lead to parasitic behaviour with regard to food resources (Emery, 1886; Santschi, 1919; Gobin *et al.*, 1998; Ito *et al.*, 2004; Menzel *et al.*, 2010; Powell *et al.*, 2014). Unlike specialized parasites (e.g. Visicchio *et al.*, 2001; Buschinger, 2009; de la Mora *et al.*, 2020), no advanced mechanisms of chemical deception exist in most of these cases, so in the eventuality of direct encounters the model species recognizes and attacks the mimic, which however is well-equipped to escape (Goetsch, 1942; 1951; Kaudewitz, 1955; Gobin *et al.*, 1998; Ito *et al.*, 2004; Menzel *et al.*, 2010). The vast majority of the hitherto well-documented cases come from the tropics: mimics mainly belong to diverse lineages from the Formicinae tribe Camponotini (mostly *Camponotus* Mayr, 1861), while their models are phylogenetically scattered, including Ectatomminae, Myrmeciinae, Myrmicinae (Crematogastrini and Stenammini) and Pseudomyrmecinae. Only one case of ant-mimicking ant species is well-documented in the West-Palearctic zone, i.e. *Camponotus lateralis* (Olivier, 1792). It chromatically mimics the similar *Crematogaster* species *Cr. ionia* Forel, 1911, *Cr. scutellaris* (Olivier, 1792) and *Cr. schmidti* (Mayr, 1853), and follows their trails (Emery, 1886; Baroni Urbani, 1969; Menzel *et al.*, 2010; Wagner, 2014; Seifert, 2018; 2019a). The three species are closely related with neighbouring geographic ranges and differ slightly chromatically (Blaimer, 2012). Interestingly, there seems to be a geographic trend in the chromatic pattern of *Ca. lateralis*, allowing it to better resemble these three *Crematogaster* species in the regions of sympatric occurrence (Wagner, 2014; Seifert, 2019a).

The ant genus *Colobopsis* Mayr, 1861 (Formicinae: Camponotini), recently separated from *Camponotus* (Ward *et al.*, 2016), currently counts 95 valid species and 21 subspecies (Bolton, 2021). It is distributed across the Holarctic, Indomalayan and Australasian regions, and is most diversified in the latter two regions (Janicki *et al.*, 2016; Guénard *et al.*, 2017). *Colobopsis* species are usually arboreal ants that nest in dead wood, form small-sized colonies and behave timidly towards other ants

(Wheeler, 1904; Ward *et al.*, 2016). In the Western-Palearctic region, *Colobopsis truncata* (Spinola, 1808) is the only recognized species of its genus. The queen caste was described by Spinola (1808) from north-western Italy (Liguria region), while the other castes were described later (Dufour & Perris, 1840; Forel, 1874; Emery, 1916). Another species, *Co. fuscipes* (Mayr, 1853) was described from Austria by Mayr (1853), but was later reclassified as a junior synonym of *Co. truncata* (Emery & Forel, 1879). *Colobopsis truncata* is therefore considered to have a wide geographic distribution, from the Caucasus to Iberia and from Central Europe to the Maghreb (Seifert, 2018; Janicki *et al.*, 2016; Guénard *et al.*, 2017). It is an arboreal-nesting species, as is typical of the genus, and it preferably nests on broadleaved trees, where it lives in monogynous and often polydomous colonies, rarely exceeding 500 workers (Seifert, 2018). Queens and soldiers are specialized for phragmosis, and soldiers may also function as repletes (living containers of liquid food), seldom leaving the safety of the nests they guard (Brun 1924; Goetsch, 1950; 1953; Seifert, 2018). Minor workers are usually active outside the nest during both day and night, forage solitarily, do not recruit nest mates to food sources, and perform very quick evasive movements when encountering other ants (Seifert, 2018).

During field observations across Italy we encountered marked divergences between *Colobopsis* colonies: workers of some colonies resembled *Cr. scutellaris* and followed its trails, while others resembled *Dolichoderus quadripunctatus* (Linnaeus, 1771), two species having remarkably different appearance. This is reflected by several contradictory reports which however contain no comment on these incongruences. Forel (1874) first referred to Swiss ants by considering *Co. truncata* a Batesian mimic of *D. quadripunctatus*. He later suggested that the two species show pre-adaptations to parabiotic nest-sharing (Forel, 1903). Zimmermann (1934) instead studied ants in Croatia and considered the occasional relationship between *Co. truncata* and *Cr. scutellaris* similar to the one between *Ca. lateralis* and *Cr. scutellaris*. Goetsch (1942) stated that in Spain *Co. truncata* behaves similarly to *Ca. lateralis,* following the trails of *Cr. scutellaris,* , yet is also chromatically very different and shows no adaptation to mimicry. Baroni Urbani (1971) reported on a case of trail-following between a *Co. truncata* queen and a *Cr. scutellaris* trail from central Italy. More recently, Tinaut (1991) claimed that in southern Iberia *Co. truncata* can be easily confused with *D. quadripunctatus* during field surveys due to their similarity. However, working in the same area, Carpintero et al. (2001; 2005) instead affirmed that *Co. truncata* is a visual mimic of *Cr. scutellaris* and follows its trails, and even speculated that after nuptial flights *Co. truncata* queens specifically choose trees occupied by *Cr. scutellaris* to found their colony. In reviewing the distribution of *Colobopsis* in Iberia, García (2020) mentioned possible chromatic similarity of *C. truncata* with *Cr. scutellaris* and its mimic *Ca. lateralis*, but also *D. quadripunctatus.* More recently, there have been reports on trail-following by *Co. truncata* on *Cr. scutellaris* ants in Italy (mentioned by Seifert 2018, no locality specified; Lake Garda according to Wagner HC, personal communication). Wagner (2019) described a close association between *Co. truncata* and *D. quadripunctatus* in Austria (Vienna), highlighted morphological and chromatic similarity between the two, and reported trail-following of *D. quadripunctatus* trails by *Co. truncata*.

We aimed to test whether the abovementioned diversity of traits represented intraspecific variation or indicated the existence of multiple *Colobopsis* species in the West-Palearctic. In order to address the different biological dimensions of this problem, we used a multidisciplinary approach which involves the description of the patterns of diversity within the traditional notion of *Co. truncata*. We relied on the principles of integrative taxonomy (Schlick-Steiner *et al.*, 2010), involving morphological, genetic, ecological, ethological and biogeographical data.

MATERIALS AND METHODS

We combined qualitative morphology through chromatic pattern evaluation, quantitative morphology through the multivariate analysis of morphometric data and genetics in the form of mtDNA (COI) sequencing, ecological surveys to study the association between *Colobopsis* and its putative model species and recorded ethological data to document cross-species trail following. Finally, we compared our results with the known biogeographic patterns of other ant species. We chose this quantitative morphological approach as it is widely regarded as the most practical and reliable single source of evidence for cryptic ant species delimitation, and as a cornerstone in integrative approaches on cryptic species complexes of ants (Seifert, 2009; 2018; Seifert *et al.*, 2014; Wagner *et al.*, 2017; Steiner *et al.*, 2011; 2018; Csősz *et al.*, 2020). Moreover, mtDNA sequencing represents a widespread and cost-effective method to gain preliminary information on species identification, biogeography and cryptic speciation (Hebert *et al.*, 2003; 2016; Ratnasingham & Hebert, 2007), which has developed into an aid to myrmecological faunistic, biogeographic and taxonomic studies (Steiner *et al.*, 2005; 2018; Csősz *et al.*, 2015; Seifert *et al.*, 2017; Schär *et al.*, 2018; 2020; Blatrix *et al.*, 2020). Ecological data on species associations and ethological data are rarely used in ant taxonomy but appear to be highly relevant to the specific case we are investigating, while biogeography is important to understand species diversity.

For our morphological and molecular analyses, we gathered type material of *Co. truncata* and *Co. fuscipes* as well as additional non-type material of *Colobopsis* from the Mediterranean region, and relied on our own efforts and the generous contribution of colleagues to achieve a satisfactory geographic coverage. In particular, the type series of *Co. truncata* consists in a single queen with the label "*Polyergus* (?) | *F.ca truncata* | Spin. in Ligur. | Genova || 6571". This queen could be safely identified as the type since it is the sole *Colobopsis* queen in the Spinola collection at the Museo di

Scienze Naturali in Turin (Italy), and matched the description given by the author (Spinola, 1808). Concerning *Co. fuscipes*, at least two syntypes are stored in the Museum für Naturkunde, University of Berlin (Germany), and their pictures are available on AntWeb (AntWeb.org, codes FOCOL2496 and FOCOL2497): these are labelled "Oesterreich | Coll. Rhd || *Colobopsis fuscipes* Mayr || Type || 29812 || GBIF-D/FoCol | 2496 | specimen + label | data documented" and "Oesterreich | Coll. Rhd || *Colobopsis fuscipes* Mayr || Type || GBIF-D/FoCol | 2497 | specimen + label | data documented". Although the label is unlikely to be an original by Gustav Mayr (B. Seifert, pers. comm.), we deem their status as types credible. We also retrieved a worker labelled *Co. fuscipes* in Mayr's collection at the Natural History Museum of Vienna, but with no explicit indication ensuring its type status. In order to gather information on chromatic variation of Euro-Mediterranean *Colobopsis*, we relied on AntWeb pictures, images from scientific papers or monographs (Glaser, 2009; Wagner, 2014; 2019; Lebas *et al.*, 2016; Seifert, 2018; Scupola, 2018; García, 2020; Salata *et al.*, 2020; Tăușan *et al.* 2020), and on georeferenced photographs uploaded on citizen science platforms (iNaturalist.org, biodiversidadvirtual.org) and on biodiversity-related Facebook groups. A complete list of the material examined, their depositories and collecting data is available as a Supplementary Material file to this paper. Ecological and behavioural data were obtained through field surveys across Italy.

PIGMENTATION: CHROMATIC MIMICRY

Preliminary observations highlighted that chromatic pattern provides the most evident difference between allopatric *Colobopsis* populations which resemble two different model ant species in Italy. We preemptively described the two chromatic forms and investigated whether these were consistently able to represent *Colobopsis* diversity across the Mediterranean basin, and whether they occurred intracolonially or sympatrically, and also checked for the possible existence of third forms. The two *Colobopsis* model patterns were pre-emptively established by observing ten workers per each form (10 from Sicily and 10 from mainland Italy), and all subsequent investigations were carried out by inspecting specimens of well-preserved pigmentation primarily belonging to the worker caste. Queens and soldiers were also examined and identified only if closely resembling one worker model pattern, while males were not considered due to their very different pigmentation. Furthermore, to better describe the differences between the two models, a ratio was calculated between head color and mesosoma color by taking dorsal pictures of specimens and calculating the average value of red (RGB colors) between 5 randomly selected pixels of the head and 5 of the mesosoma via software ImageJ (Schneider *et al.*, 2012). Calculating a ratio rather than considering the absolute values greatly reduces the variation produced by different light conditions and camera settings among different pictures, thereby allowing comparison of pictures from various sources. The same ratio was also calculated for the two putative model species *Cr. scutellaris* and *D. quadripunctatus*. Chromatic ratios were calculated on 20 workers per chromatic pattern or species from across their respective geographic range using both directly inspected specimens and images from citizen science platforms. Any differences were statistically tested by using the software R 4.0.3 and R Studio 1.3.1056 (R Core Team, 2021), and employing an ANOVA test and subsequent Tukey Post-hoc test for pairwise comparisons.

The visual examination to verify correspondence to either of the two chromatic models was conducted on 79 directly observed *Colobopsis* colonies (76 of which containing workers) plus images of 136 further specimens (including 76 isolated queens), for a total of 310 workers and 79 queens covering a total of 16 countries from across the W-Palearctic *Colobopsis* distribution (see supplementary material).

The two model patterns are defined as follows:

Cr. scutellaris-like pattern (CSL pattern): head, or head and anterior part of the mesosoma (rarely most of it) uniformly red, rest of the body evidently darker and mostly black. White stripes or dots on the second gastral tergite often absent or weak (present in 10% of the examined workers). See Fig. 1.

D. quadripunctatus-like pattern (DQL pattern): head, mesosoma and appendages from reddish to blackish (therefore chromatically more variable than the *Cr. scutellaris*-like model), head at least slightly darker than the mesosoma or less frequently concolour, gaster black. White stripes or dots on the second gastral tergite often present (80% of examined workers) and more obvious. Phragmotic heads of soldiers or queens are always reddish in their anterior, heavily sculptured part (approximately one half of the head), while the rest follows the same scheme of workers. See Fig. 1.

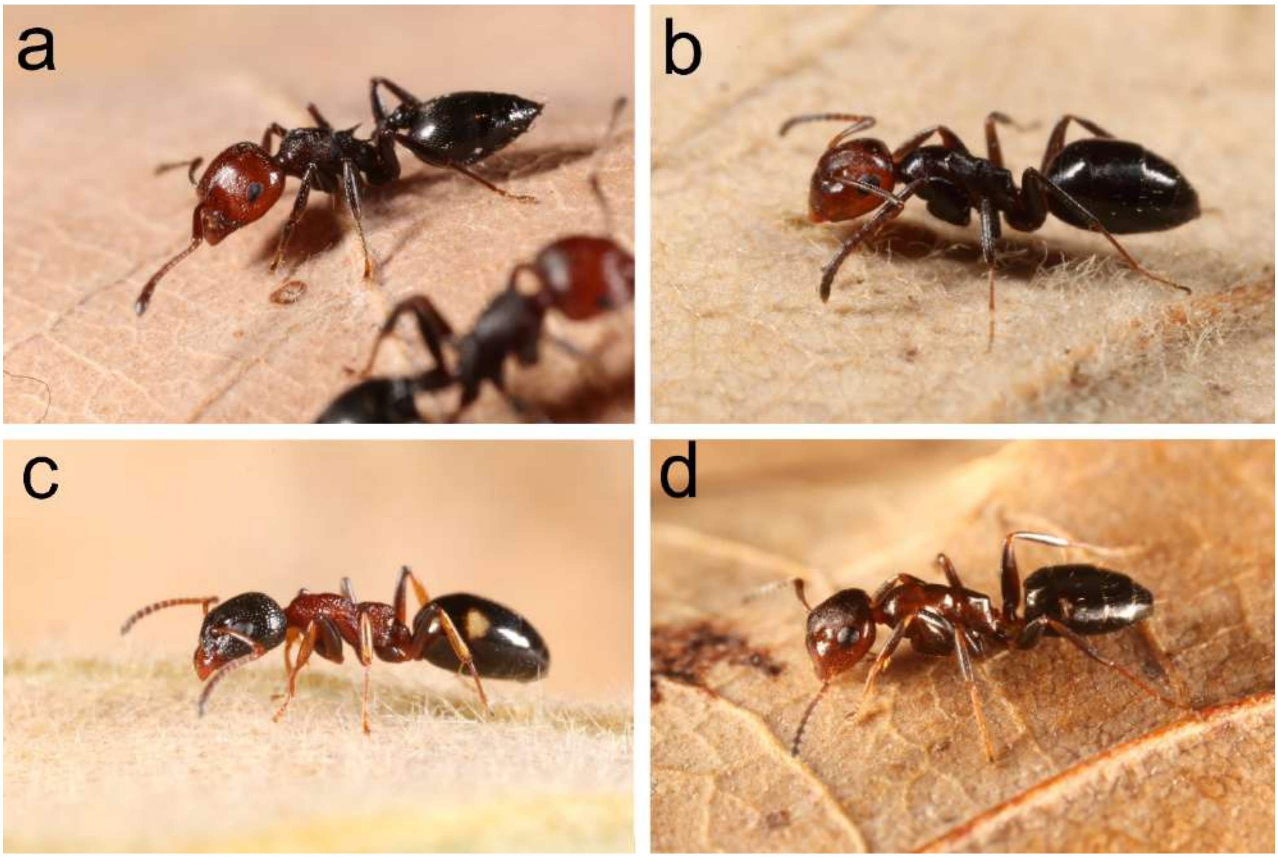

Figure 1. The model species and the two detected chromatic model patterns of *Colobopsis*: a) *Cr. scutellaris*; b) CSL *Colobopsis* from Sicily; c) *D. quadripunctatus* from Tuscany; d) DQL *Colobopsis* from Tuscany.

NUMERIC MORPHOLOGY: MULTIVARIATE ANALYSES OF MORPHOMETRIC DATA

A total of 12 continuous morphometric traits were defined following Seifert (2018) (Tab. 1) and measured on 115 *Colobopsis* workers from 44 nest samples (considering minor workers only, and not the soldiers). All measurements were made in µm by using a pin-holding stage, which allowed rotations around the X, Y, and Z axes. An Olympus SZX9 stereomicroscope was used at x150 magnification for each character; however, with characters larger than the field of view x75 magnification was applied. Due to the low number of the much rarer queens, males and soldiers in our possession, we recorded only a reduced set of 7 morphometric traits aimed at providing a brief description of these castes without using them in the following statistical analyses. Morphometric data are provided in µm throughout the whole paper.

Repeatability of the recorded size parameters were evaluated via Intraclass Correlation Coefficients (ICC) by using Package ICC (Wolak *et al.*, 2012), see Tab. 1. Variables were tested via matrix scatterplots and Pearson product-moment correlation coefficients for error variance and outliers. Each character resulted highly repeatable, except for NOL, which was considered moderately repeatable.

Exploratory analyses through NC-PART clustering

The prior species hypothesis was generated based on workers through combined application of NC clustering (Seifert *et al.*, 2014) and Partitioning Based on Recursive Thresholding (PART) (Nilsen & Lingjaerde, 2013). The script for NC-clustering combined with PART was written in R and can be found in Appendix S1 in Csősz & Fisher (2016). Our exploratory data analysis approach follows the protocol described by Csősz & Fisher (2016) with the following specific settings: bootstrap iterations in PART were set to 'b=1000', and the minimum size of clusters was set to 'minSize=5' for both 'hclust' and 'kmeans'. The optimal number of clusters and the partitioning of samples are accepted as the preliminary species hypothesis in every case in which the two clustering methods, 'hclust' and 'kmeans' through PART, have yielded the same conclusion.

Exploratory analyses via PCA using allometrically corrected data

An alternative prior species hypothesis has been generated via the ordinating Principal Component Analysis (PCA) that searches for discontinuities in continuous morphometric data and display plots in a graphic.

Using raw data (without removal of allometric variance) in PCA may lead to weaker performance in ordination because the first vector of the PCA often describes the size component, which is a useless information when cryptic species of similar size have to be separated, hence, in PCA residuals were used. Residuals, in which the head length (CL) was used as covariate, were calculated via a linear regression model according to the following steps: a) scaling properties, intercept and steepness were calculated for each nest sample separately (note: nest samples constituted by a singleton were not involved in this phase); b) a grand average for steepness and intercept was calculated from scaling properties of each nest sample; c) residuals are calculated for every nest sample (including singletons) based on the grand average. Residuals of every trait calculated against head length (CL) are given (Tab. 1). In contrast to NC-PART clustering, the PCA has no estimation on the number of clusters and "classification" of objects has been made based on subjective decision. The coefficients (x any intercept) for removal allometric variance for each trait are given in supplementary material.

Hypothesis testing by confirmatory analysis

The validity of the prior species hypothesis was tested via Linear Discriminant Analysis (LDA). Classification hypotheses were imposed for all samples that were congruently classified by partitioning methods, while wild-card settings (i.e. no prior hypothesis imposed on its classification) were given to samples that were incongruently classified by the two partitioning methods. Statistical analyses were conducted through the software R 3.6.3 (R Core Team 2021).

Abbr.	Description of the trait	ICC (R)

CL	Maximum median length of head capsule. The head must be carefully tilted so the maximum length is positioned in the measuring plane.	0.982
CW	Maximum head with including compound eyes. The largest distance between profiles of the two compound eyes in full-face view.	0.951
EL	Eye length. Maximum diameter of the compound eye.	0.967
dAN	Minimum distance of the inner margins of antennal socket rings.	0.985
ML	Diagonal length of the alitrunk in profile. Measured in lateral view from the anteriormost point of anterior pronotal slope to the caudalmost point of the lateral metapleural lobe.	0.969
MW	Maximum width of pronotum.	0.989
NOL	Petiole node length; measured in lateral view, from the center of the petiolar spiracle to the posterior profile.	0.890
PeW	Petiole width. The maximum width of petiole in dorsal view.	0.994
PreOC	Preocular distance. Use a cross-scaled ocular micrometer and adjust the head to the measuring position of CL. Frontal measuring point: median clypeal margin; caudal measuring point: reference line between the frontalmost border of the two compound eyes.	0.951
SL	Scape length. The maximum straight-line scape length excluding the articular condyle.	0.971
HTL	Hind tibia length. Measured from the distalmost point of the tibia to the proximal end where the tibia is narrowest in profile.	0.968
PeSH	Petiole scale height measured from the center of petiolar spiracle to top of the crest.	0.959

Table. 1 Abbreviation (Abbr.) of morphometric characters, definition of measurements, and ICC (R) a metric for repeatability parameter are given. Definitions of morphometri characters follow Seifert (2018).

GENETICS: MITOCHONDRIAL COI SEQUENCES

Total genomic DNA was extracted from leg tissues using the NuceloSpin DNA Insect kit (Macherey-Nagel, Düren, Germany), following the manufacturer's protocol. A 700 bp region of mitochondrial gene cytochrome *c* oxidase subunit I (COI) was amplified using the primer couple LCO1490/HCO2198 (Folmer *et al.*, 1994). PCR was carried out in 25 µL reactions using the following profile: initial denaturation step at 95 °C for 5 minutes, 35 amplification cycles (denaturation at 95 °C for 30 seconds, annealing at 52 °C for 30 seconds, elongation at 72 °C for 45 seconds), final elongation at 72 °C for 7 minutes. PCR products were sent to Macrogen Europe (Amsterdam, Netherlands) for Sanger sequencing. Chromatograms were checked and edited using SeqTrace (Stucky, 2012). Sequences were aligned using the MUSCLE (Edgar, 2004) algorithm as implemented in AliView (Larsson, 2014). Model selection and Maximum Likelihood phylogenetic analysis were performed on the IQ-TREE web server (Trifinopoulos *et al.*, 2016) using the Eastern-Palearctic *Co. nipponica* (Wheeler, W.M., 1928) and *Co. shohki* (Terayama, 1999) and the Indomalayan *Colobopsis* nr. *saundersi* (Emery, 1889) (GenBank accession numbers AB019417, AB019418 and KU975365, respectively) as outgroups. Ten separate runs were launched, each with 1000 replicates of ultrafast bootstrap, and the tree with the best likelihood value out of the ten was chosen. Twenty-three colony samples were sequenced, consisting in 41 workers from 6 countries and 18 localities. Obtained sequences have been submitted to Genbank, under accession numbers MW462045–MW462085 (see supplementary material).

ECOLOGY: COEXISTENCE WITH MODEL SPECIES

Field surveys were conducted in the Italian Peninsula (Emilia-Romagna, Tuscany; n sites = 5, DQL pattern) and Sicily (n sites = 8, CSL pattern) to test whether the local *Colobopsis* populations, showing a DQL and a CSL phenotype respectively, actually lived in close proximity with either of the two species indicated as probable mimicry models (see Supplementary material). In each site, we searched for the presence of *Colobopsis* workers on trees until a tree occupied by a *Colobopsis* colony was detected. Then, we performed a 10 minutes-long continuous sampling within a 1.5 m radius of the point of the tree trunk where *Colobopsis* was firstly observed, recording the eventual presence of *Cr. scutellaris* or *D. quadripunctatus* workers.

Occurrences of *Cr. scutellaris* or *D. quadripunctatus* on trees occupied also by *Colobopsis* according to the different DQL and CSL models were statistically tested by using the software IBM SPSS statistics, Italian version 24 and the chi-squared test. All data are presented in the Supplementary Material.

ETHOLOGY: INTERSPECIFIC TRAIL-FOLLOWING BEHAVIOUR

Field surveys were conducted in the Italian Peninsula (Emilia Romagna, Tuscany) and Sicily (sites as in the section before, also see supplementary material) with the aim of quantifying the occurrence of trail-following behaviour performed by *Colobopsis* ants in relation to *Cr. scutellaris* or *D. quadripunctatus* trails. We selected trees where *Colobopsis* colonies coexisted with either *Cr. scutellaris*, *D. quadripunctatus* or both. In accordance with the relevant literature (Gobin *et al.*, 1988; Ito *et al.*, 2004; Menzel *et al.*, 2010; Powell *et al.*, 2014), trail-following was defined as the event of *Colobopsis* workers moving along an established pheromone trail of *Cr. scutellaris* or *D. quadripunctatus* within 1 cm from the trail itself. A 10 minutes continuous sampling was used to record the presence or absence of this behaviour on each of the examined tree.

To study trail-following on *Cr. scutellaris* trails, we selected a total of 59 trees inhabited by this species: 29 trees hosted *Colobopsis* colonies exhibiting the CSL pattern (Sicily, 4 sites) and 30 hosted *Colobopsis* with the DQL pattern (Emilia-Romagna and Tuscany, 5 sites). Observations on *D. quadripunctatus* trails could be performed only in 23 *Colobopsis* colonies exhibiting the DQL pattern (Emilia-Romagna and Tuscany): since no *D. quadripunctatus* colonies could be found in the studied sites in Sicily (where the species is known to be very rare, see Schifani & Alicata, 2018), no

Colobopsis colonies exhibiting the CSL pattern could be tested in this regard. All data are summarized in the supplementary material.

SPECIES CONCEPT

Integration of the evidence provided by different complementary disciplines into an evolutionarily credible species hypothesis is performed according to the principles emphasized by Schlick-Steiner *et al.* (2010), i.e. resolving eventual disagreements by invoking solid evolutionary explanations. Biogeography is here treated as an additional source of information, holding an important advisory role to the formation of the final species-hypothesis. We abide by the universal Gene and Gene Expression (GAGE) species concept proposed by Seifert (2020), which, although recently formulated, convincingly summarizes the main theoretical and practical formulae most commonly adopted during the last few decades as a rigorous approach on alpha taxonomy of cryptic ants, especially in Europe.

RESULTS

PIGMENTATION: CHROMATIC MIMICRY

All the examined colonies are safely assignable to one of the two models and no transitional or third forms are detected (see Supplementary Material). No intracolonial coexistence of the two models is detected either. The type series of both *Co. truncata* and *Co. fuscipes* show the DQL pattern (Fig. 2). The two models occur strictly allopatrically according to the examined material. Samples from the south-western Mediterranean basin, namely Algeria, Sicily (Italy), Morocco, southern Portugal and Andalusia (southern Spain) are assigned to the CSL pattern. All the rest is assigned to the DQL pattern, that is samples from Austria, Bulgaria, Croatia, Czech Republic, France, Germany, Greece, Hungary, Israel, Italian peninsula (Apulia, Campania, Emilia-Romagna, Liguria, Tuscany), Romania, Serbia, Slovenia, Switzerland, the rest of Spain (Aragon, Catalonia, Balearic Islands, Castilla-La Mancha), and Turkey. In addition, photographs of *Co. truncata* specimens present in the European ant fauna guides by Lebas *et al.* (2016) and Seifert (2018), regional faunistic guides by Glaser (2009) (Liechtenstein), Wagner (2014) (Austria's Carinthia), Scupola (2018) (Italy's Veneto) as well as in the Crete's ant fauna monograph by Salata *et al.* (2020) and in the papers by Wagner (2019) (Austria), García (2020) (Spain) and Tăușan *et al.* (2020) (Romania) all show the DQL pattern.

Figure 2. Type material of the so far described West-Palearctic *Colobopsis*, all adhering to the "*D. quadripunctatus*-like" pattern. **a)** holotype queen of *Colobopsis truncata* from Liguria, Italy, preserved at the Turin Natural History Museum (Italy). **b)** syntype worker of *Colobopsis fuscipes* from Austria (picture from AntWeb.org, FOCOL2496; photographer: Christiana Klingenberg), preserved at the Museum für Naturkunde der Humboldt-Universität Berlin (Berlin, Germany). Note that the queen's red color in the anterior heavily sculptured part of the phragmotic head is not relevant to evaluate its chromatic pattern. Scale bars: 0.5 mm.

The head red/mesosoma red ratio is statistically different among the two *Colobopsis* patterns and their models ($F_{3,76} = 152.4$, $p < 0.001$) (also see supplementary material). Pairwise comparisons show no statistically significant difference between CSL *Colobopsis* and *Cr. scutellaris* ($p = 0.817$; mean ± sd = 1.96 ± 0.36 for CSL *Colobopsis*; mean ± sd = 2.05 ± 0.38 for *Cr. scutellaris*) and between DQL *Colobopsis* and *D. quadripunctatus* ($p = 0.299$; mean ± sd = 0.60 ± 0.27 for DQL *Colobopsis*; mean ± sd = 0.43 ± 0.20 for *D. quadripunctatus*), while all other comparisons are significantly different ($p < 0.001$) (Fig. 3).

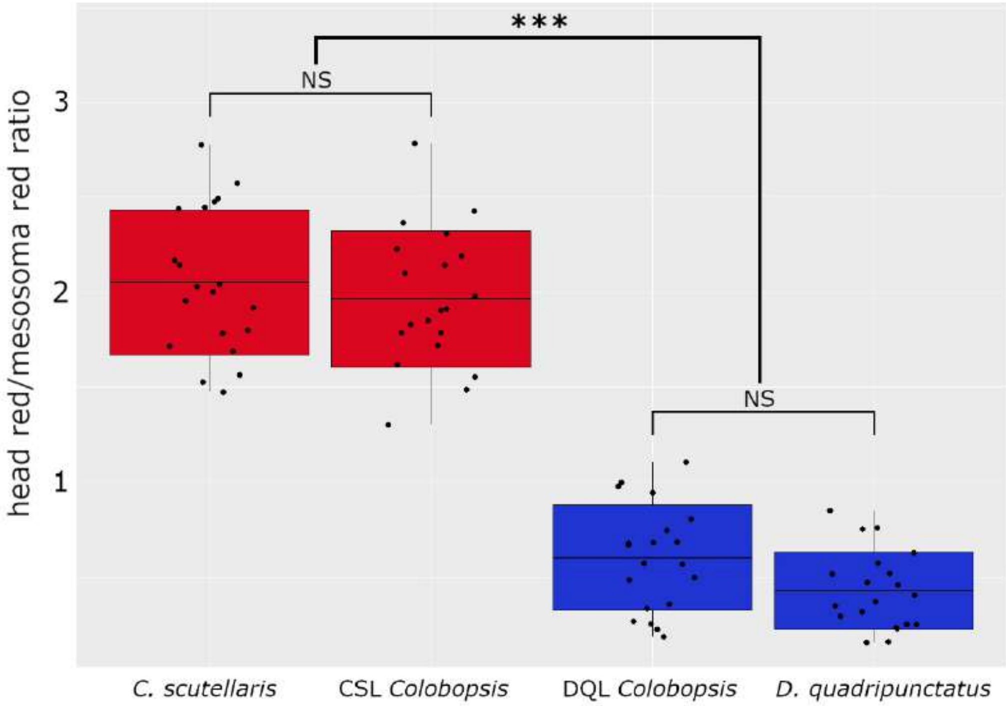

Figure. 3. Chromatic ratios calculated from pictures of the *Colobopsis* CSL and DQL patterns and from pictures of the two putative model species *Cr. scutellaris* and *D. quadripunctatus* (N =2 0 for each species or chromatic form). Boxplots show mean and standard deviation, while whiskers represent minimum and maximum values. Dots are measured individuals. Their dispersal on the x-axis is a randomized graphical effect to avoid overlaps.

NUMERIC MORPHOLOGY: MULTIVARIATE ANALYSES OF MORPHOMETRIC DATA

Two morphological clusters are identified via NC-clustering combined with “kmeans”, and “hclust” (Figs. 4). These two clusters correspond to the CSL pattern and DQL pattern specimens, respectively. All but two samples are congruently classified via both partitioning methods. The two incongruently placed samples (ITA:Mondello-VillaMercadante_col-12, ITA:Mondello-VillaMercadante_col-16; both CSL pattern from Sicily) are classified as belonging to the CSL cluster (posterior p = 0.85 and 0.81, geometric means of 3 workers each). Without running samples as wild-cards, the overall classification success is 96.3% using all variables in the analysis.

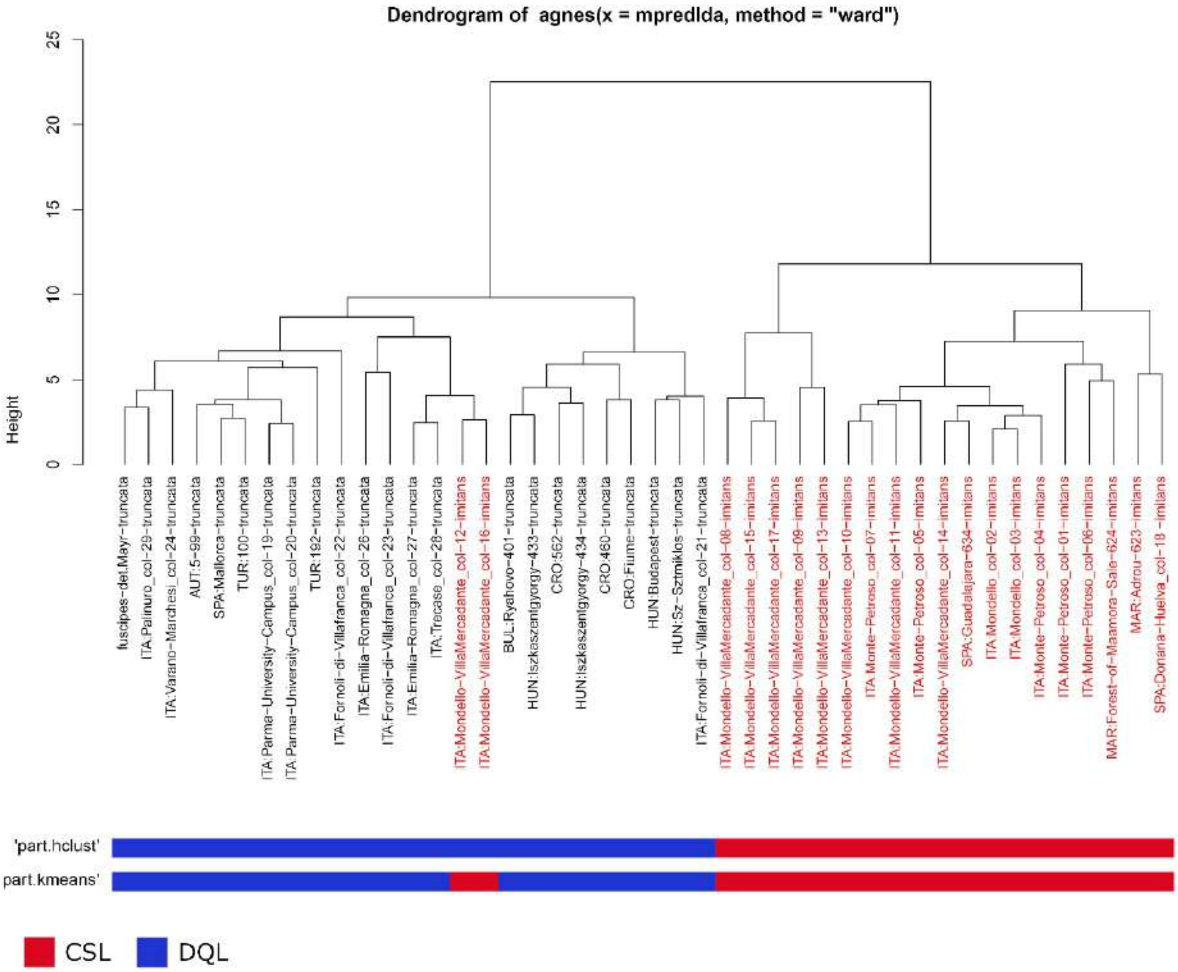

Figure 4. Figure 4. Dendrogram comparing the results of "kmeans", and "hclust" in NC Clustering of Colobopsis morphometric raw data. Two samples (4.5% of the total) are misplaced by both the dendrogram and one of the partitioning analyses, NC-part.kmeans; partially different samples being affected in each of the three analyses. The

other partitioning analysis, NC-part.hclust returned the same sample assignment as the LDA did.

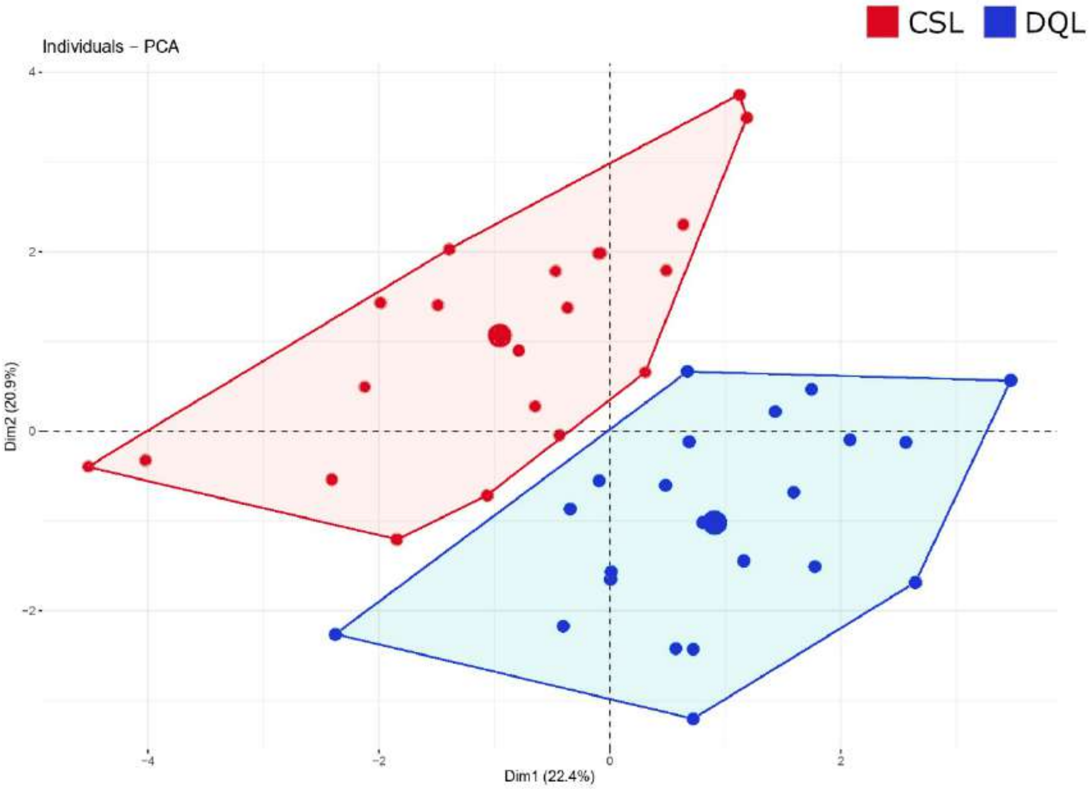

Figure 5. Principal Component Analyses of morphometric data of analyzed *Colobopsis* nest samples according to the two clusters evidenced by NC-PART Clustering. Each small dot represents a colony sample. Large dots represent centroids.

T-tests were calculated to assess significant differences (p) of body size ratios between specimens of the two different clusters, resulting in significant differences for 7 ratios (Tab. 2). Unfortunately, there is not a single numeric body size ratio available for reliable separation of these clusters on individual level (Tab. 2): the most reduced multivariate function that can reach the goal of attaining an acceptably high rate of classification success (>95%) requires a minimum 6 morphometric characters achieved via backward stepwise method.

The most simple D(6) function that yields 4.3% of error rate at the individual level is as follows:

$$D(6) = 0.03501 * CW - 0.03384 * SL - 0.03144 * HTL - 0.01762 * ML + 0.03653 * PeSH + 0.07458 * EL + 16.61469$$

D(6) scores for CSL pattern cluster (n = 55) = mean - 1.59 [- 4.17, + 0.66] ± 1.05

D(6) scores for DQL pattern cluster (n = 60) = mean - 1.54 [- 0.37, + 3.76] ± 0.96

character	CSL (n = 55)	p	DQL (n = 60)
CS	897 ± 51 [725, 1025]	0.924	898 ± 55 [803, 1042]
PreOc/CL	**0.546 ± 0.01** **[0.517, 0.571]**	**0.000**	**0.537 ± 0.01** **[0.517, 0.570]**
CL/CW	1.152 ± 0.02 [1.113, 1.198]	0.052	1.145 ± 0.02 [1.106, 1.189]
dAN/CS	0.387 ± 0.01 [0.345, 0.431]	0.128	0.391 ± 0.02 [0.358, 0.426]
SL/CS	**0.872 ± 0.03** **[0.798, 0.931]**	**0.000**	**0.846 ± 0.02** **[0.798, 0.906]**
MW/CS	0.682 ± 0.02 [0.648, 0.717]	0.476	0.680 ± 0.02 [0.648, 0.723]
PeW/CS	0.332 ± 0.02 [0.268, 0.372]	0.257	0.336 ± 0.02 [0.306, 0.395]
HTL/CS	**0.931 ± 0.02** **[0.888, 0.978]**	**0.000**	**0.902 ± 0.02** **[0.845, 0.957]**
ML/CS	**1.485 ± 0.03** **[1.395, 1.543]**	**0.000**	**1.460 ± 0.02** **[1.410, 1.526]**
NOL/CS	**0.139 ± 0.01** **[0.117, 0.165]**	**0.008**	**0.134 ± 0.01** **[0.112, 0.157]**
PeSH/CS	**0.239 ± 0.02** **[0.193, 0.284]**	**0.000**	**0.253 ± 0.02** **[0.203, 0.293]**
EL/CS	**0.312 ± 0.01** **[0.290, 0.335]**	**0.000**	**0.321 ± 0.01** **[0.304, 0.343]**

Table 2. Mean of morphometric ratios calculated for CSL pattern and DQL pattern clusters based on individuals (raw data). Morphometric traits are divided by cephalic size (CS), namely the arithmetic mean of CL and CW. The upper row in each data field gives arithmetic mean ± standard deviation, the lower one, in square brackets, lower and upper extremes. Significant differences are highlighted in bold.

GENETICS: MITOCHONDRIAL COI SEQUENCES

The Maximum Likelihood phylogenetic analysis on mtDNA COI sequences identifies four main clusters with good nodal support (Fig. 6). The clade A is formed by specimens exhibiting the CSL pattern and collected from Andalusia (Spain) and Morocco. The specimens of the clade B exhibited the DQL pattern and were sampled from Bulgaria, Castilla La Mancha (Spain), Hungary, the Italian

Peninsula, and the Occitanic region of France. The clade C groups specimens with the DQL pattern, sampled in the Spanish regions of Aragona and Catalonia, and from the Balearic Islands. Finally, the clade D is formed by all specimens from Sicily, showing the CSL pattern, and one of the Spanish specimens from Catalonia actually exhibiting the DQL pattern.

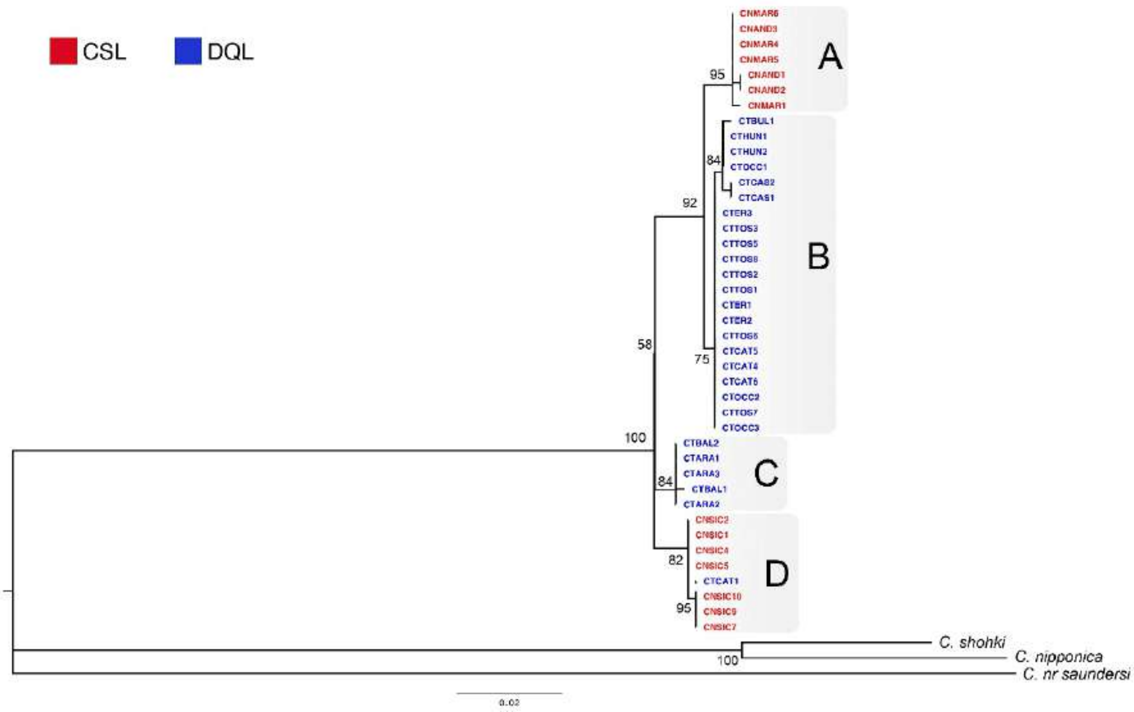

Figure 6. Maximum likelihood phylogenetic tree based on the barcode fragment of the mtCOI gene from the sequenced *Colobopsis* specimens.

ECOLOGY: COEXISTENCE WITH MODEL SPECIES

Crematogaster scutellaris is present in 97% of the investigated trees occupied by CSL *Colobopsis* and in 20% of those occupied by DQL *Colobopsis*, the difference is statistically significant (χ^2_1 = 26.23, $p < 0.001$). *Dolichoderus quadripunctatus* was never detected in trees occupied by CSL *Colobopsis*. On the other hand, *D. quadripunctatus* occurrs on 40% of the investigated trees occupied by DQL *Colobopsis* (6% of which also hosted *Cr. scutellaris*). Results are illustrated in Fig. 7, and detailed data is provided in the supplementary material.

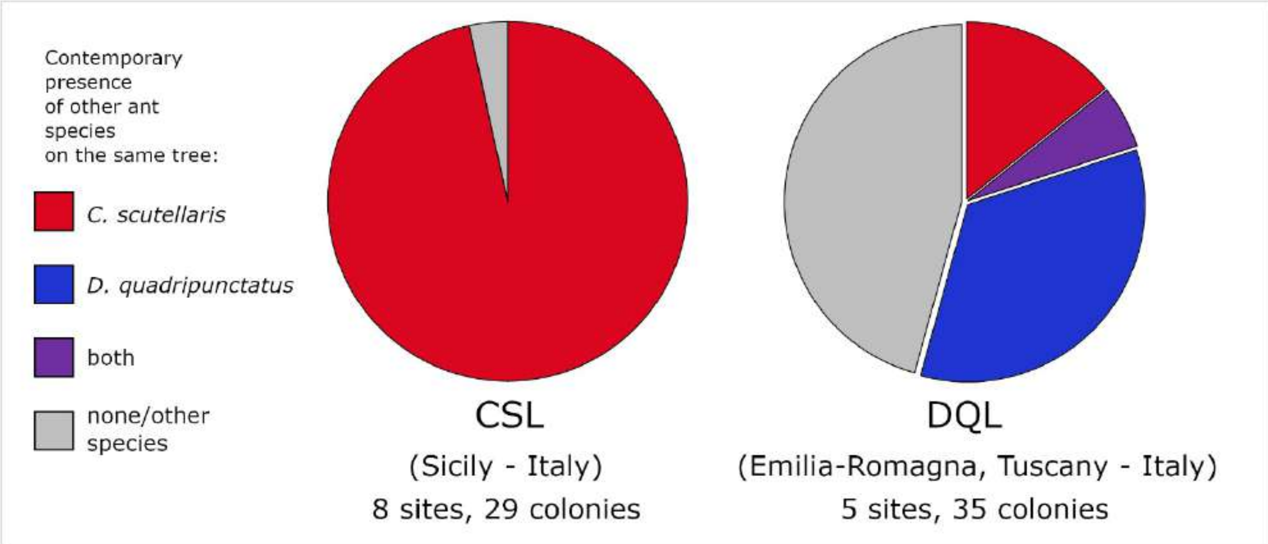

Figure 7. Coexistence between *Colobopsis* and their putative model species on the same tree.

ETHOLOGY: INTERSPECIFIC TRAIL-FOLLOWING BEHAVIOUR

During field observations, trail-following behaviour was never performed by *Colobopsis* colonies exhibiting the DQL pattern (neither to *Cr. scutellaris* nor *D. quadripunctatus* trails). Conversely, 77% of the observed *Colobopsis* colonies exhibiting a CSL pattern had workers following the *Cr. scutellaris* trails (Fig. 8). Detailed data are shown in the supplementary material.

CSL *Colobopsis* followed trails of *Cr. scutellaris* by either walking directly on them (more scarcely populated worker trails with considerable gaps) or slightly sideways (crowded trails without or with very small gaps only). If coming into contact with a *Cr. scutellaris* worker, they immediately performed sudden accelerations and evasive movements. Trail-following often began a few moments after the *Colobopsis* worker left its nest and encounter a *Cr. scutellaris* trail on the tree trunk and ended with the *Colobopsis* worker leaving the trail and directing towards some specific twigs, no longer following *Cr. scutellaris* workers.

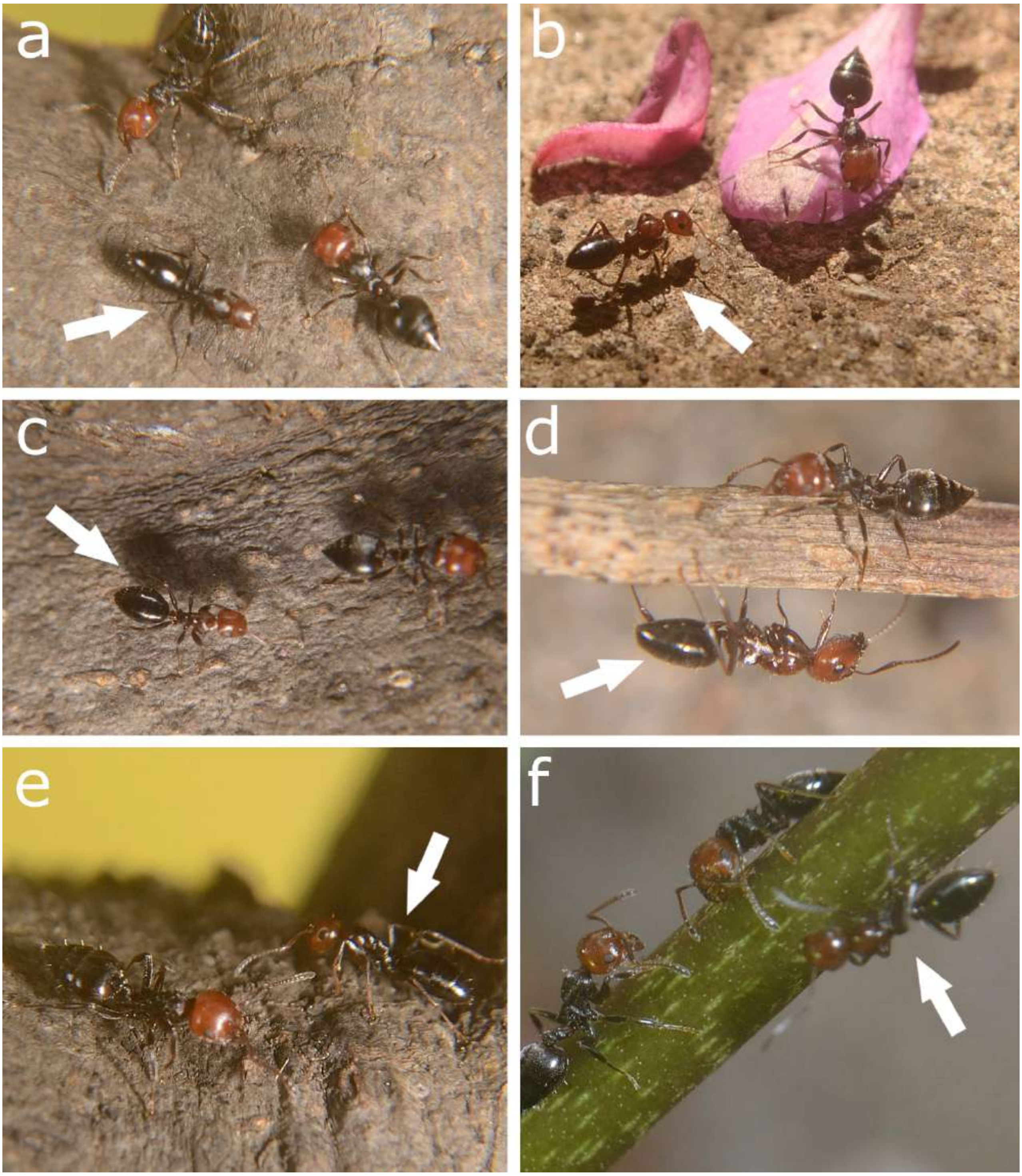

Figure 8. Trail-following behaviour on *Crematogaster scutellaris* trails by other ants (indicated with arrows). On the left (a,c,e) CSL *Colobopsis*, on the right (b,d,f) *Camponotus lateralis* observed in the same locality performing the same behaviour (photos taken in Palermo (Sicily) during field surveys).

BIOGEOGRAPHY, EVIDENCE DISCUSSION AND FINAL SPECIES HYPOTHESIS

CSL and DQL chromatic patterns are found to effectively split into two the Mediterranean *Colobopsis* into two populations, occurring allopatrically and each covering a vast geographic region (Fig. 9). The DQL pattern characterizes almost the entire European distribution of *Colobopsis* in addition to

Western Asia, while the CSL pattern occurs mainly in the Maghreb region (North-Western Africa), a well-recognized ant biodiversity hotspot (Borowiec, 2014), and in the European regions of greater biogeographic proximity to it (Sicily and Southern Iberia) (e.g. Alicata & Schifani, 2019; Tinaut & Ruano, 2021). In particular, this distribution mirrors strikingly well those of some camponotine ant species such as *Camponotus barbaricus* Emery, 1905, *Ca. micans* (Nylander, 1856) and *Ca. ruber* Emery, 1925 (Fig. 9; for their distribution see de Haro *et al.*, 1996; Forel, 1890; 1905; Santschi, 1925; Finzi, 1940; Menozzi, 1940; Cagniant, 1968; 1996; Collingwood & Yarrow, 1969; Baroni Urbani, 1971; Cagniant & Espadaler, 1993; Schembri & Collingwood, 1995; Janicki *et al.*, 2016; Guénard *et al.*, 2017; Schär *et al.*, 2020) and to a slightly lesser extent the distribution of myrmicine ants as the *Aphaenogaster crocea* species group, *A. sardoa* Mayr, 1855 or the *Temnothorax algiricus-mediterraneus* complex (see Mayr, 1853; Emery, 1880; Forel, 1909; Santschi, 1929; Galkowski & Cagniant, 2017; Alicata & Schifani, 2019). Ecological and behavioural field surveys across different Italian regions suggest that the two chromatic patterns are related to quite different lifestyles: the CSL pattern often coexists with *Cr. scutellaris* and very often follows its trails, while the DQL pattern is associated with *D. quadripunctatus* without the involvement of frequent trail-following. The CSL pattern characterized specimens from the Spanish locality where mimicry, close nesting association and extensive trail-following of *Cr. scutellaris* were described by Carpintero et al. (2001; 2005). On the other hand, the DQL pattern characterized samples from the Austrian region where Wagner (2019) based his suggestions of close association and mimicry between *Colobopsis* and *D. quadripunctatus*. A survey conducted in the region of Vienna (Austria) employing similar methodologies to ours estimated that 36% of the investigated *Colobopsis* colonies (n = 110) nested on trees occupied by *D. quadripunctatus*, confirming the trend observed in our study (Wagner, pers. comm.). However, interspecific trail-following between DQL pattern *Colobopsis* and either *D. quadripunctatus* or *Cr. scutellaris* as reported in Wagner (2019; personal communication) was never observed during our surveys and seems to represent a considerably less frequent phenomenon. Such differences between the two groups in chromatic pattern, biogeography and life history traits could arguably be sufficient to suggest a separation of the West-Palearctic *Colobopsis* into two species even according to a conservative classical taxonomical approach. Moreover, examined specimens from the two chromatic patterns are also classified into two morphometric clusters, whose separation reaches a significant threshold indicating heterospecificity according to the current procedures of cryptic ant species separation (Seifert, 2020). At the same time, the morphometric separation between the two clusters is relatively narrow, possibly indicating that the two species may have separated quite recently. Concerning the mtDNA phylogenetic analysis, each clade is unambiguously monophyletic with respect to morphometric and chromatic evidences (A and D = CSL pattern; B and C = DQL pattern), with only one misplaced DQL specimen (a 2.4% error rate). On the other hand, with respect to mtDNA, CSL and DQL patterns resulted in polyphy. This can be explained with possible retention of ancestral polymorphisms and/or introgression of mtDNA (see Chan & Levin, 2005; Willis *et al.*, 2013). These phenomena appear, in fact, largely responsible for the actual estimate of paraphyly emerging from mtDNA phylogenies analyses in about 20% of animal species (Funk & Omland, 2003; Ross, 2014). Mitochondrial DNA introgression is, like in other eukaryotic groups, quite frequent in ants (e.g. Darras & Aron 2015; Beresford et al. 2017; Seifert, 2018), and coalescence during speciation commonly results in species undergoing through phases of polyphyly and paraphyly – averagely longer in arthropods than in other groups – before normally reaching monophyly due to the stochastic process of complete lineage sorting (Avise, 2004; Ross 2014). In the presently analyzed taxa, this would support the hypothesis of the recent divergence. Due to their geographic origins, the ambiguous placement of a few specimens during morphometric or genetic analyses also seems better supported by this hypothesis than by hybridization (despite the latter being relatively frequent in European ants, e.g. Steiner *et al.*, 2011; Seifert, 2018; 2019b).

In conclusion, the CSL and DQL *Colobopsis* clusters are considerable separate species in accordance with the good practices of ants' alpha-taxonomy: all available sources of evidence suggest monophyly with the exception of mtDNA, whose advisory role to infer species boundaries may be relatively weak in comparison with nuclear genes or nuclear genes' expression products for the arguments given by Seifert (2020). As a result, the formal naming of CSL and DQL *Colobopsis* species holds a key informative value over their biology and life history traits. The type material of *Co. truncata*, consisting of a single queen, could not be part of the morphometric or genetic analyses, but shows very clearly the DQL pattern and its geographic origin is unambiguous (with the type locality at mountains of Orero, near Genoa, in Italy's Liguria, placed in the middle of a highly investigated area within the DQL *Colobopsis* geographic range and about 780 km away from the closest area inhabited by CSL *Colobopsis*). The same arguments of safe chromatic identification apply for *Co. fuscipes*, and in this case they are supplemented by an even stronger biogeographic argument.As a result, the *Colobopsis* characterized by the CSL pattern is an undescribed species. Accordingly, a formal description is provided below.

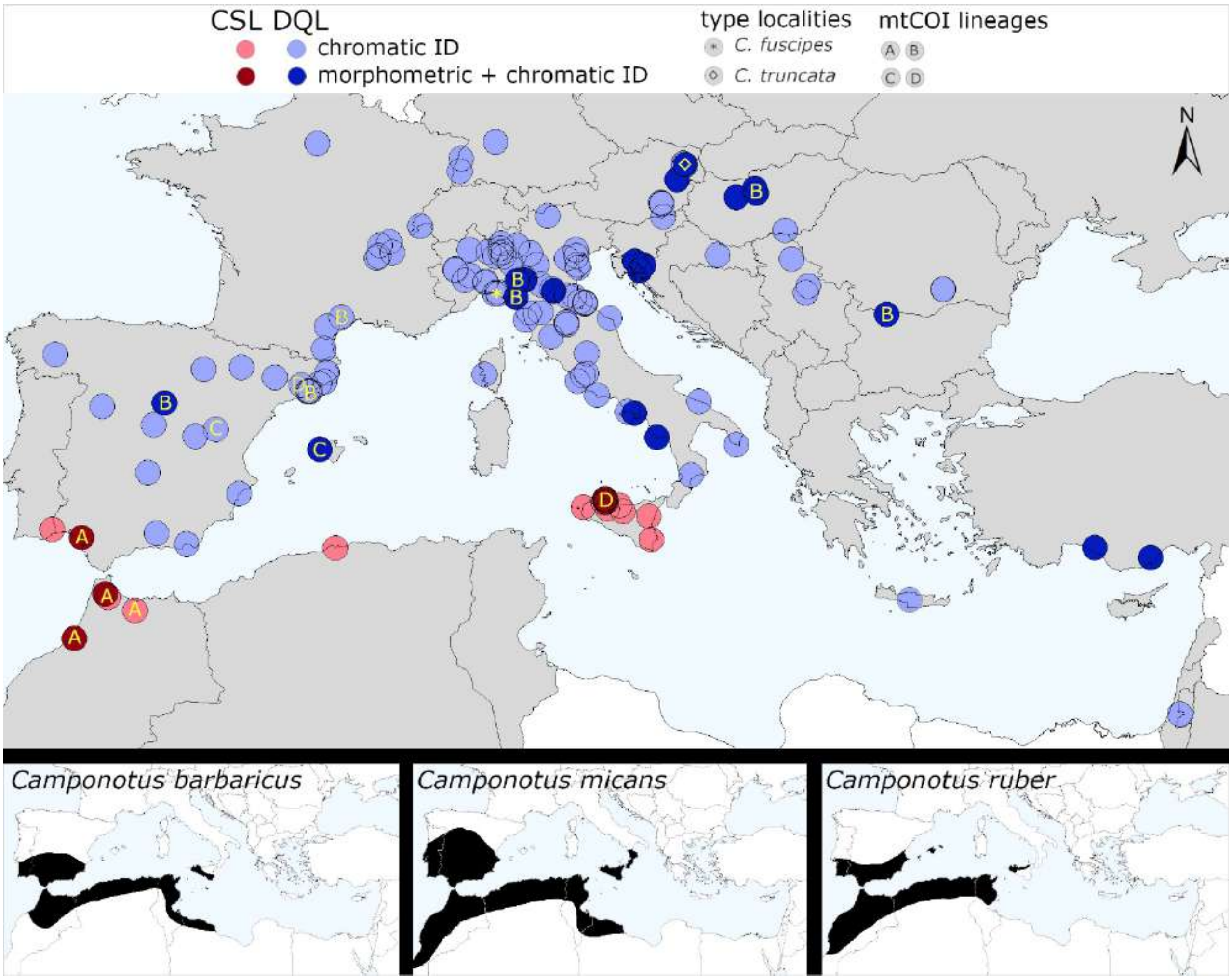

Figure 9. Above: distribution map of examined *Colobopsis* samples – countries where *Colobopsis* presence is known from literature are highlighted in grey. Below: approximate distributions of other Camponotini (*Camponotus barbaricus*, of *C. micans* and of *C. ruber*) which resemble that of CSL *Colobopsis*.

DESCRIPTION OF ***COLOBOPSIS IMITANS*** SP. NOV.

Etymology: imitans is the present participle of the latin verb imitor, meaning "imitating", and is here used in apposition. It refers to the interpretation that this species resembles *Cr. scutellaris*.

Type series: 1 holytpe worker (Figure 10) and 14 paratype workers from Mondello, Sicily (Italy), 38.1953, 13.3354, 5 m, 14.X.2018, E. Schifani leg. The holotype is stored in the Hungarian Natural History Museum collection.

Worker description: Morphometric indexes are shown in Tab. 2. Head subrectangular, on all sides rounded. A straight, central furrow runs from the frontal triangle to the level at which the frontal carinae end. Eyes large, ocelli extremely reduced. Antennae of 12 segments, without a distinct antennal club. Pronotum significantly wider than the rest of the mesosoma. In lateral profile, pronotum and mesonotum gently convex, propodeum profile often showing a central concavity thus having a saddle-like appearance. Petiolar scale profile anteriorly roundly concave and posteriorly straight, its dorsal crest excavated in frontal view. Promesonotal and mesoepinotal sutures as well as metathoracic and propodeal spiracles well-visible. All legs with well-developed tibial spurs, but more so in the anterior legs which are characterized by strikingly large femurs (identical to *Co. truncata*, function unknown). Pigmentation as described in the CSL model. Very fine alveolate to areolate sculpture covering the whole body and appendages. Few erect hairs near the posterior margin of the vertex, between the frons and on the clypeus, and few others on the gaster tergites. See Figs 1, 8, 10, 13.

Soldier (= phragmotic major worker) description: Measurements (2 specimens from Sicily): CL = 1327, 1419; CW = 1262, 1470; SL = 865, 942; ML = 1752, 1774; MW = 921, 1103; EW = 264, 331; EL = 409, 459; CS = 1294, 1444; CL/CW = 0.96, 1.05; SL/CS = 0.65, 0.67; ML/CS = 1.23, 1.35. Large phragmotic head with a cylindrical shape, and a flattened anterior part formed by the mandibles, part of the clypeus and of the genae. In the distalmost half, it is characterized by a strong areolate-rugose sculpture and a dense coverage of thick and short erect hairs. Rest of the shape, sculpture and pigmentation generally similar to the worker but white dots or stripe on the first gastral tergite sometimes very evident. See Fig. 10.

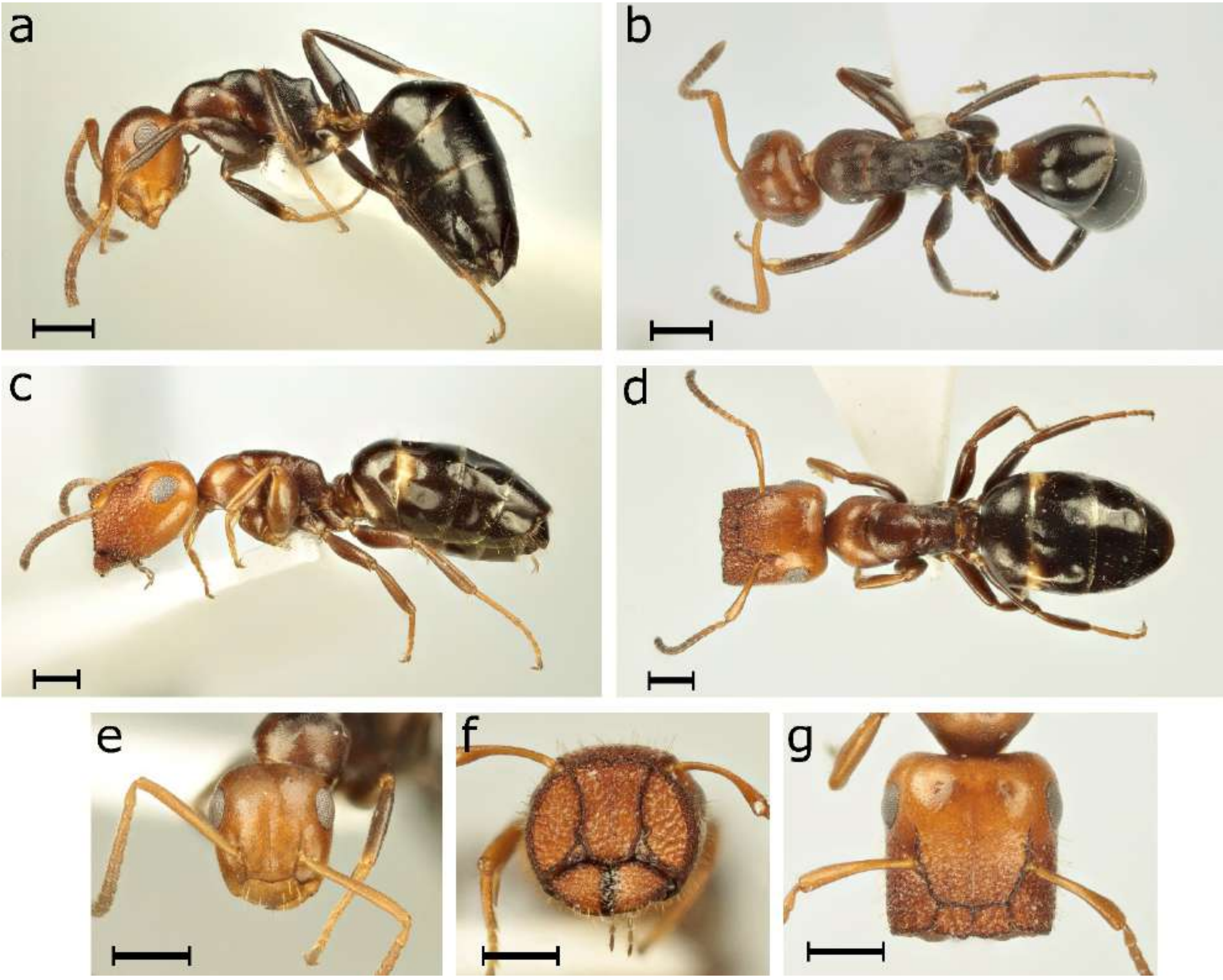

Figure 10. *Colobopsis imitans* sp. nov.: a,b,e) worker (holotypus), c,d,f,g) soldier (specimen from the type locality). Scale bars: 0.5 mm. Pictures also available on AntWeb.org database, specimen codes: ANTWEB1041481 and ANTWEB1041482.

Queen description: Measurements (3 specimens from Sicily): CL = 1437-1531; CW = 1281-1406; SL = 1156-1218; ML = 2687-3031; MW = 1281-1312; EW = 325-362; EL = 525-537; CS = 1359-1468; CL/CW = 1.08-1.11; SL/CS = 0.83-0.87; ML/CS = 1.93-2.22. Large phragmotic head very similar to the soldier not only in shape but also in size (despite larger body size), but well-developed ocelli, eyes much larger and much longer scapi. Immediately distinguishable by the larger, dorsally flatter mesosoma, which is largely unsculptured and shiny. Propodeum profile similar to the end of soldiers' propodeum. Head red as in the worker, but the mesosoma is brownish and the white dots or stripe on the first gaster tergite are/is evident. See Fig. 11.

Male description: Measurements (3 specimens from Sicily): CL = 875-1093; CW = 781-1000; SL = 937-1001; ML = 2281-2437; MW = 1062-1218; EW = 300-387; EL = 462-525; CS = 828-1046; CL/CW = 1.09-1.17; SL/CS = 0.92-1.20; ML/CS = 2.32-2.75. Small, subrectangular head with large ocelli and very large eyes protruding laterally. Toothless mandibles. Relatively large mesosoma, propodeum more gently rounded than in queens or workers. Petiolar node very low and round. Sculpture very weak, mesosoma shiny. Mandibles very hairy, other hairs on clypeus and gaster. Entire body ferruginous or brownish, gaster blackish. See Fig. 11. Genitalia as in Fig. 12.

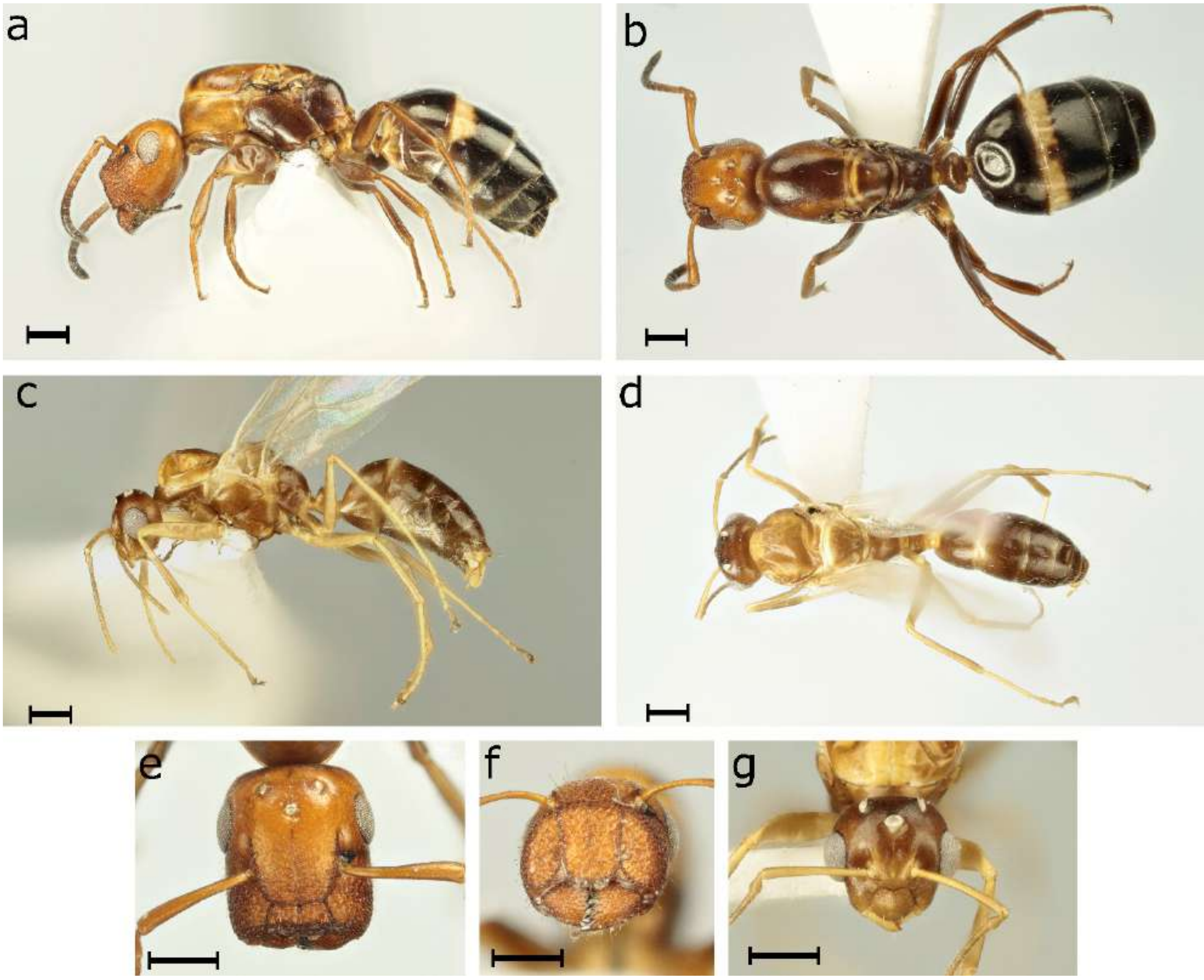

Figure 11. *Colobopsis imitans* sp. nov.: a,b,e,f) queen, c,d,g) male. Specimens from the type locality. Scale bars: 0.5 mm. Pictures also available on AntWeb.org database, specimen codes: ANTWEB1041483 and ANTWEB1041484.

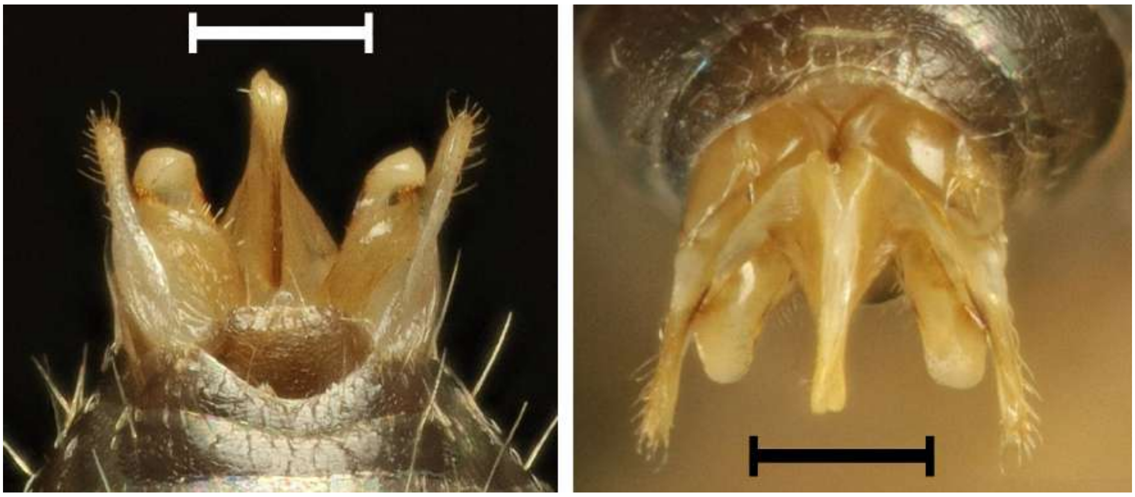

Figure 12. Male genitalia of *Colobopsis imitans* sp. nov. in ventral and dorsal view, specimen from the type locality. Scale bars = 0.25 mm.

Diagnosis: Generally easy to determine on the basis of worker material due to strong chromatic differentiation from *Co. truncata* and allopatric distribution (although further investigation is required for possible contact regions in southern Iberia and southern Italy). Some very small worker specimens may appear almost completely black, therefore lacking the typical chromatic pattern, and workers with entirely red mesosoma can seldom be observed. Tentative identifications of isolated soldier or queen specimens should be much more cautious, although their chromatic appearance may sometimes appear to be very explicit. The low number of males and the lack of particularly evident distinctive characters from *Co. truncata* do not allow a safe species-level identification of this caste based on morphology. In respect to workers, the morphometric linear discriminant function provided in the results section should be helpful to determine dubious cases including decolored specimens. Finally, DNA barcoding, which can be used for the same purpose and also be employed on the other castes, shows a relatively low error rate but may present some risks due to the polyphyletic pattern that we observed.

Biological, ecological and phenological notes: Relatively thermophilous, in Sicily occurring from few meters above the sea level to at least 1015 m a.s.l., in Morocco ascending up to 1290 m a.s.l. and in Spain so far known from coastal lowland areas. Probably very common but also heavily under-recorded due to cryptic arboreal lifestyle, low colony population (most-likely monogynous), effective mimicry and long periods of inactivity during the most arid and coldest times of the year. Workers and soldiers are unlikely to descend to the ground but were observed to do so at least once, following a sparsely populated *Cr. scutellaris* trail. Soldiers in general are very difficult to be found outside the nest and usually seen acting as gatekeepers of the nest entrance. Founding queens were observed to do the same. Nests are hidden in minute holes on the dead parts of arboreal trunks, where *Co. imitans* sp. nov. often seems to act as a secondary user of cavities excavated by xylophagous insects. It exploits *Andricus quercustozae* (Bosc, 1792) oak galls as nests (occupying about 15% of galls collected in Sicily's Bosco della Ficuzza in a recent survey, authors' unpublished data), in a similar way to *Co. truncata* (see Giannetti *et al.*, 2019; 2021; Fürjes-Mikó *et al.*, 2020). Polydomy appears probable due to repeated findings of groups of workers without queens within oak-galls. Observed nesting on several and diverse plant species, including at least: *Citrus reticulata* Blanco, 1837, *Ci. sinensis* (L.) Osbeck, 1765*, Laurus nobilis* L., *Olea europaea* L., *Quercus ilex* L., *Q. pubescens*-group, *Q. suber* L., *Pyrus communis* L., *Pittosporum tobira* (Thunb.) W.T.Aiton. Apparently dense populations were found in old *Citrus* orchards and relatively sparse *Q. suber* woods, but also in deciduous oak forests. However, it occurs in a broad range of habitats from cities to agricultural lands to natural forest habitats, but information available so far is insufficient to depict a satisfactory picture of habitat preferences. Despite the earlier claim by Carpintero *et al.* (2005), there is currently no evidence backing the fascinating hypothesis that *C. imitans* sp. nov. foundress queens prefer trees hosting *Cr. scutellaris* to found their colonies. A focused investigation on this topic would be interesting. Nuptial flights for *Co. imitans* sp. nov. occur approximately in the same period of *Co. truncata* (alates in Sicily observed from June 30 to July 13, n = 5, see supplementary material). Winged queens and males were repeatedly seen attracted by artificial lights at night.

FINAL REMARKS

Body pigmentation pattern is the only qualitative character that makes *Co. imitans* sp. nov. identifiable without recurring to quantitative data, as it is otherwise morphologically extremely similar to *Co. truncata* up to a significant level of crypsis (see Wagner *et al.*, 2018). These pigmentation differences among West-Palearctic *Colobopsis* so far went completely unnoticed, the sole exception being a brief statement by Santschi (1929) noting that the chromatic aspect of the Moroccan *Co. truncata* is different than the typus one by its lighter head color. The case we documented can be considered one of the few where such element is important for species discrimination in European ants. While body pigmentation has been used without scientific rigor by some past ant taxonomists (see the example described by Boer, 2008), it can be important for the morphological identification of species such as *Formica clara* Forel, 1886 and *F. cunicularia* Latreille, 1798 or even fundamental for many *Temnothorax* spp. (Seifert & Schulz, 2009; Seifert, 2018) and should not be overlooked in multi-character approaches for taxonomic purposes. Under these conditions, checking pictures uploaded on citizen science platforms and social media proved to be significantly helpful to obtain data on these species distribution, evidencing once more the uncovered potentials of citizen science in the study of ant distribution (e.g. Lucky *et al.*, 2014; Zhang *et al.*, 2019; Castracani *et al.*, 2020; Sheard *et al.*, 2020) and more in general of platforms hosting these kind of data in the study of insect distribution (e.g. Schifani & Paolinelli 2018; Hochmair *et al.*, 2020; Ruzzier *et al.*, 2020; Winterton, 2020). Moreover, behavioural data are seldom considered in integrative taxonomic approaches dealing with ants, but they may prove valuable in some cases (see also Ronque *et al.*, 2016). Finally, while mtDNA has a decent identification performance, our data clearly support the idea that it should not be used as the primary source of information to take taxonomic decision on species delimitation (see Seifert 2020).

The taxonomic status of the West-Palearctic *Colobopsis* populations appears now well-resolved. Still, our analyses missed data from what the existing literature describes as the easternmost distribution of *Co. truncata* east to the Mediterranean region, which reaches to the Kopet Dag in Turkmenistan (Dlussky *et al.*, 1990; Gratiashvili & Barjadze, 2008; Dubovikoff & Yusupov, 2018; Bračko, 2019; Samin *et al.*, 2020). In biogeographic terms, they are extremely unlikely to represent a disjunct *Co. imitans* sp. nov. population, while conspecificity with *Co. truncata* appears likely due to the existence of several ant species with similar distributions (e.g. Wagner *et al.*, 2017; Seifert, 2018). Within the Mediterranean, the range limits of *Co. imitans* sp. nov. and *Co. truncata* or their eventual sympatry in contact zones should be appropriately investigated in areas of biogeographic transition (southern Iberia, Sicily, Calabria and perhaps Sardinia, see Alicata & Schifani, 2019; García, 2020; Schifani *et al.*, 2020; 2021; Tinaut & Ruano, 2021).

The fact that *Co. imitans* sp. nov. and *Co. truncata* greatly differ chromatically is interesting if one considers that phylogenetics and morphometry suggest a recent differentiation. In evolutionary terms, the most likely interpretation is to link such differentiation to a shared strategy based on ant-mimicry modulated according to the presence or absence of certain good models across different Mediterranean regions. Both *D. quadripunctatus* and *Cr. scutellaris* have much more populous colonies than *Co. imitans* sp. nov. and *Co. truncata*, while both are likely less palatable for predators and armed with effective toxic substances (Cavill & Hinterberger, 1960; Wagner, 2019). Therefore, even though only *Cr. scutellaris* is truly recognized as an aggressive and dominant species (Santini *et al.*, 2007; Frizzi *et al.*, 2015; Castracani *et al.*, 2017; Seifert, 2018), both appear to possess the required traits to be considered good Batesian models to the non-aggressive and relatively unarmed *Colobopsis* (which still possess some formic acid). However, across the distribution range of *Co. imitans* sp. nov., *D. quadripunctatus* is almost completely absent: it does not inhabit the Maghreb, its Iberian distribution is concentrated to the North and in Sicily it is considered to bevery rare (Schifani & Alicata, 2018; Cabanillas *et al.*, 2019). Yet it is interesting to note that the opposite is not true for *Co. truncata*: the latter is not only sympatric with *D. quadripunctatus* along its entire range (including in the hypothesis that easternmost *Colobopsis* are *Co. truncata*: see Reznikova, 2003; Ghahari *et al.*, 2015), but also sympatric with *Cr. scutellaris* in south-western Europe and with *Cr. schmidti* in the east. Finally, it is worth noting that the white dots or stripe that have been linked to mimicry of *D. quadripunctatus* in *Co. truncata* (Forel, 1886; Wagner, 2019) are/is absent or hardly visible in *Co. imitans* sp. nov. workers but at the same time well-visible in at least a few soldiers and especially queens that we inspected. Following the mimicry interpretation of the chromatic patterns, it is imaginable that this character is an ancestral remnant but that selective (predatory) pressures leading to perfect mimicry are stronger on workers than on queens or soldiers which rarely leave the safety of their nest.

Mimicry may be considered as a third defensive strategy of *Colobopsis* unique or very rare among ants after suicidal authothysis and phragmosis (Emery, 1925; Maschwitz & Maschwitz, 1974; Davidson *et al.*, 2012; Shorter & Rueppel, 2012; Ward *et al.*, 2016; Laciny *et al.*, 2018). Apart from the two species we treated, the only existing claims of mimicry in the genus come from morphologically very different and likely unrelated species from Fiji Islands (Santschi 1928; Wheeler 1934). However, since several other Palearctic *Colobopsis* species share a general morphological similarity with *Co. imitans* sp. nov. and *Co. truncata*, likely belonging to the same evolutionary lineage, it is possible that some of them represent yet undiscovered mimics. It also appears that mimicry may have played a powerful role driving phenotypic diversification of West-Palearctic *Colobopsis*: *Co. imitans* sp. nov. and *Co. truncata* can be considered as the only well-documented example among ants that suggests mimicry-driven phenotypic divergence of sister species. In comparison, the intraspecific case of mimicry pattern divergence in *Ca. lateralis* is one of much more modest differentiation (Wagner, 2014; Seifert, 2019a). Similar accounts are not particularly common in other organisms either, but recently an interesting scenario of strong diverging aposematic patterns coupled with minimal genetic differentiation was described by for a group of frogs (Tarvin *et al.*, 2017).

It is still unknown which visual predators may have been responsible for determining the selective pressures that lead to the emergence of ant-mimicry across different ant lineages. Birds and lizards appear to be good candidates to start with (Ito *et al.*, 2004; Wagner, 2014). Our surveys around the colonies and trails of *Cr. scutellaris* and *D. quadripunctatus* led us to find several possible mimics of either species that belong to different insect and spider groups already known for ant mimicry (Fig. 13). In particular, Santschi (1919) suggested in the the Canarian relative of *Ca. ruber* (*Ca. guanchus* Santschi, 1908) the existence of an association similar to that between *Ca. lateralis* and *Cr. scutellaris*, while Harvey *et al.* (2018) described the anti-predatory function of ant-mimicry in *Gelis* spp., Komatsu (1961) reported on *Phrurolithus*-ant associations, Corcobado *et al.* (2016) reported on *Leptorchestes*-ant associations, and finally Chandler (2010) mentions myrmecomprhism among

Anthicidae. Although some of these findings may have been coincidental and deserve further investigation, it is imaginable that *Co. imitans* sp. nov. and *Co. truncata* are each part of a larger cohort of different arthropods that evolved mimicry to resemble *Cr. scutellaris* or *D. quadripunctatus* in response to visually hunting generalist insectivores, similarly to the “golden mimicry complex” described by Pekár *et al.* (2017). Further investigation is also required to understand whether the advantages of mimicry for *Co. imitans* sp. nov. and *Co. truncata* may lay in a dilution effect, if Batesian mimicry is truly implied and if Müllerian mimicry also plays a role (see Speed, 1999; Pekár et al., 2017) –, keeping in mind that different evolutionary relations may exist between the same prey and different predators.

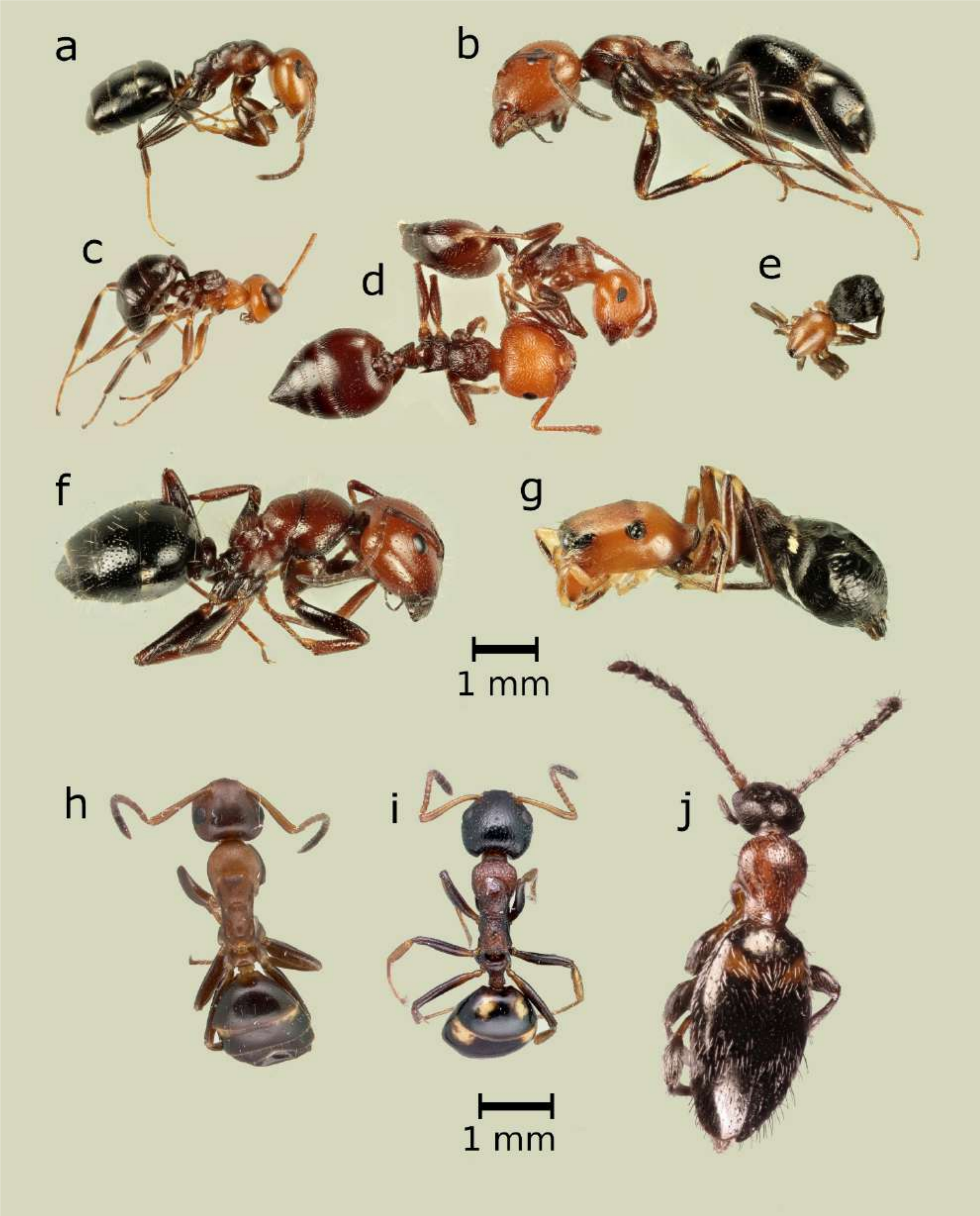

Figure 13. Above *Cr. scutellaris* and species showing a very similar chromatic pattern that were collected near *Cr. scutellaris* trails in Sicily (Italy): a) *Co. imitans* sp. nov. (worker from Mondello), b) *Ca. lateralis* (worker from Monte Pellegrino), c) *Gelis* sp. (Hymenoptera: Braconidae) from Monte Petroso, d) *Cr. scutellaris* from Levanzo island, e) *Phrurolithus* sp. (Araneae: Phrurolitidae) from Mondello, f) *Ca. ruber* (worker from Monte Pellegrino) and g) *Leptorchestes* sp. (Araneae: Salticidae) from Monte Petroso. Below, *D. quadripunctatus* and species with a very similar chromatic pattern that were collected near its trails or in the same trees in the Italian Peninsula: h) *Co. truncata* (specimen

from Bulgaria, AntWeb code CASENT0280000, photographer Michele Esposito), i) *D. quadripunctatus* (specimen from Czech Republic, AntWeb code CASENT0179916, photographer Michele Esposito), j) *Formicomus pedestris* (Rossi, 1790) (Coleoptera: Anthicidae) from Parma (Italy).

Interspecific but intrageneric trail-following described for some ants is likely relatable to phylogenetic proximity and morphofunctional and behavioural similarities or similar foraging strategies among species (e.g. Grasso *et al.*, 2002 and references therein). On the other hand, the significance of the recorded *Colobopsis*-*Crematogaster* trail-following is not yet fully clear to us. Similar cases (such as that of *Ca. lateralis*) have often been referred to as parabiosis, but we avoided this term since quite different interpretations of its meaning coexist creating ambiguity: it is sometimes used to simply indicate trail-following but in other occasions it implies also nest-sharing (see Forel, 1898; Swain, 1980; Vantaux *et al.*, 2007; Menzel *et al.*, 2008; 2010; 2014a; 2104b; Seifert, 2018). Outside of *Co. imitans* sp. nov. and *Co. truncata*, many other camponotine ants follow *Crematogaster* trails without always acting as mimics (Ito *et al.*, 2004; Vantaux *et al.*, 2007; Menzel *et al.*, 2008; 2014). Baroni Urbani (1969) and Menzel *et al.* (2014) speculated that the compounds used as trails pheromones by *Crematogaster* are generally easily perceived by *Camponotus*, this capacity representing an important pre-adaptation to trail-following. During our field surveys, we unexpectedly observed several workers of *Camponotus piceus* (Leach, 1825) (a relative of *Ca. lateralis* with no resemblance of *Cr. scutellaris*, see Seifert, 2019a) easily following part of a *Cr. scutellaris* trail to the canopy of a tangerine tree while avoiding *Cr. scutellaris* attacks. It may be possible that many other similar camponotine ants rarely perform the same without possessing a specific mimicry adaptation, which can partly explain the occasional observations of trail-following between *Co. truncata* and *Cr. scutellaris* (Zimmermann 1934; Goetsch 1942; Baroni Urbani 1969; Wagner 2014). Still, in the overwhelming majority of the documented cases inter-specific trail-following is associated either with mimicry (as for *Colobopsis imitans* sp. nov., see Gobin *et al.*, 1998; Ito *et al.*, 2004; Menzel *et al.*, 2010; Powell *et al.*, 2014) or with nest-sharing (Vantaux *et al.*, 2007; Menzel *et al.*, 2008; 2014). For mimics, it appears to be primarily a way to better hide within the ranks of the model species, an example of dilution effect (Lehtonen & Jaatinen, 2016), which may also apply to a certain degree non-mimic ant species as well. However, the trail-followers may be able to obtain additional benefits in their success of locating trophic resources, sometimes even establishing somewhat parasitic relationships (see Vantaux et al. 2007; Menzel et al. 2010; 2014a; 2014b). It is unclear whether *Colobopsis* ants may also benefit from a similar mechanism although a parasitic aspect of its trail-following behaviour has been suggested by Baroni Urbani (1969).

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