



RESEARCH ARTICLE - ANTS

Description of the male in the ant *Proformica longipilosa* Galkowski et al., 2017 (Hymenoptera, Formicidae, Formicinae) and notes on European *Proformica*

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Abstract

In most ant species with flightless queens, such as the genus *Proformica* Ruzsky, 1902, winged males are crucial for allowing proper gene flow between and within populations. Furthermore, since these taxa often have a complex taxonomy, it is all the more interesting to study this often-neglected caste to gain a better understanding of the speciation dynamics at work. Here, we describe for the first time the male of *Proformica longipilosa* Galkowski et al., 2017, based on two individuals collected on the slopes of Mont Ventoux, France. This description completes our knowledge of the genus *Proformica* in France, as all the castes are now known for the three species occurring in the country. Consequently, we provide a preliminary key to the French *Proformica* males. Additionally, comparing our specimens with those of other European species, we distinguish two morphological groups in the genus: one characterised by males with very developed eyes (*nasuta* type male) and the other by males with more reduced eyes (*ferreri* type male). Finally, we provide informal but unique observations of *Proformica nasuta* (Nylander, 1856) reproductive behavior, illustrating the probably very weak dispersal capacity of the species within this genus.

Introduction

The ant genus *Proformica* Ruzsky, 1902 is a small Formicinae genus containing 30 valid species and two valid subspecies (Bolton, 2025), and is distributed discontinuously throughout the Palearctic. A few species inhabit thermophilous plains and plateaus in Western Europe, from the Iberian Peninsula to the first slopes of the Southern Alps in France, whereas the others occur from the Balkan dry mountains to the Chinese and Mongolian steppes (Antmaps.org: Janicki et al., 2016; Guénard et al., 2017). The taxonomic state of *Proformica* is currently impressively chaotic, and despite recent revisions of Greek (Borowiec & Salata, 2022, 2025) and of Shaanxi Province, China (Zhu et al., 2022) faunas, most species remain poorly understood. Decades-long undersampling, lack of

interest from the scientific community, and many biological features made this genus a black box among Palearctic ants. For example, the high intraspecific but relatively weak interspecific morphological variations in workers – the traditional taxonomic unit in myrmecology – significantly impede species delimitation and identification of most samples (Galkowski et al., 2017; Lebas et al., 2023). Also, the queens often being apterous or brachypterous, a strong female philopatry coupled with weak male dispersion hardens the population/species differentiation, especially in mountainous environments where two closely related populations (both geographically and evolutionarily) can diverge quite quickly (Sanllorente et al., 2015). In the last decade, sampling efforts in Greece, Spain and France allowed to collect more material and particularly nest series with males, queens and their



conspecific workers, bettering our understanding of the genus (Galkowski et al., 2017; Lebas & Galkowski, 2019a, 2019b; Galkowski et al., 2022; Salata & Borowiec 2022, 2025; Lebas et al., 2023). Such complete collections are essential for taxonomic purposes, as doing morphology on other castes than workers may be pretty successful in many problematic taxa, especially when using male individuals. This has been demonstrated recently in various genera across different subfamilies: in the Ponerine *Dinoponera* Roger, 1861 (Dias & Lattke, 2021), the Myrmicine *Aphaenogaster* Mayr, 1853 (Schifani et al., 2023), the Dolichoderine *Tapinoma* Foerster, 1850 (Seifert et al., 2024), or the Formicine *Nylanderia* Emery, 1906 (Williams et al., 2024).

Following the redescription of *P. nasuta* (Nylander, 1856) and the description of *P. cerdanyensis* Galkowski et al., 2022, with all castes, we propose to expand the knowledge of the genus in France by describing here the male of *P. longipilosa* Galkowski et al., 2017. We then provide a preliminary key for French *Proformica* males, as well as a brief behavioral note on reproduction in *P. nasuta*. Finally, we discuss these findings at the European scale.

Material and Methods

Depositories and Specimens

CGPC – Christophe Galkowski Personal Collection, Saint-Aubin-de-Médoc, France.

LFPC – Lorenzo FRAYSSE Personal Collection, Montpellier, France.

Fieldwork took place around Chalet Reynard, on the southern slope of Mont Ventoux, in Southeastern France, where *P. longipilosa* was initially described (Galkowski et al., 2017). At an altitude of 1450m, the collecting site is essentially a limestone scree with sparse *Pinus spp*, *Juniperus communis*, and *Lavandula sp* as the main woody cover, a few herbaceous plants thriving between rocks (Fig 1). There, *P. longipilosa* is very common and nests under stones of all sizes. The other ant species we encountered at the collecting site were *Formica cunicularia* Latreille, 1798, *Tapinoma erraticum* (Latreille, 1798), *Temnothorax tuberum* (Fabricius, 1775), and *Tetramorium alpestre* Steiner, Schlick-Steiner & Seifert, 2010.

FRANCE • 1 male; Bédoin, Mont Ventoux, Chalet Reynard; 44.153, 5.321 ± 50 m ; 1450 m; 25 Jul. 2019, 14:00; L. FRAYSSE leg.; Pine-Juniper-Lavandula scree, sweeping low vegetation; L. FRAYSSE Rec.; deposited in LFPC under LFPC003248 (also on Antweb.org) • 1 male, same data as for preceding but deposited in CGPC.

For comparison with males of *P. cerdanyensis* and *P. nasuta*, we imaged specimens used in previous studies (Galkowski et al., 2017; Galkowski et al., 2022).

Measurements and indices

We recorded morphometric traits using a Perflex Zoom Pro 10.26 stereomicroscope, equipped with a micrometer, which allowed for magnification ranging from x40 to x100. Measurements are expressed in mm.



Fig 1. Typical habitat of *Proformica longipilosa* on Mont Ventoux, showing the many stones under which nests are built. Picture taken the day of males' sampling, by LF.

HW Maximal head width in frontal view, eyes included.

HL Maximal head length in frontal view, from the vertex to the anterior clypeal margin.

MW In dorsal view, maximal mesosoma width.

SL With the scape in the visual plan, maximal scape length (bilateral mean).

EL With the eye in the visual plan, maximal eye diameter (bilateral mean).

CI = $(HW / HL) * 100$, Cephalic Index

SI = $(SL / HW) * 100$, Scape Index

REL = $(EL / HL) * 100$, Relative Eye Length

Imaging

We imaged our specimens with a Keyence VHX-500 hosted by the Centre de Biologie et Gestion des Populations in Montferrier-sur-Lez, using a x100 magnification.

Behavioral observations

A colony of *Proformica nasuta* was regularly observed by one of us (LF) in a private garden in Nézignan l- Evêque (43.426569, 3.407168; 26 m). Observations took place during sunny mornings in 2015 and 2016, roughly from July 10th to July 20th, and from 10:00 to 12:00.

Results

Identification of male specimens

The two collected individuals were identified as *P. longipilosa* due to: (i) their morphological divergence with those of *P. nasuta*, the only other species known in the region; (ii) the geographic distance and topology between Mont Ventoux and the Pyrenees where lives *P. cerdanyensis*; (iii) the very high density of *P. longipilosa* nests at the collecting site, that is also the type locality of the species (Galkowski et al., 2017).

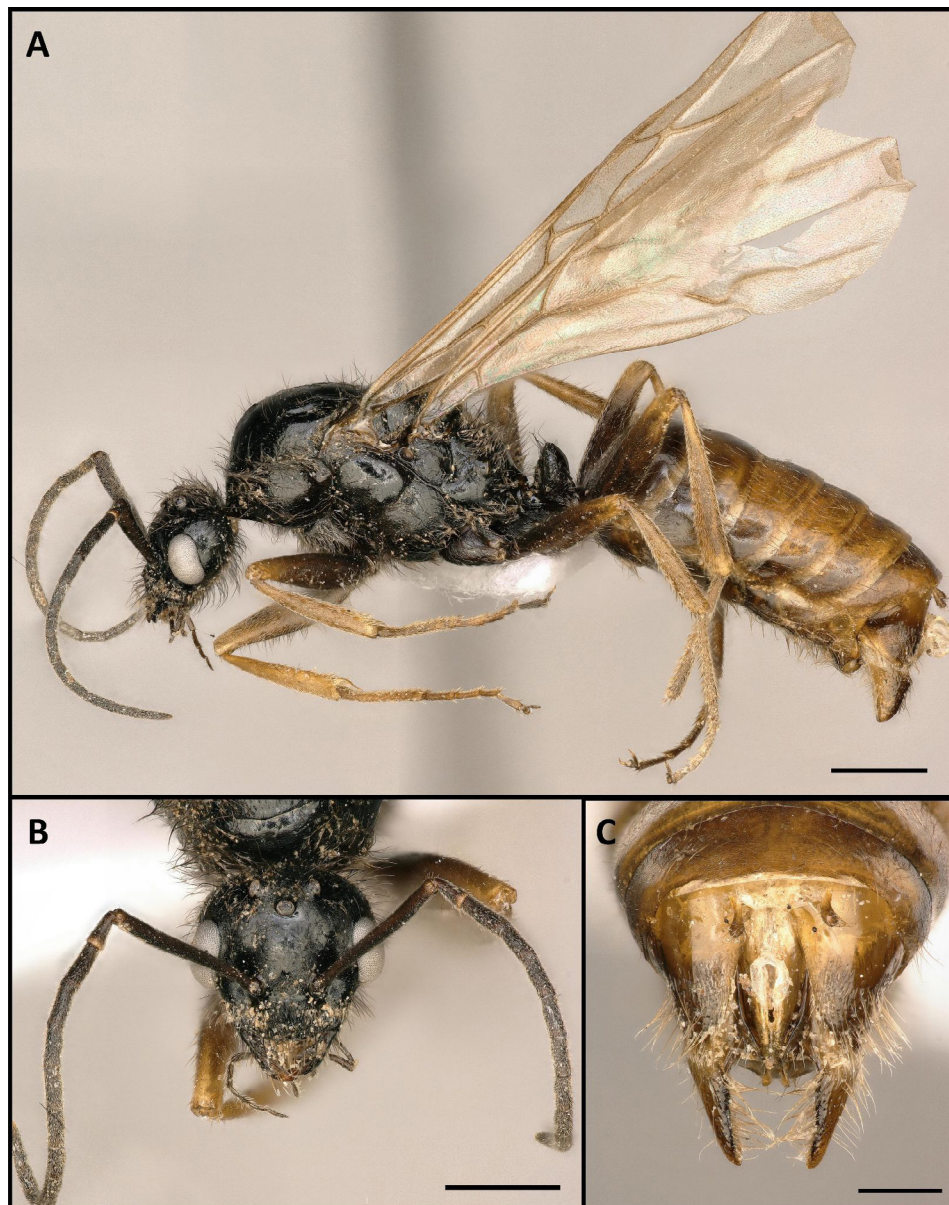


Fig 2. Illustration of *Proformica longipilosa* male, LFPC003248. Note that pilosity has been damaged, and is usually densely homogeneous on the whole head and mesosoma. **A.** Body in lateral view, **B.** Head in frontal view, **C.** Genitalia in dorsal view. Scale bar: 1 mm (**A**, **C**); 0.5 mm (**B**).

Description of *Proformica longipilosa* male

Mean measurements values, expressed in mm (n = 2, details in Table 1): HW 1.44; HL 1.25; SL 1.23; EL 0.57; CI 114; SI 86.15; REL 44.9

Mandibles thin with only an acute apical tooth and a blunt but wide basal tooth that forms a right angle between the masticatory margin and the inner mandibular margin. Surface with sparse and deeply impressed elongated fovea, separated by large smooth and shiny interspaces. Palp formula 6:4. Clypeus distinctly microreticulate, with poorly defined longitudinal rugae in its central third that do not reach the posterior margin. Clypeal carina incomplete, ridging progressively from the posterior margin to a bit less than half clypeal length where it brutally interrupts, forming a tooth-like tubercle visible both in frontal view and in lateral view. Eyes large and globular, elongated. Ocelli protruding from vertex. Head and mesosoma surfaces globally shiny with very thin and weak microreticulations. Wings are fully developed and yellowish. Appendages appear duller due to stronger impression of microreticulations. One tibial spur is very developed on each leg, pectinated on protibiae but simple and curved on mid and hind tibiae. Petiole forming a big and thick scale, dorsal crest slightly but asymmetrically emarginated. Gaster shining despite visible microreticulation. Genitalia strongly protruding, they represent nearly a quarter of gaster length and volume. Head, mesosoma and petiole blackish brown, as well as head appendages, coxae and the proximal femoral half. Remaining of legs and gaster reddish brown. Dark erect pilosity long and dense, especially on the mandibles, the cephalic capsule, mesosoma and petiole. On the gaster, pilosity brown and less dense, mainly restricted to tergites' posterior border, while being more homogenous on the sternites and parameres. Also dense on appendages, particularly on profemora where some setae are as long as the femoral diameter. Scapes with only a few short erect setae and, like the funiculi, covered with short and dense appressed pubescence. Appressed pubescence also present on the gaster, shorter and very sparse on the tergites, longer and denser on the sternites that are quite covered with it. Remaining parts of the body lacking pubescence.

Preliminary key to French *Proformica* species based on the male caste

Few male specimens have been studied from France (n = 6 for *P. nasuta*, n = 5 for *P. cerdanyensis*, n = 2 for *P. longipilosa*), and the basic measurements are insufficient to provide strong support for safely discriminating all species on this basis. However, we consider that the combination of

qualitative morphology, morphometrics, and biogeography is sufficient to produce this preliminary key.

1 - Eye relatively large (REL > 50). Gaster light brown to yellowish red, with sparse relatively short erect pilosity, which is almost restricted to the first tergite. Erect setae on profemora are relatively sparse and short, their maximal length at most equal to or shorter than the maximal femoral width. Overall pilosity light brown (Fig 3C-D). Clypeus without rugae or carina, appearing very shiny despite thin microreticulations. Mandible thin with only an acute apical tooth, the masticatory margin merging with the inner margin in a continuous curve (Fig 3D). Known from the Central and Eastern plains and low mountains of Southern France (between 3.35°E and 6.35°E, south to 44.5°N)..... ***P. nasuta***

- Eye relatively short (REL < 50). Gaster dark brown to brownish red, with relatively long and dense erect setae on most tergites posterior plates, also numerous on the anterior half of the first tergite. Erect setae on profemora dense and long, as long or longer than the maximal femoral width. Overall pilosity darker, from brown on gaster and appendages to blackish brown on the head, the mesosoma and the coxae. Clypeus with a more or less developed carina running from its posterior margin to half of his length. Carina's sides and anterior part of clypeus with more or less impressed longitudinal rugae. Mandible variable. Western Pyrenees and South-Western Pre-Alps..... **2**

2 - Mandibles thin with only an acute apical tooth, the masticatory margin merging with the inner margin in a continuous curve. Clypeus with a simple and poorly defined carina on its posterior half, with few rugae anterior to it (Fig 3B). General coloration dark brown to black with gaster nearly concolorous with head and mesosoma, only tibiae and tarsi being yellowish brown (Fig 3A). Eyes longer (REL = 46.7). Known only from a few close localities in Cerdagne, Western Pyrenees (between 1.85°E and 1.95°E)..... ***P. cerdanyensis***

- Mandibles wider, with an acute apical tooth and a more or less blunt basal tooth, forming a right angle between the masticatory margin and the inner margin. Clypeus with a small carina that interrupts in a small protruding process, best visible in lateral view. Anterior clypeal half weakly but distinctly rugose, some rugae running up to the carina (Fig 2B). General coloration dark brown to black with gaster slightly brighter than head and mesosoma (Fig 2A). Eyes shorter (REL = 44.9). Restricted to Southern pre-Alps mountains (between 4.8°E and at least 7.2°E) ***P. Longipilosa***

Table 1. Individual measurements of our two males of *Proformica longipilosa* (expressed in mm).

Individual	HW	HL	SL	EL	CI	REL	SI
Male 1	1,37	1,21	1,23	0,54	112	44,62	90,3
Male 2	1,5	1,29	1,22	0,59	116	45,18	82

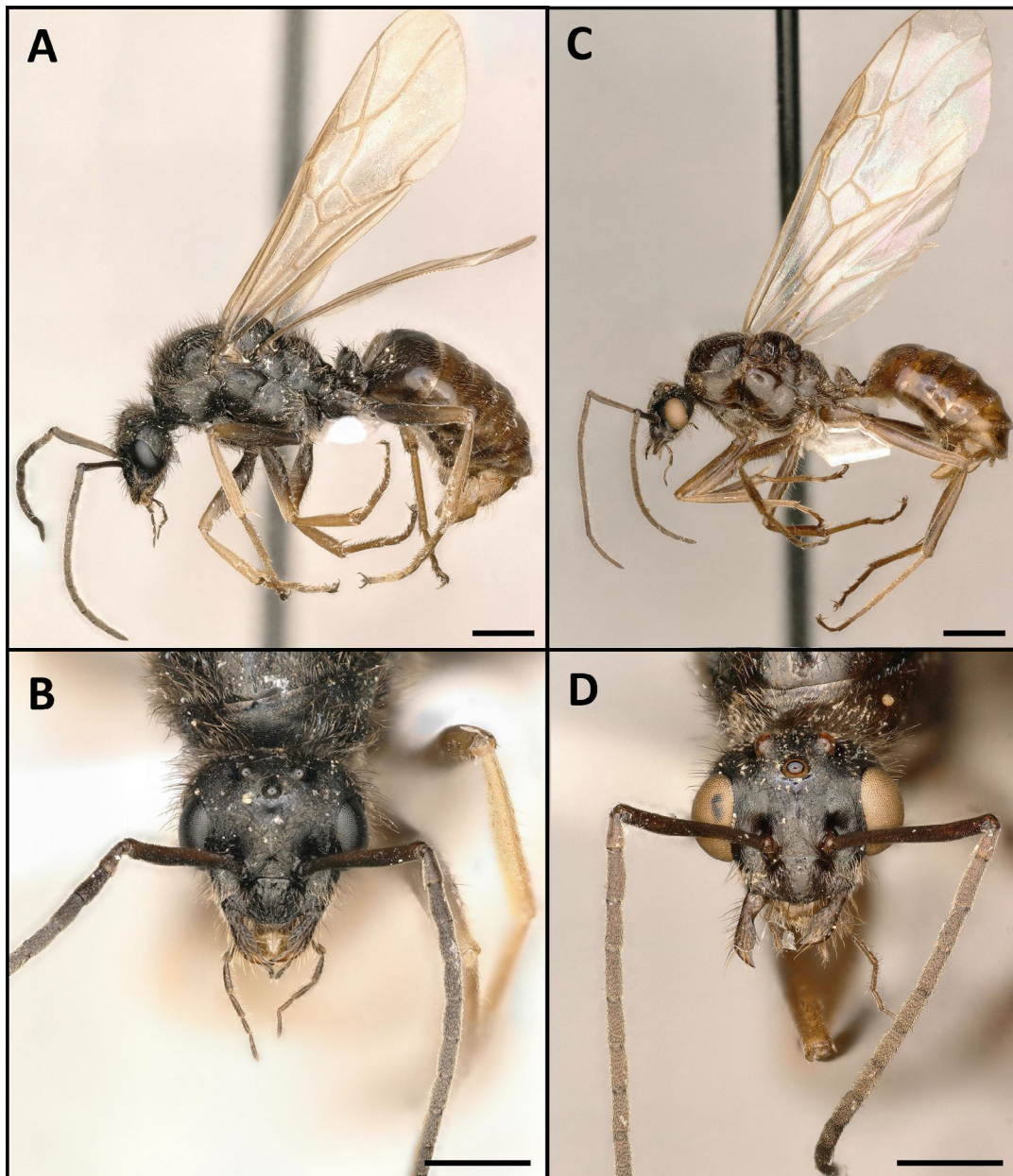


Fig 3. Illustration of French *Proformica* males. **A.** Body of *P. cerdanyensis* in lateral view, **B.** Head of *P. cerdanyensis* in frontal view, **C.** Body of *P. nasuta* in lateral view, **D.** Head of *P. nasuta* in frontal view. Scale bar: 1 mm (A, C); 0.5 mm (B, D).

Notes about Proformica nasuta reproductive behavior

Around 10:00, when the ground was sufficiently warmed by strong sunlight, the workers removed the few debris that were obstructing the nest entrance for the night. Soon, foragers left the nest, while many other workers were excavating soil pellets. Between 30 minutes and one hour after initiating the nest activity, one or two males timidly exited and then quickly reentered the nest a few times, before taking off. During the next 20 to 30 minutes, only workers were visible, before one to four queens started emerging from the entrance. Again, numerous back-and-forths were necessary before they moved away 5 to 50 cm from the entrance and climbed onto a clear support, such as a stone or stalk of grass, where they waited for males. Within at most a minute, a male travelled across the

lawn, flying at grass level very quickly and in a zigzag pattern. When the male spotted a queen, he interrupted his zigzag and threw himself on it. Mating was brief, lasting between 15 and 40 seconds, after the queen quickly returned to the nest, while the male resumed his search. On three occasions, the same male was observed fertilizing all the queens in the nest in succession, flying only a few meters away before returning and spotting a new queen. Only once two males were observed simultaneously patrolling the same zone, but there were no queens. Two freshly mated queens were sampled and kept in breeding glass tubes: one alone and the other with two small workers from her native colony. Both queens were able to lay eggs and raise them to advanced larval stages within a month. However, we never obtained new workers, likely due to inappropriate maintenance conditions during pupation.

Discussion

The description of the male of *Proformica longipilosa* improved the understanding of the diversity of the genus in the Western Palearctic, especially since all three species known from France now have their three castes described. There is no doubt that understanding the characteristics of males in this taxonomically challenging genus is highly beneficial for comprehending its peculiar evolutionary history, as well as for improving species delimitation. This thought is not new, as historically, Bondroit (1918) described *P. ferreri* based on a male exhibiting characters considered more distinctive than those of the worker, which were used to distinguish this species from *P. nasuta*, the only species known in Western Europe at the time. Thus, the description provided above allows us to draw some interesting parallels with the males known from other species in the region. First, the male of *P. longipilosa* presents a combination of characters that brings it morphologically closer to the male of *P. cerdanyensis* from the French Pyrenees, but also to the males of the *P. ferreri* complex from Sierra de Guadarrama northwest of Madrid (Galkowski et al., 2022) or even to the males of *P. chelmosensis* Lebas & Galkowski, 2019 and of *P. borowieci* Lebas et al., 2023 from the Greek mountains (Lebas & Galkowski, 2019b; Lebas et al., 2023). These characters concern the size of the eyes, the setosity of the femurs I, as well as the coloration and setosity of the gaster. Interestingly, known males of the other European species (*P. nasuta* from Southern France, *Proformica sp* from the Ebro Valley in Spain, and males of *P. oculatissima* (Forel, 1886) from Attica and the Corinth region in Greece) also share common characters that distinguish them from the previous ones (Table 2). In addition to these morphological arguments,

it is also worth noting that there appears to be an ecological differentiation: species with large-eyed males (*nasuta*, *oculatissima*, *sp.* Ebro Valley) are lowland or low-altitude taxa, while the ones with small-eyed males (*ferreri* complex, *longipilosa*, *cerdanyensis*, *chelmosensis*, *borowieci*) are mid-mountain species, most often living in locations at or above an altitude of 1000 m. Hence, it would be very interesting to continue these morphological investigations in other regions hosting species of the genus *Proformica*, such as the Iberian Peninsula, Anatolia-Caucasus, and Central Asia. However, we want to emphasize that these two groups have not yet proved to be evolutively consistent, and additional data – especially molecular – will be needed to test them, as well as large scale confrontation with females' morphologies.

To our knowledge, nearly nothing is known about reproductive behavior in *Proformica*, with only a short sentence published about *P. longiseta* Collingwood, 1978 (Fernandez-Escudero et al., 2002). Hence, even though they are quite informal, our mating observations in *P. nasuta* provide new insights into the ecology of this genus. The strong female philopatry associated with colony budding, as demonstrated genetically (Fernandez-Escudero et al., 2001; Sanllorente et al., 2015), is very likely a common characteristic in the genus, as is the apparent absence of macropterous flying queens. Males are hence the primary vector of genetic diversity between and within local populations. However, their ability to disperse – little or not studied at all – might be quite reduced despite them being agile fliers (Sanllorente et al., 2015). This last observation may be due to the very high density of nests locally, implying that males do not have to fly far to find partners. Another explanation might be that males flying low above the ground in open spaces, small reliefs could prevent them from long-range dispersal. All these facts

Table 2. Comparison of the two male-based morphological groups in European *Proformica* and of their respective features.

Morphological group	Species	Eyes	Profemora pilosity	Gaster	Habitat
<i>nasuta</i> type male	<i>Proformica nasuta</i> (FRA)	Relatively big and globular, REL > 50 (from 50.5 in some <i>P. nasuta</i> individuals to 74 in <i>P. oculatissima</i>)	Less abundant and shorter, longest hairs at most as long as maximal profemora length, in general shorter	Lighter, from yellowish brown to reddish brown, with scarce and light brown erect setae	Taxa inhabiting plains and low valley (< 1000m)
	<i>Proformica oculatissima</i> (GRE)				
	<i>Proformica sp.</i> Ebro Valley (SPA)				
<i>ferreri</i> type male	<i>Proformica ferreri</i> complex (SPA)	Relatively small and flatter, REL < 50 (from 44.6 in <i>P. longipilosa</i> to 49.5 in some <i>P. ferreri</i> complex individuals)	Abundant and long, longest hairs as long or longer than maximal profemora length	Often brown to dark brown with several dark erect setae, at least on the first tergite and on sternites	Taxa inhabiting mountains (from 1000m to more than 2000m)
	<i>Proformica longipilosa</i> (FRA)				
	<i>Proformica cerdanyensis</i> (FRA)				
	<i>Proformica chelmosensis</i> (GRE)				
	<i>Proformica borowieci</i> (GRE)				

may explain the difficulty in differentiating species based on morphology: On one hand, mountain populations are subject to strong genetic structuration (Sanllorrente et al., 2015), which is likely associated with cryptic morphological variation. On the other hand, plain species present morphological gradients (Galkowski et al., 2017), probably associated with the limited dispersal capacity of males, which struggle to homogenize the gene pool on a large scale. These considerations are crucial for future taxonomic studies in *Proformica*, which will need to integrate both morphological variations and the fragmented distributions of taxa, as well as a population genomics approach, to gain a sufficient understanding of this very particular genus.

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