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

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# 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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Running title: Mimicry-driven diversification in *Colobopsis* ants?

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1 ABSTRACT

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

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

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## INTRODUCTION

30

31 Ants (Insecta: Formicidae) are a hyperdiverse group of organisms which counts about 13,860 species  
32 (Bolton, 2021) and is extraordinarily successful in most terrestrial ecosystems (Hölldobler & Wilson,  
33 1990; Gibb *et al.*, 2017; Seifert, 2017). Such high diversification stems from several evolutionary  
34 strategies and lifestyles, and enables even hundreds of different ant species to coexist in the same  
35 habitat (Hölldobler & Wilson, 1990; 2008). However, only one or very few dominant species  
36 generally characterize even the most species-rich ant communities: these species form very populous  
37 colonies, with large, often permanent foraging trails, and they defend territories that may extend over  
38 hectares (Hölldobler & Wilson, 1990; Andersen, 1995; 1997; Grasso *et al.*, 1998; 1999; 2005; Arnan  
39 *et al.*, 2018). These ants are exposed to higher predation risk compared the ones whose workers forage  
40 solitarily or in small groups, and are accordingly equipped with effective defensive mechanisms  
41 (Buschinger & Maschwitz, 1984; Hölldobler & Wilson, 1990; Dornhaus & Powell, 2010; Seifert,  
42 2018). Most ant species live in small colonies and forage solitarily or in small groups, only  
43 occasionally form trails, and develop evasive anti-predatory strategies (e.g. Hölldobler & Wilson,  
44 1990; Tautz *et al.*, 1994; Andersen, 1995; Dornhaus & Powell, 2010; Helms *et al.*, 2014; Larabee &  
45 Suarez, 2015; Seifert, 2018; Grasso *et al.*, 2020). Of the species that live in small colonies, the only  
46 ones armed with dangerous defences are some predatory ants which retain the primitive feature of a  
47 powerful functional stinger to hunt (Buschinger & Maschwitz, 1984; Hölldobler & Wilson, 1990;  
48 Dornhaus & Powell, 2010).

49 Well-armed ant species, in particular the ones that build large colonies, are a very good model for  
50 several mimicking organisms, mostly arthropods. Some of these mimics are myrmecophilous  
51 organisms: commonly ant predators or parasites, they have adapted to live within or close to ant  
52 colonies by relying on chemical or acoustic mimicry (e.g. Geiselhardt *et al.*, 2007; Barbero *et al.*,  
53 2009; Cushing, 2012; Parker & Grimaldi, 2014; Parker, 2016; Scarparo *et al.*, 2019). On the other  
54 hand, myrmecomorph species resemble their ant model thanks to morphological and/or behavioural  
55 adaptations (e.g. Komatsu 1961; Jackson & Drummond, 1974; Oliveira & Sazima, 1984; Oliveira  
56 1988; Cobben, 1986; McIver, 1987; McIver & Stonedahl, 1993; Trjapitzin & Trjapitzin, 1995; Cassis  
57 & Wall, 2010; Chandler, 2010; Durkee *et al.*, 2011; Huang *et al.*, 2011; Cushing, 2012; Pekár, 2014;  
58 Corcobado *et al.*, 2016; Pekár *et al.*, 2017; Harvey *et al.*, 2018; de L. Nascimento & Perger, 2018;  
59 Gnezdilov, 2019). The main aim of myrmecomorphism is predation avoidance: compared to the  
60 mimics, models usually possess superior defensive mechanisms and are also more numerous. As  
61 such, they are usually interpreted as Batesian mimics (e.g. Jackson & Drummond, 1974; McIver,  
62 1987; Durkee *et al.*, 2011; Huang *et al.*, 2011; Cushing, 2012; Harvey *et al.*, 2018), whose evolution  
63 can be favoured by model abundance (Kikuchi & Pfenning, 2010).

64 Many ant mimics are ants themselves. Some are parasites (e.g. inquilines) that act similarly to  
65 myrmecophilous organisms (Buschinger, 2009), relying on chemical adaptations to interact with the  
66 host species. However, there are some free-living ant species that act as mimics of more aggressive  
67 or dominant ant species and are therefore interpreted as Batesian mimics. Nonetheless, solid empirical  
68 evidence to reject the alternative hypothesis of Müllerian mimicry (see Müller, 1879; Pasteur, 1982;  
69 Ritland, 1991) is rarely available (Ito *et al.*, 2004; Wagner, 2014). In these species, chromatic mimicry  
70 is the prevalent mechanism, while behavioural or morphological adaptations are more rarely  
71 documented (Emery, 1886; Forel, 1886; Santschi, 1919; Gobin *et al.*, 1998; Merrill & Elgar, 2000; Ito  
72 *et al.*, 2004; Ward, 2009; Gallego-Ropero & Feitosa, 2014; Powell *et al.*, 2014; Pekár *et al.*, 2017;  
73 Rasoamanana *et al.*, 2017; Seifert, 2019a). In addition, recurrent behaviour among mimicking ant  
74 species is interspecific trail-following, which consists in the mimics regularly infiltrating into the  
75 foraging trails of the model and may lead to parasitic behaviour with regard to food resources (Emery,  
76 1886; Santschi, 1919; Gobin *et al.*, 1998; Ito *et al.*, 2004; Menzel *et al.*, 2010; Powell *et al.*, 2014).  
77 Unlike specialized parasites (e.g. Visicchio *et al.*, 2001; Buschinger, 2009; de la Mora *et al.*, 2020),  
78 no advanced mechanisms of chemical deception exist in most of these cases, so in the eventuality of  
79 direct encounters the model species recognizes and attacks the mimic, which however is well-  
80 equipped to escape (Goetsch, 1942; 1951; Kaudewitz, 1955; Gobin *et al.*, 1998; Ito *et al.*, 2004;  
81 Menzel *et al.*, 2010). The vast majority of the hitherto well-documented cases come from the tropics:  
82 mimics mainly belong to diverse lineages from the Formicinae tribe Camponotini (mostly  
83 *Camponotus* Mayr, 1861), while their models are phylogenetically scattered, including  
84 Ectatomminae, Myrmeciinae, Myrmicinae (Crematogastrini and Stenammini) and  
85 Pseudomyrmecinae. Only one case of ant-mimicking ant species is well-documented in the West-  
86 Palearctic zone, i.e. *Camponotus lateralis* (Olivier, 1792). It chromatically mimics the similar  
87 *Crematogaster* species *Cr. ionia* Forel, 1911, *Cr. scutellaris* (Olivier, 1792) and *Cr. schmidtii* (Mayr,  
88 1853), and follows their trails (Emery, 1886; Baroni Urbani, 1969; Menzel *et al.*, 2010; Wagner,  
89 2014; Seifert, 2018; 2019a). The three species are closely related with neighbouring geographic  
90 ranges and differ slightly chromatically (Blaimer, 2012). Interestingly, there seems to be a geographic  
91 trend in the chromatic pattern of *Ca. lateralis*, allowing it to better resemble these three  
92 *Crematogaster* species in the regions of sympatric occurrence (Wagner, 2014; Seifert, 2019a).

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

98 (Wheeler, 1904; Ward *et al.*, 2016). In the Western-Palearctic region, *Colobopsis truncata* (Spinola,  
99 1808) is the only recognized species of its genus. The queen caste was described by Spinola (1808)  
100 from north-western Italy (Liguria region), while the other castes were described later (Dufour &  
101 Perris, 1840; Forel, 1874; Emery, 1916). Another species, *Co. fuscipes* (Mayr, 1853) was described  
102 from Austria by Mayr (1853), but was later reclassified as a junior synonym of *Co. truncata* (Emery  
103 & Forel, 1879). *Colobopsis truncata* is therefore considered to have a wide geographic distribution,  
104 from the Caucasus to Iberia and from Central Europe to the Maghreb (Seifert, 2018; Janicki *et al.*,  
105 2016; Guénard *et al.*, 2017). It is an arboreal-nesting species, as is typical of the genus, and it  
106 preferably nests on broadleaved trees, where it lives in monogynous and often polydomous colonies,  
107 rarely exceeding 500 workers (Seifert, 2018). Queens and soldiers are specialized for phragmosis,  
108 and soldiers may also function as repletes (living containers of liquid food), seldom leaving the safety  
109 of the nests they guard (Brun 1924; Goetsch, 1950; 1953; Seifert, 2018). Minor workers are usually  
110 active outside the nest during both day and night, forage solitarily, do not recruit nest mates to food  
111 sources, and perform very quick evasive movements when encountering other ants (Seifert, 2018).

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



132 no locality specified; Lake Garda according to Wagner HC, personal communication). Wagner (2019)  
133 described a close association between *Co. truncata* and *D. quadripunctatus* in Austria (Vienna),  
134 highlighted morphological and chromatic similarity between the two, and reported trail-following of  
135 *D. quadripunctatus* trails by *Co. truncata*.

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

## 142 MATERIALS AND METHODS

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

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

165 Scienze Naturali in Turin (Italy), and matched the description given by the author (Spinola, 1808).  
166 Concerning *Co. fuscipes*, at least two syntypes are stored in the Museum für Naturkunde, University  
167 of Berlin (Germany), and their pictures are available on AntWeb (AntWeb.org, codes FOCOL2496  
168 and FOCOL2497): these are labelled “Oesterreich | Coll. Rhd || *Colobopsis fuscipes* Mayr || Type ||  
169 29812 || GBIF-D/FoCol | 2496 | specimen + label | data documented” and “Oesterreich | Coll. Rhd ||  
170 *Colobopsis fuscipes* Mayr || Type || GBIF-D/FoCol | 2497 | specimen + label | data documented”.  
171 Although the label is unlikely to be an original by Gustav Mayr (B. Seifert, pers. comm.), we deem  
172 their status as types credible. We also retrieved a worker labelled *Co. fuscipes* in Mayr’s collection at  
173 the Natural History Museum of Vienna, but with no explicit indication ensuring its type status. In  
174 order to gather information on chromatic variation of Euro-Mediterranean *Colobopsis*, we relied on  
175 AntWeb pictures, images from scientific papers or monographs (Glaser, 2009; Wagner, 2014; 2019;  
176 Lebas *et al.*, 2016; Seifert, 2018; Scupola, 2018; García, 2020; Salata *et al.*, 2020; Täuşan *et al.* 2020),  
177 and on georeferenced photographs uploaded on citizen science platforms (iNaturalist.org,  
178 biodiversidadvirtual.org) and on biodiversity-related Facebook groups. A complete list of the material  
179 examined, their depositories and collecting data is available as a Supplementary Material file to this  
180 paper. Ecological and behavioural data were obtained through field surveys across Italy.

#### 181 PIGMENTATION: CHROMATIC MIMICRY

182 Preliminary observations highlighted that chromatic pattern provides the most evident difference  
183 between allopatric *Colobopsis* populations which resemble two different model ant species in Italy.  
184 We preemptively described the two chromatic forms and investigated whether these were consistently  
185 able to represent *Colobopsis* diversity across the Mediterranean basin, and whether they occurred  
186 intracolony or sympatrically, and also checked for the possible existence of third forms. The two  
187 *Colobopsis* model patterns were pre-emptively established by observing ten workers per each form  
188 (10 from Sicily and 10 from mainland Italy), and all subsequent investigations were carried out by  
189 inspecting specimens of well-preserved pigmentation primarily belonging to the worker caste.  
190 Queens and soldiers were also examined and identified only if closely resembling one worker model  
191 pattern, while males were not considered due to their very different pigmentation. Furthermore, to  
192 better describe the differences between the two models, a ratio was calculated between head color  
193 and mesosoma color by taking dorsal pictures of specimens and calculating the average value of red  
194 (RGB colors) between 5 randomly selected pixels of the head and 5 of the mesosoma via software  
195 ImageJ (Schneider *et al.*, 2012). Calculating a ratio rather than considering the absolute values greatly  
196 reduces the variation produced by different light conditions and camera settings among different  
197 pictures, thereby allowing comparison of pictures from various sources. The same ratio was also  
198 calculated for the two putative model species *Cr. scutellaris* and *D. quadripunctatus*. Chromatic ratios

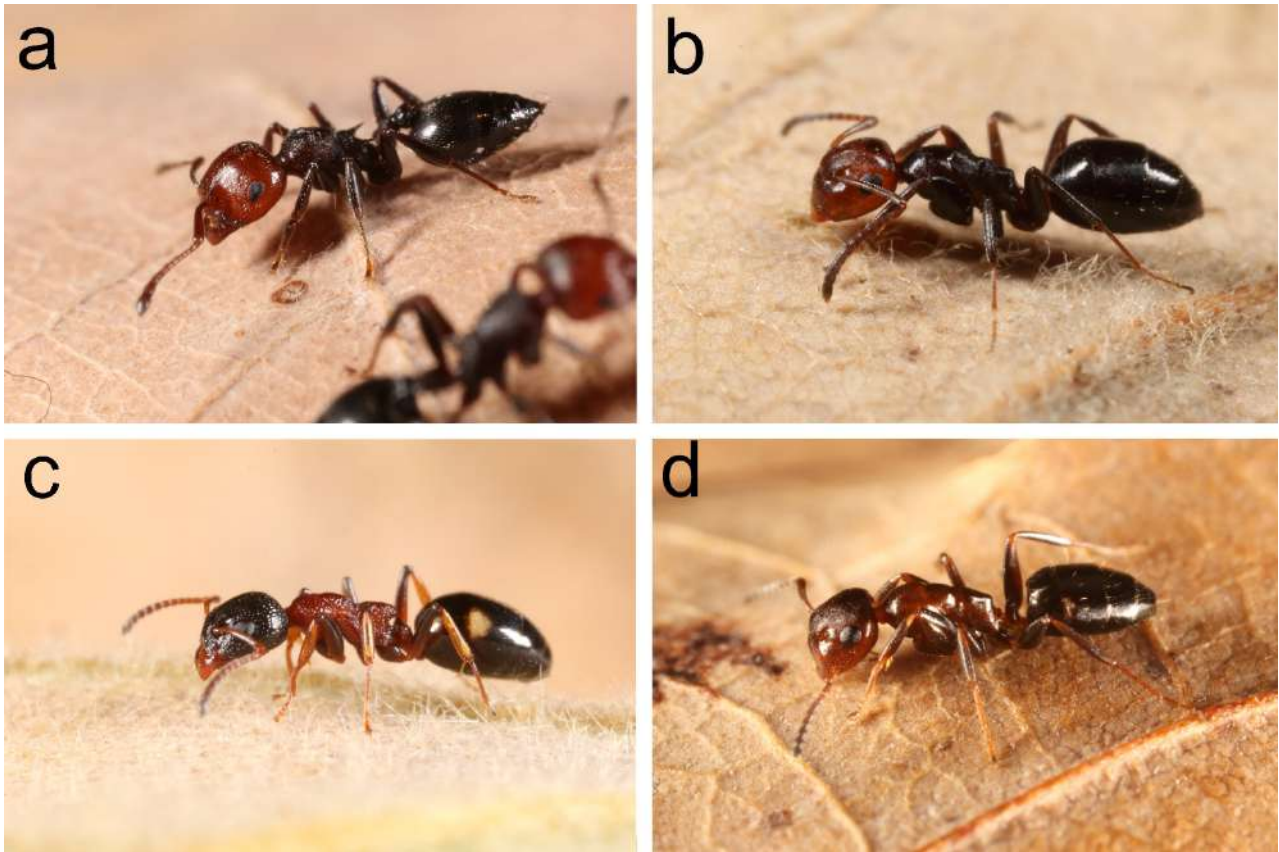
199 were calculated on 20 workers per chromatic pattern or species from across their respective  
200 geographic range using both directly inspected specimens and images from citizen science platforms.  
201 Any differences were statistically tested by using the software R 4.0.3 and R Studio 1.3.1056 (R Core  
202 Team, 2021), and employing an ANOVA test and subsequent Tukey Post-hoc test for pairwise  
203 comparisons.

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

209 The two model patterns are defined as follows:

210 *Cr. scutellaris*-like pattern (CSL pattern): head, or head and anterior part of the mesosoma (rarely  
211 most of it) uniformly red, rest of the body evidently darker and mostly black. White stripes or dots  
212 on the second gastral tergite often absent or weak (present in 10% of the examined workers). See Fig.  
213 1.

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



220

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

223 NUMERIC MORPHOLOGY: MULTIVARIATE ANALYSES OF MORPHOMETRIC DATA

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

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

237 *Exploratory analyses through NC-PART clustering*

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

#### 247 *Exploratory analyses via PCA using allometrically corrected data*

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

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

#### 263 *Hypothesis testing by confirmatory analysis*

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

Abbr.	Description of the trait	ICC (R)
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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

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

271 GENETICS: MITOCHONDRIAL COI SEQUENCES

272 Total genomic DNA was extracted from leg tissues using the NucleoSpin DNA Insect kit (Macherey-  
273 Nagel, Düren, Germany), following the manufacturer's protocol. A 700 bp region of mitochondrial  
274 gene cytochrome *c* oxidase subunit I (COI) was amplified using the primer couple  
275 LCO1490/HCO2198 (Folmer *et al.*, 1994). PCR was carried out in 25  $\mu$ L reactions using the  
276 following profile: initial denaturation step at 95 °C for 5 minutes, 35 amplification cycles  
277 (denaturation at 95 °C for 30 seconds, annealing at 52 °C for 30 seconds, elongation at 72 °C for 45  
278 seconds), final elongation at 72 °C for 7 minutes. PCR products were sent to MacroGen Europe  
279 (Amsterdam, Netherlands) for Sanger sequencing. Chromatograms were checked and edited using  
280 SeqTrace (Stucky, 2012). Sequences were aligned using the MUSCLE (Edgar, 2004) algorithm as  
281 implemented in AliView (Larsson, 2014). Model selection and Maximum Likelihood phylogenetic  
282 analysis were performed on the IQ-TREE web server (Trifinopoulos *et al.*, 2016) using the Eastern-  
283 Palearctic *Co. nipponica* (Wheeler, W.M., 1928) and *Co. shohki* (Terayama, 1999) and the  
284 Indomalayan *Colobopsis nr. saundersi* (Emery, 1889) (GenBank accession numbers AB019417,  
285 AB019418 and KU975365, respectively) as outgroups. Ten separate runs were launched, each with  
286 1000 replicates of ultrafast bootstrap, and the tree with the best likelihood value out of the ten was

287 chosen. Twenty-three colony samples were sequenced, consisting in 41 workers from 6 countries and  
288 18 localities. Obtained sequences have been submitted to Genbank, under accession numbers  
289 MW462045–MW462085 (see supplementary material).

#### 290 ECOLOGY: COEXISTENCE WITH MODEL SPECIES

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

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

#### 303 ETHOLOGY: INTERSPECIFIC TRAIL-FOLLOWING BEHAVIOUR

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

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

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

## 321 SPECIES CONCEPT

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

## 331 RESULTS

### 332 PIGMENTATION: CHROMATIC MIMICRY

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

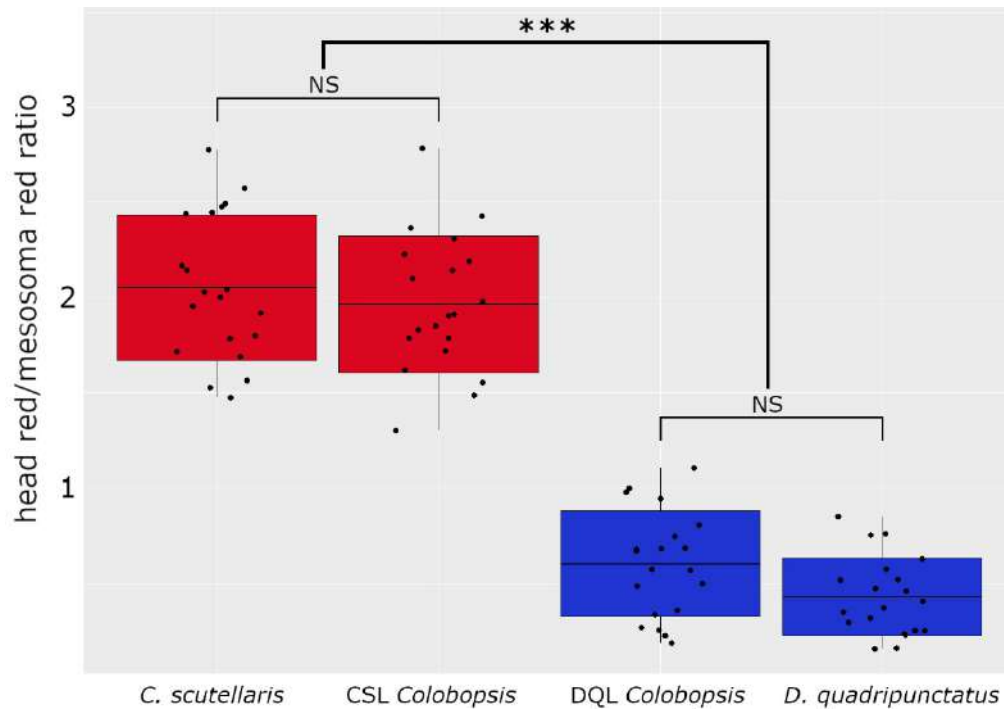




347

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

354 The head red/mesosoma red ratio is statistically different among the two *Colobopsis* patterns and their  
 355 models ( $F_{3,76} = 152.4, p < 0.001$ ) (also see supplementary material). Pairwise comparisons show no  
 356 statistically significant difference between CSL *Colobopsis* and *Cr. scutellaris* ( $p = 0.817$ ; mean  $\pm$  sd  
 357 =  $1.96 \pm 0.36$  for CSL *Colobopsis*; mean  $\pm$  sd =  $2.05 \pm 0.38$  for *Cr. scutellaris*) and between DQL  
 358 *Colobopsis* and *D. quadripunctatus* ( $p = 0.299$ ; mean  $\pm$  sd =  $0.60 \pm 0.27$  for DQL *Colobopsis*; mean  
 359  $\pm$  sd =  $0.43 \pm 0.20$  for *D. quadripunctatus*), while all other comparisons are significantly different ( $p$   
 360  $< 0.001$ ) (Fig. 3).

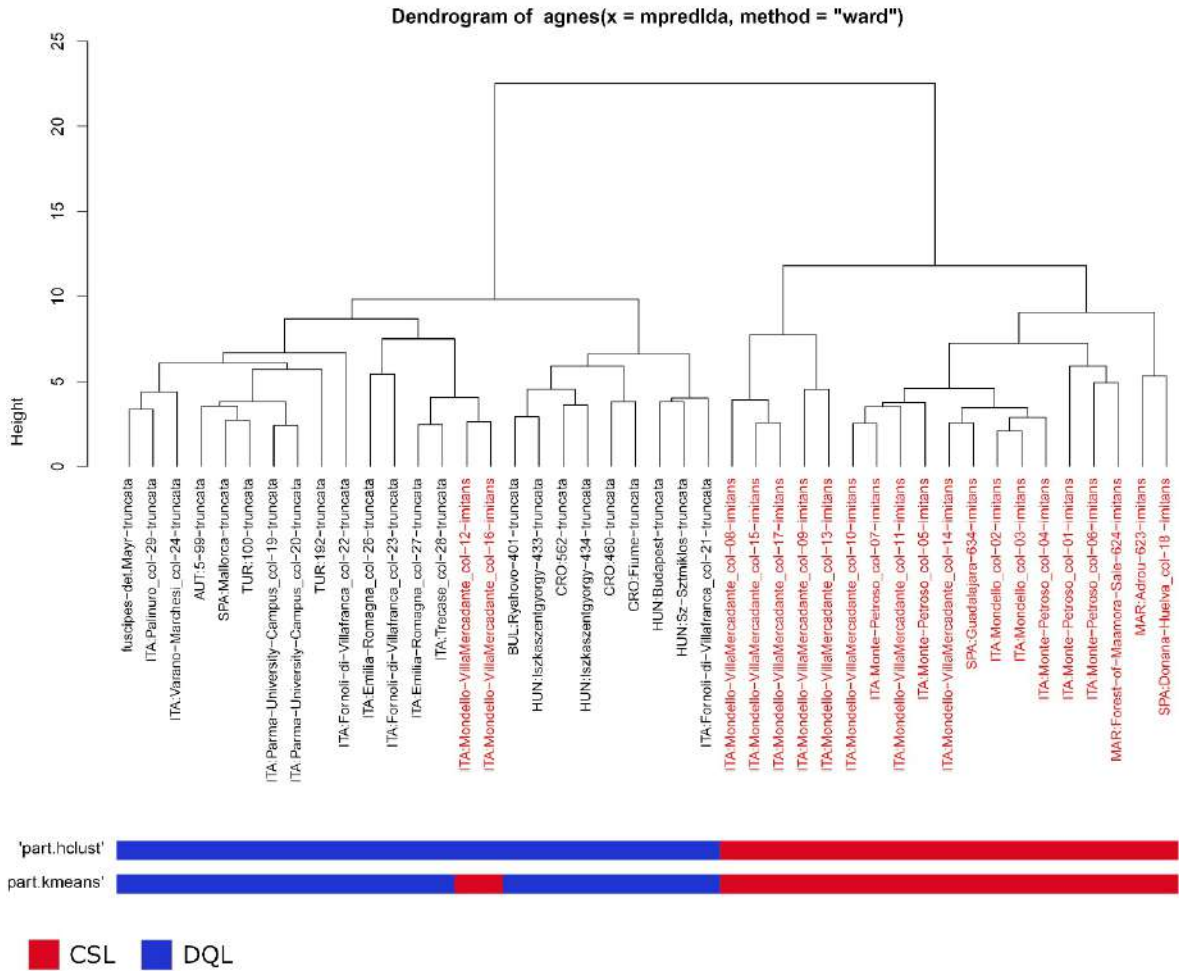


361

362 Figure. 3. Chromatic ratios calculated from pictures of the *Colobopsis* CSL and DQL patterns and from pictures of the  
 363 two putative model species *Cr. scutellaris* and *D. quadripunctatus* (N=20 for each species or chromatic form). Boxplots  
 364 show mean and standard deviation, while whiskers represent minimum and maximum values. Dots are measured  
 365 individuals. Their dispersal on the x-axis is a randomized graphical effect to avoid overlaps.

366 NUMERIC MORPHOLOGY: MULTIVARIATE ANALYSES OF MORPHOMETRIC DATA

367 Two morphological clusters are identified via NC-clustering combined with “kmeans”, and “hclust”  
 368 (Figs. 4). These two clusters correspond to the CSL pattern and DQL pattern specimens, respectively.  
 369 All but two samples are congruently classified via both partitioning methods. The two incongruently  
 370 placed samples (ITA:Mondello-VillaMercadante\_col-12, ITA:Mondello-VillaMercadante\_col-16;  
 371 both CSL pattern from Sicily) are classified as belonging to the CSL cluster (posterior p = 0.85 and  
 372 0.81, geometric means of 3 workers each). Without running samples as wild-cards, the overall  
 373 classification success is 96.3% using all variables in the analysis.

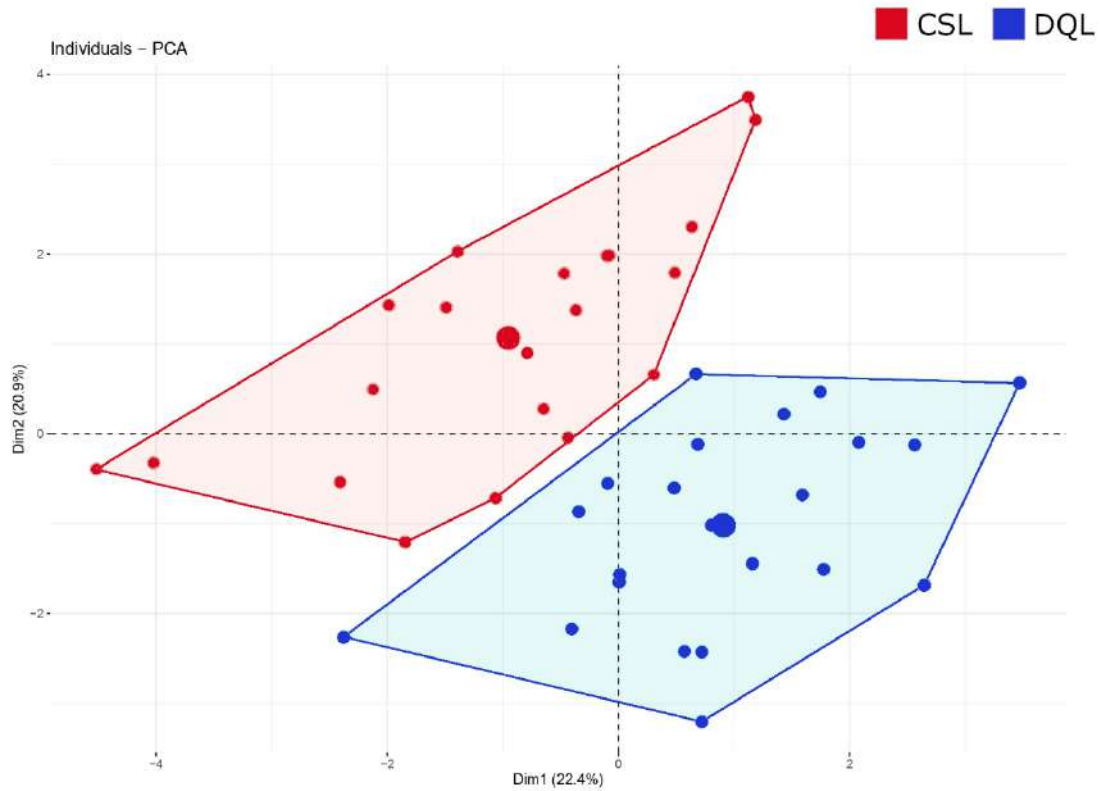


374

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

378

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



379

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

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

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

390  $D(6) = 0.03501 * CW - 0.03384 * SL - 0.03144 * HTL - 0.01762 * ML + 0.03653 * PeSH +$   
 391  $0.07458 * EL + 16.61469$

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

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

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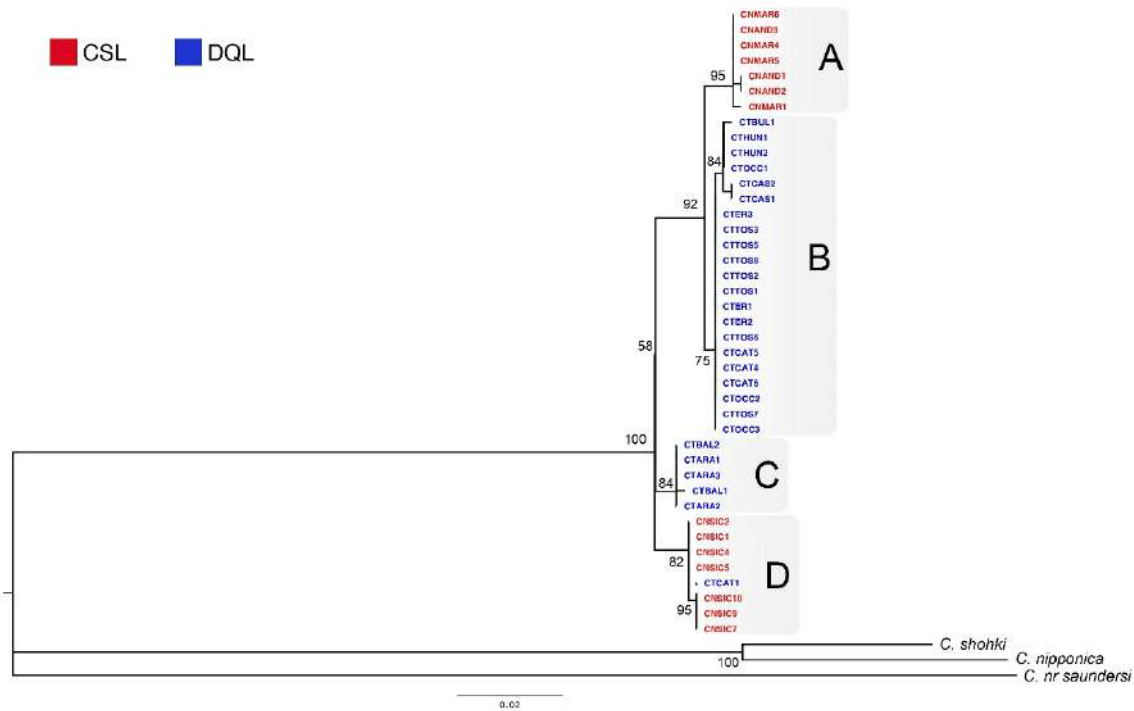
character	CSL (n = 55)	p	DQL (n = 60)
CS	897 ± 51 [725, 1025]	0.924	898 ± 55 [803, 1042]
<b>PreOc/CL</b>	<b>0.546 ± 0.01</b> <b>[0.517, 0.571]</b>	<b>0.000</b>	<b>0.537 ± 0.01</b> <b>[0.517, 0.570]</b>
CL/CW	1.152 ± 0.02 [1.113, 1.198]	0.052	1.145 ± 0.02 [1.106, 1.189]
dAN/CS	0.387 ± 0.01 [0.345, 0.431]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

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

#### 401 GENETICS: MITOCHONDRIAL COI SEQUENCES

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

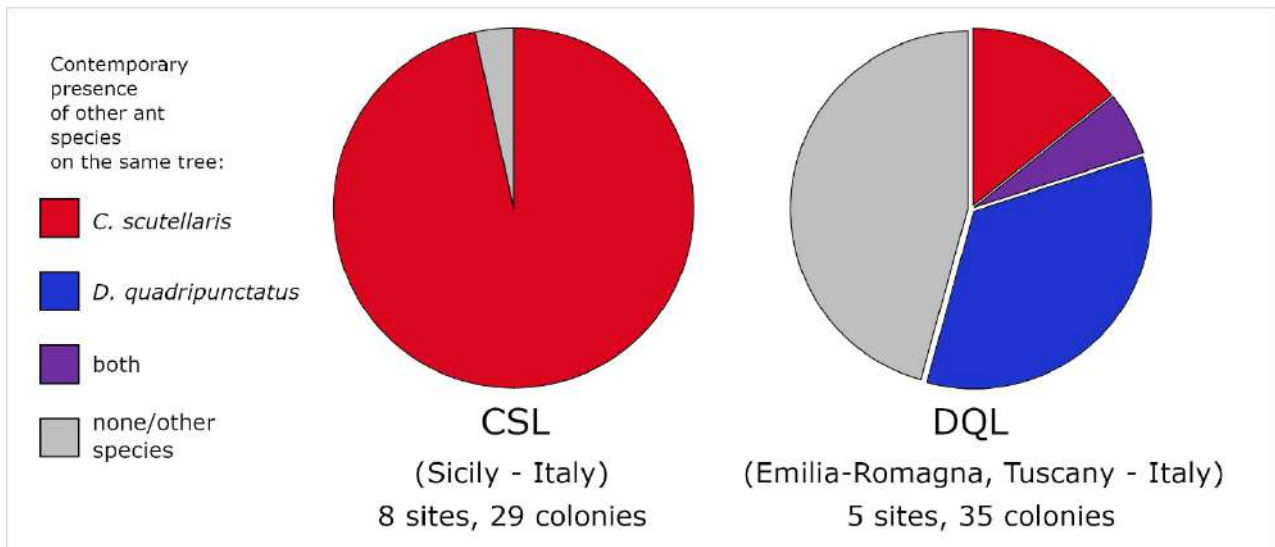
406 Peninsula, and the Occitanic region of France. The clade C groups specimens with the DQL pattern,  
 407 sampled in the Spanish regions of Aragona and Catalonia, and from the Balearic Islands. Finally, the  
 408 clade D is formed by all specimens from Sicily, showing the CSL pattern, and one of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



410  
 411 Figure 6. Maximum likelihood phylogenetic tree based on the barcode fragment of the mtCOI gene from the sequenced  
 412 *Colobopsis* specimens.

### 413 ECOLOGY: COEXISTENCE WITH MODEL SPECIES

414 *Crematogaster scutellaris* is present in 97% of the investigated trees occupied by CSL *Colobopsis*  
 415 and in 20% of those occupied by DQL *Colobopsis*, the difference is statistically significant ( $\chi^2_1 =$   
 416 26.23,  $p < 0.001$ ). *Dolichoderus quadripunctatus* was never detected in trees occupied by CSL  
 417 *Colobopsis*. On the other hand, *D. quadripunctatus* occurs on 40% of the investigated trees occupied  
 418 by DQL *Colobopsis* (6% of which also hosted *Cr. scutellaris*). Results are illustrated in Fig. 7, and  
 419 detailed data is provided in the supplementary material.



420

421

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

422

#### ETHOLOGY: INTERSPECIFIC TRAIL-FOLLOWING BEHAVIOUR

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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.

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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.

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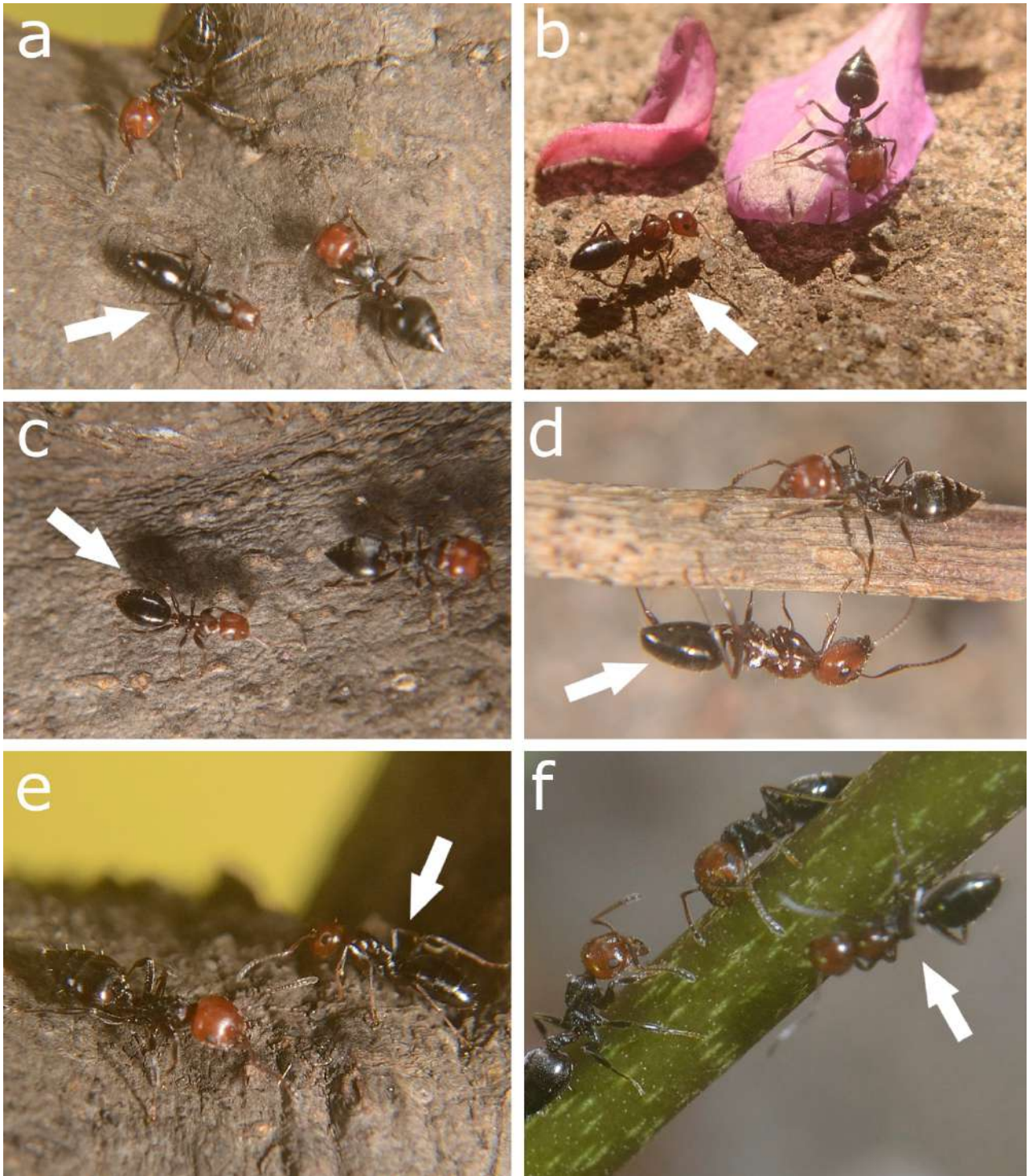
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435 Figure 8. Trail-following behaviour on *Crematogaster scutellaris* trails by other ants (indicated with arrows). On the  
 436 left (a,c,e) CSL *Colobopsis*, on the right (b,d,f) *Camponotus lateralis* observed in the same locality performing the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

438

#### BIOGEOGRAPHY, EVIDENCE DISCUSSION AND FINAL SPECIES HYPOTHESIS

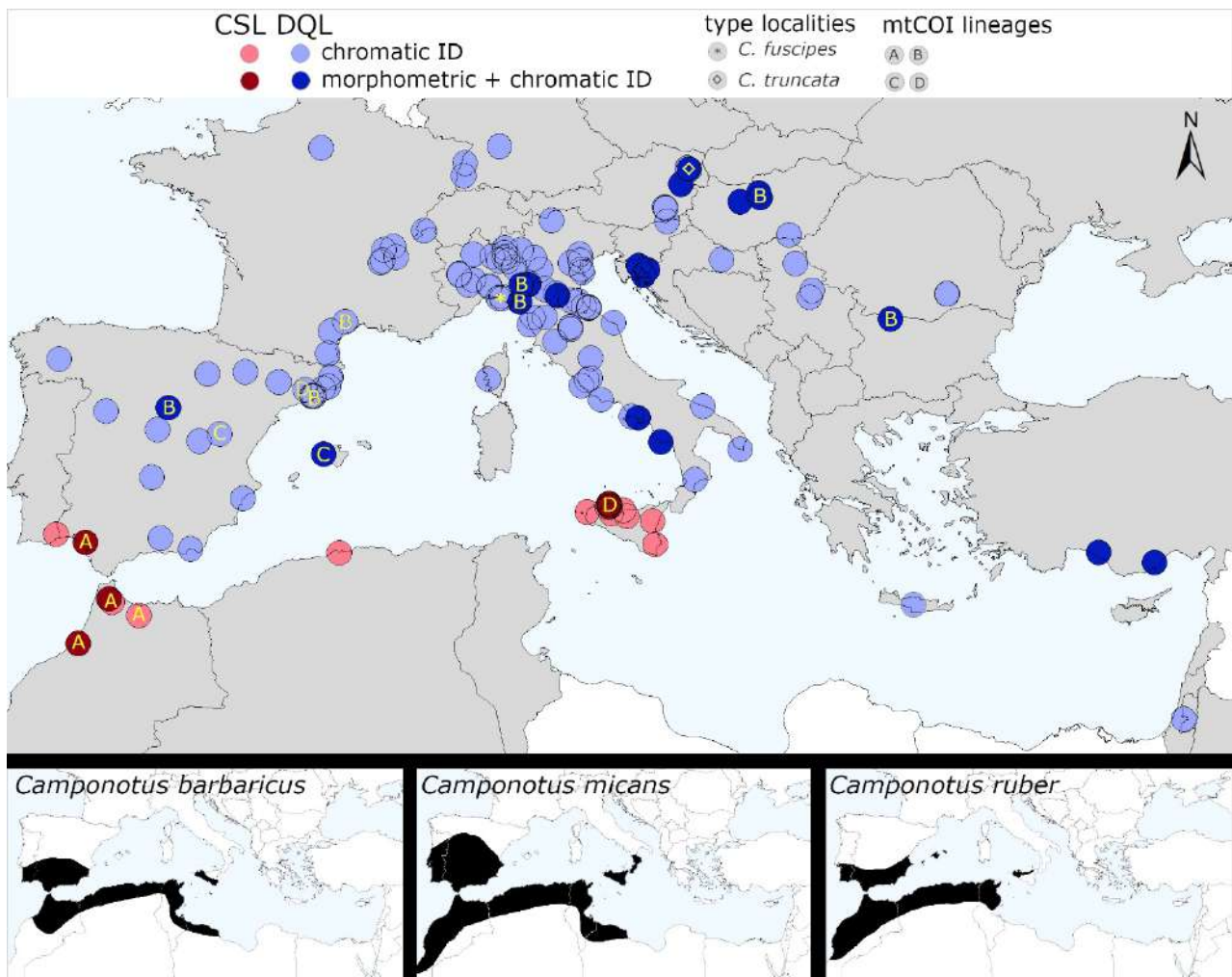
439 CSL and DQL chromatic patterns are found to effectively split into two the Mediterranean *Colobopsis*  
 440 into two populations, occurring allopatrically and each covering a vast geographic region (Fig. 9).  
 441 The DQL pattern characterizes almost the entire European distribution of *Colobopsis*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



442 Western Asia, while the CSL pattern occurs mainly in the Maghreb region (North-Western Africa),  
443 a well-recognized ant biodiversity hotspot (Borowiec, 2014), and in the European regions of greater  
444 biogeographic proximity to it (Sicily and Southern Iberia) (e.g. Alicata & Schifani, 2019; Tinaut &  
445 Ruano, 2021). In particular, this distribution mirrors strikingly well those of some camponotine ant  
446 species such as *Camponotus barbaricus* Emery, 1905, *Ca. micans* (Nylander, 1856) and *Ca. ruber*  
447 Emery, 1925 (Fig. 9; for their distribution see de Haro *et al.*, 1996; Forel, 1890; 1905; Santschi, 1925;  
448 Finzi, 1940; Menozzi, 1940; Cagniant, 1968; 1996; Collingwood & Yarrow, 1969; Baroni Urbani,  
449 1971; Cagniant & Espadaler, 1993; Schembri & Collingwood, 1995; Janicki *et al.*, 2016; Guénard *et*  
450 *al.*, 2017; Schär *et al.*, 2020) and to a slightly lesser extent the distribution of myrmicine ants as the  
451 *Aphaenogaster crocea* species group, *A. sardoa* Mayr, 1855 or the *Temnothorax algiricus-*  
452 *mediterraneus* complex (see Mayr, 1853; Emery, 1880; Forel, 1909; Santschi, 1929; Galkowski &  
453 Cagniant, 2017; Alicata & Schifani, 2019). Ecological and behavioural field surveys across different  
454 Italian regions suggest that the two chromatic patterns are related to quite different lifestyles: the CSL  
455 pattern often coexists with *Cr. scutellaris* and very often follows its trails, while the DQL pattern is  
456 associated with *D. quadripunctatus* without the involvement of frequent trail-following. The CSL  
457 pattern characterized specimens from the Spanish locality where mimicry, close nesting association  
458 and extensive trail-following of *Cr. scutellaris* were described by Carpintero *et al.* (2001; 2005). On  
459 the other hand, the DQL pattern characterized samples from the Austrian region where Wagner (2019)  
460 based his suggestions of close association and mimicry between *Colobopsis* and *D. quadripunctatus*.  
461 A survey conducted in the region of Vienna (Austria) employing similar methodologies to ours  
462 estimated that 36% of the investigated *Colobopsis* colonies (n = 110) nested on trees occupied by *D.*  
463 *quadripunctatus*, confirming the trend observed in our study (Wagner, pers. comm.). However,  
464 interspecific trail-following between DQL pattern *Colobopsis* and either *D. quadripunctatus* or *Cr.*  
465 *scutellaris* as reported in Wagner (2019; personal communication) was never observed during our  
466 surveys and seems to represent a considerably less frequent phenomenon. Such differences between  
467 the two groups in chromatic pattern, biogeography and life history traits could arguably be sufficient  
468 to suggest a separation of the West-Palaearctic *Colobopsis* into two species even according to a  
469 conservative classical taxonomical approach. Moreover, examined specimens from the two chromatic  
470 patterns are also classified into two morphometric clusters, whose separation reaches a significant  
471 threshold indicating heterospecificity according to the current procedures of cryptic ant species  
472 separation (Seifert, 2020). At the same time, the morphometric separation between the two clusters  
473 is relatively narrow, possibly indicating that the two species may have separated quite recently.  
474 Concerning the mtDNA phylogenetic analysis, each clade is unambiguously monophyletic with  
475 respect to morphometric and chromatic evidences (A and D = CSL pattern; B and C = DQL pattern),

476 with only one misplaced DQL specimen (a 2.4% error rate). On the other hand, with respect to  
477 mtDNA, CSL and DQL patterns resulted in polyphy. This can be explained with possible retention  
478 of ancestral polymorphisms and/or introgression of mtDNA (see Chan & Levin, 2005; Willis *et al.*,  
479 2013). These phenomena appear, in fact, largely responsible for the actual estimate of paraphyly  
480 emerging from mtDNA phylogenies analyses in about 20% of animal species (Funk & Omland, 2003;  
481 Ross, 2014). Mitochondrial DNA introgression is, like in other eukaryotic groups, quite frequent in  
482 ants (e.g. Darras & Aron 2015; Beresford *et al.* 2017; Seifert, 2018), and coalescence during  
483 speciation commonly results in species undergoing through phases of polyphyly and paraphyly –  
484 averagely longer in arthropods than in other groups – before normally reaching monophyly due to the  
485 stochastic process of complete lineage sorting (Avice, 2004; Ross 2014). In the presently analyzed  
486 taxa, this would support the hypothesis of the recent divergence. Due to their geographic origins, the  
487 ambiguous placement of a few specimens during morphometric or genetic analyses also seems better  
488 supported by this hypothesis than by hybridization (despite the latter being relatively frequent in  
489 European ants, e.g. Steiner *et al.*, 2011; Seifert, 2018; 2019b).

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



504

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

508

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

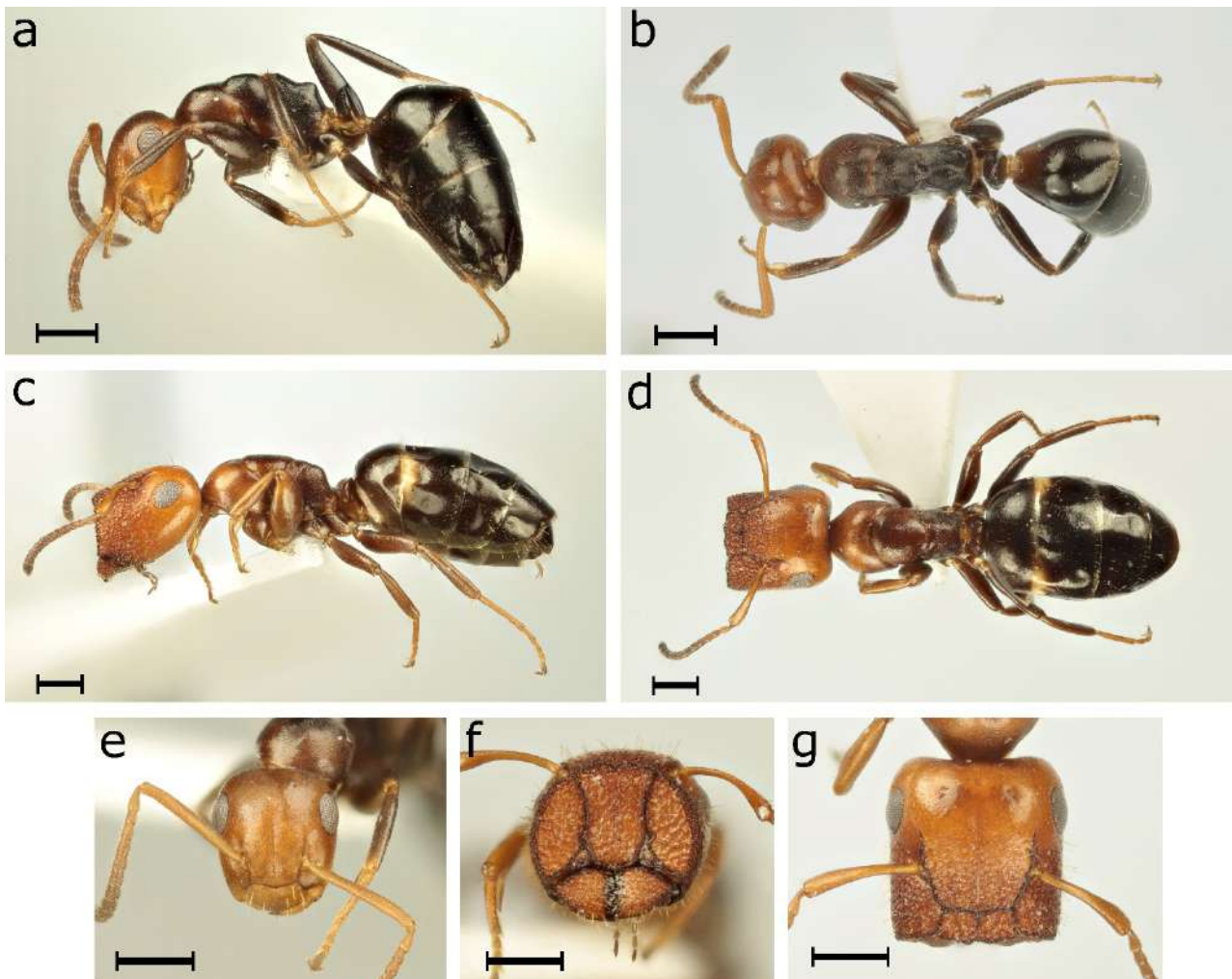
509 **Etymology:** imitans is the present participle of the latin verb imitor, meaning “imitating”, and is here  
 510 used in apposition. It refers to the interpretation that this species resembles *Cr. scutellaris*.

511 **Type series:** 1 holotype worker (Figure 10) and 14 paratype workers from Mondello, Sicily (Italy),  
 512 38.1953, 13.3354, 5 m, 14.X.2018, E. Schifani leg. The holotype is stored in the Hungarian Natural  
 513 History Museum collection.

514 **Worker description:** Morphometric indexes are shown in Tab. 2. Head subrectangular, on all sides  
 515 rounded. A straight, central furrow runs from the frontal triangle to the level at which the frontal  
 516 carinae end. Eyes large, ocelli extremely reduced. Antennae of 12 segments, without a distinct  
 517 antennal club. Pronotum significantly wider than the rest of the mesosoma. In lateral profile,  
 518 pronotum and mesonotum gently convex, propodeum profile often showing a central concavity thus

519 having a saddle-like appearance. Petiolar scale profile anteriorly roundly concave and posteriorly  
520 straight, its dorsal crest excavated in frontal view. Promesonotal and mesoepinotal sutures as well as  
521 metathoracic and propodeal spiracles well-visible. All legs with well-developed tibial spurs, but more  
522 so in the anterior legs which are characterized by strikingly large femurs (identical to *Co. truncata*,  
523 function unknown). Pigmentation as described in the CSL model. Very fine alveolate to areolate  
524 sculpture covering the whole body and appendages. Few erect hairs near the posterior margin of the  
525 vertex, between the frons and on the clypeus, and few others on the gaster tergites. See Figs 1, 8, 10,  
526 13.

527 **Soldier (= phragmotic major worker) description:** Measurements (2 specimens from Sicily): CL  
528 = 1327, 1419; CW = 1262, 1470; SL = 865, 942; ML = 1752, 1774; MW = 921, 1103; EW = 264,  
529 331; EL = 409, 459; CS = 1294, 1444; CL/CW = 0.96, 1.05; SL/CS = 0.65, 0.67; ML/CS = 1.23,  
530 1.35. Large phragmotic head with a cylindrical shape, and a flattened anterior part formed by the  
531 mandibles, part of the clypeus and of the genae. In the distalmost half, it is characterized by a strong  
532 areolate-rugose sculpture and a dense coverage of thick and short erect hairs. Rest of the shape,  
533 sculpture and pigmentation generally similar to the worker but white dots or stripe on the first gastral  
534 tergite sometimes very evident. See Fig. 10.



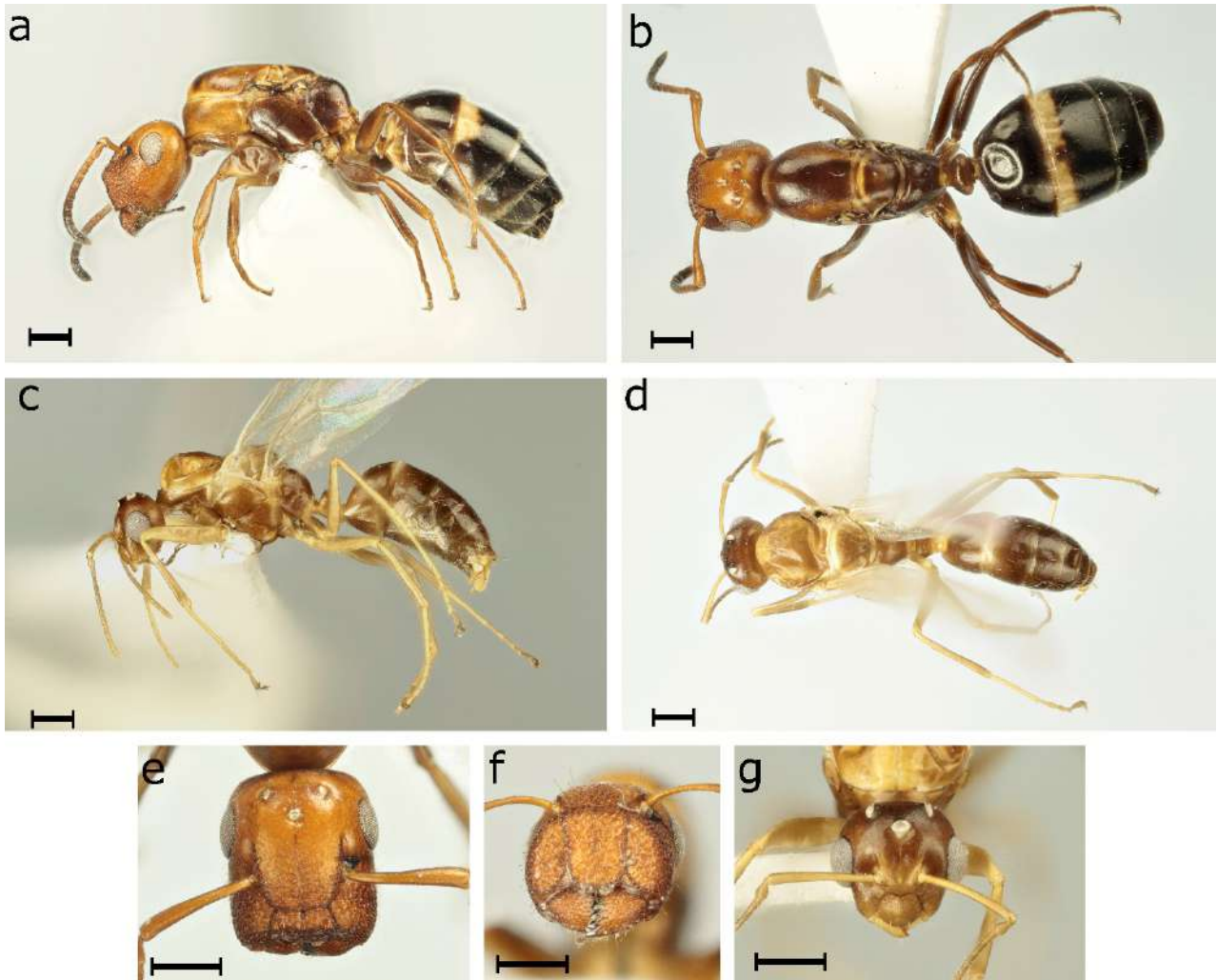
535

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

539 **Queen description:** Measurements (3 specimens from Sicily): CL = 1437-1531; CW = 1281-1406;  
 540 SL = 1156-1218; ML = 2687-3031; MW = 1281-1312; EW = 325-362; EL = 525-537; CS = 1359-  
 541 1468; CL/CW = 1.08-1.11; SL/CS = 0.83-0.87; ML/CS = 1.93-2.22. Large phragmotic head very  
 542 similar to the soldier not only in shape but also in size (despite larger body size), but well-developed  
 543 ocelli, eyes much larger and much longer scapi. Immediately distinguishable by the larger, dorsally  
 544 flatter mesosoma, which is largely unsculptured and shiny. Propodeum profile similar to the end of  
 545 soldiers' propodeum. Head red as in the worker, but the mesosoma is brownish and the white dots or  
 546 stripe on the first gaster tergite are/is evident. See Fig. 11.

547 **Male description:** Measurements (3 specimens from Sicily): CL = 875-1093; CW = 781-1000; SL  
 548 = 937-1001; ML = 2281-2437; MW = 1062-1218; EW = 300-387; EL = 462-525; CS = 828-1046;  
 549 CL/CW = 1.09-1.17; SL/CS = 0.92-1.20; ML/CS = 2.32-2.75. Small, subrectangular head with large  
 550 ocelli and very large eyes protruding laterally. Toothless mandibles. Relatively large mesosoma,

551 propodeum more gently rounded than in queens or workers. Petiolar node very low and round.  
552 Sculpture very weak, mesosoma shiny. Mandibles very hairy, other hairs on clypeus and gaster. Entire  
553 body ferruginous or brownish, gaster blackish. See Fig. 11. Genitalia as in Fig. 12.



554  
555 Figure 11. *Colobopsis imitans* sp. nov.: a,b,e,f) queen, c,d,g) male. Specimens from the type locality. Scale  
556 bars: 0.5 mm. Pictures also available on AntWeb.org database, specimen codes: ANTWEB1041483 and  
557 ANTWEB1041484.



558

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

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

574 **Biological, ecological and phenological notes:** Relatively thermophilous, in Sicily occurring from  
575 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  
576 in Spain so far known from coastal lowland areas. Probably very common but also heavily under-  
577 recorded due to cryptic arboreal lifestyle, low colony population (most-likely monogynous), effective  
578 mimicry and long periods of inactivity during the most arid and coldest times of the year. Workers  
579 and soldiers are unlikely to descend to the ground but were observed to do so at least once, following  
580 a sparsely populated *Cr. scutellaris* trail. Soldiers in general are very difficult to be found outside the  
581 nest and usually seen acting as gatekeepers of the nest entrance. Founding queens were observed to  
582 do the same. Nests are hidden in minute holes on the dead parts of arboreal trunks, where *Co. imitans*

583 sp. nov. often seems to act as a secondary user of cavities excavated by xylophagous insects. It  
584 exploits *Andricus quercustozae* (Bosc, 1792) oak galls as nests (occupying about 15% of galls  
585 collected in Sicily's Bosco della Ficuzza in a recent survey, authors' unpublished data), in a similar  
586 way to *Co. truncata* (see Giannetti *et al.*, 2019; 2021; Fürjes-Mikó *et al.*, 2020). Polydomy appears  
587 probable due to repeated findings of groups of workers without queens within oak-galls. Observed  
588 nesting on several and diverse plant species, including at least: *Citrus reticulata* Blanco, 1837, *Ci.*  
589 *sinensis* (L.) Osbeck, 1765, *Laurus nobilis* L., *Olea europaea* L., *Quercus ilex* L., *Q. pubescens*-  
590 group, *Q. suber* L., *Pyrus communis* L., *Pittosporum tobira* (Thunb.) W.T.Aiton. Apparently dense  
591 populations were found in old *Citrus* orchards and relatively sparse *Q. suber* woods, but also in  
592 deciduous oak forests. However, it occurs in a broad range of habitats from cities to agricultural lands  
593 to natural forest habitats, but information available so far is insufficient to depict a satisfactory picture  
594 of habitat preferences. Despite the earlier claim by Carpintero *et al.* (2005), there is currently no  
595 evidence backing the fascinating hypothesis that *C. imitans* sp. nov. foundress queens prefer trees  
596 hosting *Cr. scutellaris* to found their colonies. A focused investigation on this topic would be  
597 interesting. Nuptial flights for *Co. imitans* sp. nov. occur approximately in the same period of *Co.*  
598 *truncata* (alates in Sicily observed from June 30 to July 13, n = 5, see supplementary material).  
599 Winged queens and males were repeatedly seen attracted by artificial lights at night.

600

## FINAL REMARKS

601 Body pigmentation pattern is the only qualitative character that makes *Co. imitans* sp. nov.  
602 identifiable without recurring to quantitative data, as it is otherwise morphologically extremely  
603 similar to *Co. truncata* up to a significant level of crypsis (see Wagner *et al.*, 2018). These  
604 pigmentation differences among West-Palearctic *Colobopsis* so far went completely unnoticed, the  
605 sole exception being a brief statement by Santschi (1929) noting that the chromatic aspect of the  
606 Moroccan *Co. truncata* is different than the typus one by its lighter head color. The case we  
607 documented can be considered one of the few where such element is important for species  
608 discrimination in European ants. While body pigmentation has been used without scientific rigor by  
609 some past ant taxonomists (see the example described by Boer, 2008), it can be important for the  
610 morphological identification of species such as *Formica clara* Forel, 1886 and *F. cunicularia*  
611 Latreille, 1798 or even fundamental for many *Temnothorax* spp. (Seifert & Schulz, 2009; Seifert,  
612 2018) and should not be overlooked in multi-character approaches for taxonomic purposes. Under  
613 these conditions, checking pictures uploaded on citizen science platforms and social media proved to  
614 be significantly helpful to obtain data on these species distribution, evidencing once more the  
615 uncovered potentials of citizen science in the study of ant distribution (e.g. Lucky *et al.*, 2014; Zhang



616 *et al.*, 2019; Castracani *et al.*, 2020; Sheard *et al.*, 2020) and more in general of platforms hosting  
617 these kind of data in the study of insect distribution (e.g. Schifani & Paolinelli 2018; Hochmair *et al.*,  
618 2020; Ruzzier *et al.*, 2020; Winterton, 2020). Moreover, behavioural data are seldom considered in  
619 integrative taxonomic approaches dealing with ants, but they may prove valuable in some cases (see  
620 also Ronque *et al.*, 2016). Finally, while mtDNA has a decent identification performance, our data  
621 clearly support the idea that it should not be used as the primary source of information to take  
622 taxonomic decision on species delimitation (see Seifert 2020).

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

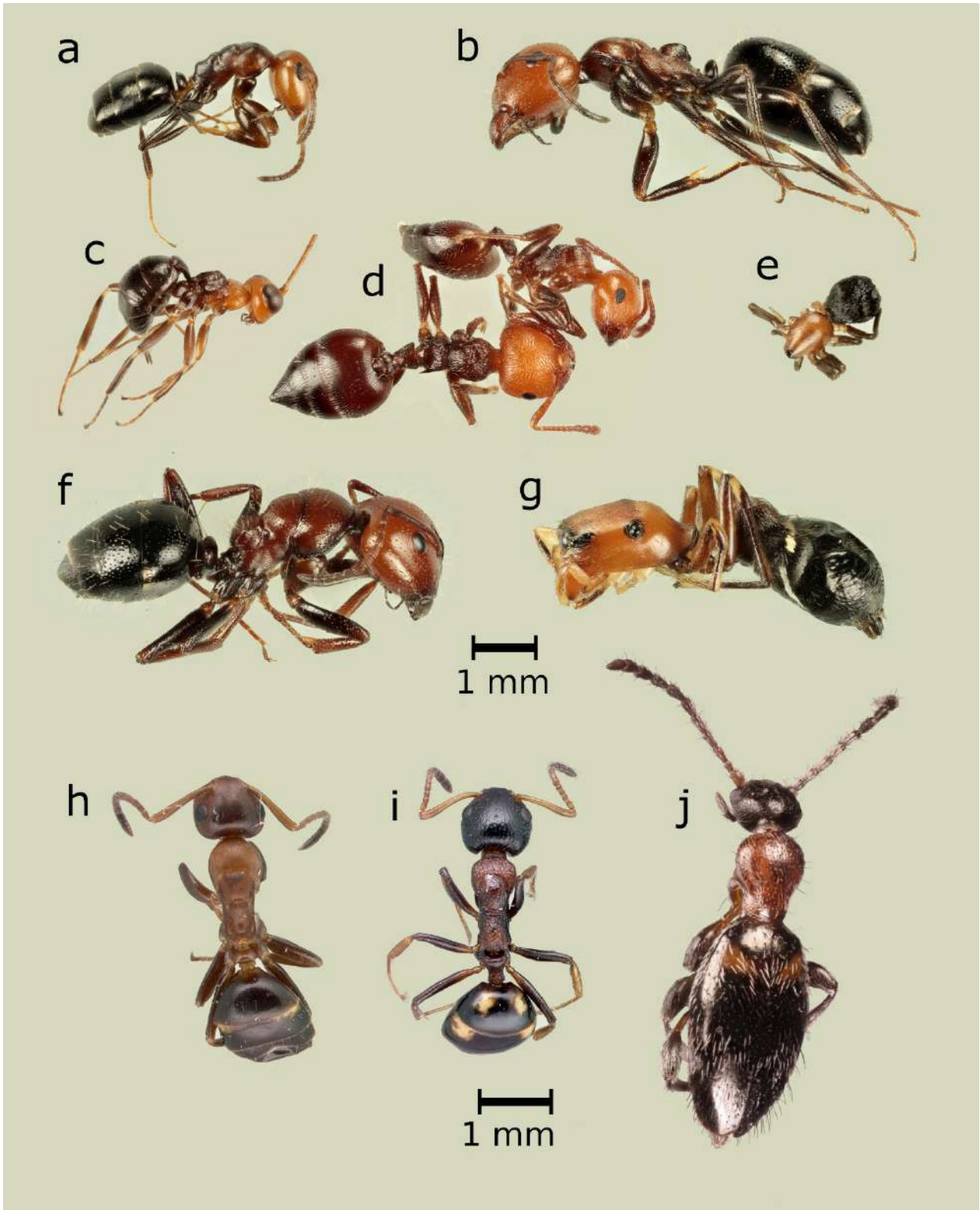
634 The fact that *Co. imitans* sp. nov. and *Co. truncata* greatly differ chromatically is interesting if one  
635 considers that phylogenetics and morphometry suggest a recent differentiation. In evolutionary terms,  
636 the most likely interpretation is to link such differentiation to a shared strategy based on ant-mimicry  
637 modulated according to the presence or absence of certain good models across different  
638 Mediterranean regions. Both *D. quadripunctatus* and *Cr. scutellaris* have much more populous  
639 colonies than *Co. imitans* sp. nov. and *Co. truncata*, while both are likely less palatable for predators  
640 and armed with effective toxic substances (Cavill & Hinterberger, 1960; Wagner, 2019). Therefore,  
641 even though only *Cr. scutellaris* is truly recognized as an aggressive and dominant species (Santini  
642 *et al.*, 2007; Frizzi *et al.*, 2015; Castracani *et al.*, 2017; Seifert, 2018), both appear to possess the  
643 required traits to be considered good Batesian models to the non-aggressive and relatively unarmed  
644 *Colobopsis* (which still possess some formic acid). However, across the distribution range of *Co.*  
645 *imitans* sp. nov., *D. quadripunctatus* is almost completely absent: it does not inhabit the Maghreb, its  
646 Iberian distribution is concentrated to the North and in Sicily it is considered to be very rare (Schifani  
647 & Alicata, 2018; Cabanillas *et al.*, 2019). Yet it is interesting to note that the opposite is not true for  
648 *Co. truncata*: the latter is not only sympatric with *D. quadripunctatus* along its entire range (including  
649 in the hypothesis that easternmost *Colobopsis* are *Co. truncata*: see Reznikova, 2003; Ghahari *et al.*,

650 2015), but also sympatric with *Cr. scutellaris* in south-western Europe and with *Cr. schmidti* in the  
651 east. Finally, it is worth noting that the white dots or stripe that have been linked to mimicry of *D.*  
652 *quadripunctatus* in *Co. truncata* (Forel, 1886; Wagner, 2019) are/is absent or hardly visible in *Co.*  
653 *imitans* sp. nov. workers but at the same time well-visible in at least a few soldiers and especially  
654 queens that we inspected. Following the mimicry interpretation of the chromatic patterns, it is  
655 imaginable that this character is an ancestral remnant but that selective (predatory) pressures leading  
656 to perfect mimicry are stronger on workers than on queens or soldiers which rarely leave the safety  
657 of their nest.

658 Mimicry may be considered as a third defensive strategy of *Colobopsis* unique or very rare among  
659 ants after suicidal autothysis and phragmosis (Emery, 1925; Maschwitz & Maschwitz, 1974;  
660 Davidson *et al.*, 2012; Shorter & Rueppel, 2012; Ward *et al.*, 2016; Laciny *et al.*, 2018). Apart from  
661 the two species we treated, the only existing claims of mimicry in the genus come from  
662 morphologically very different and likely unrelated species from Fiji Islands (Santschi 1928; Wheeler  
663 1934). However, since several other Palearctic *Colobopsis* species share a general morphological  
664 similarity with *Co. imitans* sp. nov. and *Co. truncata*, likely belonging to the same evolutionary  
665 lineage, it is possible that some of them represent yet undiscovered mimics. It also appears that  
666 mimicry may have played a powerful role driving phenotypic diversification of West-Palearctic  
667 *Colobopsis*: *Co. imitans* sp. nov. and *Co. truncata* can be considered as the only well-documented  
668 example among ants that suggests mimicry-driven phenotypic divergence of sister species. In  
669 comparison, the intraspecific case of mimicry pattern divergence in *Ca. lateralis* is one of much more  
670 modest differentiation (Wagner, 2014; Seifert, 2019a). Similar accounts are not particularly common  
671 in other organisms either, but recently an interesting scenario of strong diverging aposematic patterns  
672 coupled with minimal genetic differentiation was described by for a group of frogs (Tarvin *et al.*,  
673 2017).

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

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



693

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

700 from Bulgaria, AntWeb code CASENT0280000, photographer Michele Esposito), i) *D. quadripunctatus* (specimen from  
701 Czech Republic, AntWeb code CASENT0179916, photographer Michele Esposito), j) *Formicomus pedestris* (Rossi,  
702 1790) (Coleoptera: Anthicidae) from Parma (Italy).

703 Interspecific but intrageneric trail-following described for some ants is likely relatable to  
704 phylogenetic proximity and morphofunctional and behavioural similarities or similar foraging  
705 strategies among species (e.g. Grasso *et al.*, 2002 and references therein). On the other hand, the  
706 significance of the recorded *Colobopsis-Crematogaster* trail-following is not yet fully clear to us.  
707 Similar cases (such as that of *Ca. lateralis*) have often been referred to as parabiosis, but we avoided  
708 this term since quite different interpretations of its meaning coexist creating ambiguity: it is  
709 sometimes used to simply indicate trail-following but in other occasions it implies also nest-sharing  
710 (see Forel, 1898; Swain, 1980; Vantaux *et al.*, 2007; Menzel *et al.*, 2008; 2010; 2014a; 2014b; Seifert,  
711 2018). Outside of *Co. imitans* sp. nov. and *Co. truncata*, many other camponotine ants follow  
712 *Crematogaster* trails without always acting as mimics (Ito *et al.*, 2004; Vantaux *et al.*, 2007; Menzel  
713 *et al.*, 2008; 2014). Baroni Urbani (1969) and Menzel *et al.* (2014) speculated that the compounds  
714 used as trails pheromones by *Crematogaster* are generally easily perceived by *Camponotus*, this  
715 capacity representing an important pre-adaptation to trail-following. During our field surveys, we  
716 unexpectedly observed several workers of *Camponotus piceus* (Leach, 1825) (a relative of *Ca.*  
717 *lateralis* with no resemblance of *Cr. scutellaris*, see Seifert, 2019a) easily following part of a *Cr.*  
718 *scutellaris* trail to the canopy of a tangerine tree while avoiding *Cr. scutellaris* attacks. It may be  
719 possible that many other similar camponotine ants rarely perform the same without possessing a  
720 specific mimicry adaptation, which can partly explain the occasional observations of trail-following  
721 between *Co. truncata* and *Cr. scutellaris* (Zimmermann 1934; Goetsch 1942; Baroni Urbani 1969;  
722 Wagner 2014). Still, in the overwhelming majority of the documented cases inter-specific trail-  
723 following is associated either with mimicry (as for *Colobopsis imitans* sp. nov., see Gobin *et al.*,  
724 1998; Ito *et al.*, 2004; Menzel *et al.*, 2010; Powell *et al.*, 2014) or with nest-sharing (Vantaux *et al.*,  
725 2007; Menzel *et al.*, 2008; 2014). For mimics, it appears to be primarily a way to better hide within  
726 the ranks of the model species, an example of dilution effect (Lehtonen & Jaatinen, 2016), which may  
727 also apply to a certain degree non-mimic ant species as well. However, the trail-followers may be  
728 able to obtain additional benefits in their success of locating trophic resources, sometimes even  
729 establishing somewhat parasitic relationships (see Vantaux *et al.* 2007; Menzel *et al.* 2010; 2014a;  
730 2014b). It is unclear whether *Colobopsis* ants may also benefit from a similar mechanism although a  
731 parasitic aspect of its trail-following behaviour has been suggested by Baroni Urbani (1969).

732

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