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# Chemotaxonomy of *Tapinoma* and some Dolichoderinae ants from Europe and North Africa

Alain Lenoir, Elfie Perdereau, Laurence Berville

Institut de Recherche sur la Biologie de l'Insecte (IRBI), Université de Tours, Faculté des Sciences, Parc de Grandmont, 37200 Tours, France

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**Corresponding author**
Alain Lenoir
Institut de Recherche sur la Biologie de l'Insecte (IRBI), UMR CNRS 7261,
Université de Tours, Faculté des Sciences
Parc de Grandmont, 37200 Tours, France.
E-Mail: alain-cataglyphis@orange.fr

**Abstract**

Cuticular hydrocarbons of some Dolichoderinae ant species from France and various places like Spain, North Africa, and Italy were studied. The *Tapinoma nigerrimum* group was particularly analyzed and replaced in the genus *Tapinoma*. All species were correctly discriminated, and a new hydrocarbon profile was found in the Spanish mountains in the *T. nigerrimum* group, which was provisionally named *T. sp. Spain*. We added numerous unknown spots for the distribution of these ants. We also tested aggression between some *T. magnum* colonies. It appeared that this species forms supercolonies like other invasive species but does not form giant supercolonies like the Argentine ant.

## Introduction

Cuticular hydrocarbon profiles (CHCs) are a good indicator of species discrimination in insects (Bagnères & Wicker-Thomas, 2010) and more particularly in social insects for example in termites (Kaib et al., 1991), wasps (Dani et al., 2001) and honeybees (Page et al., 1991). In ants, Martin and Drijfhout (2009) found more than 1000 cuticular hydrocarbons in 78 ant species, and each species possess its unique pattern. In 12 species of European *Myrmica* (Guillem et al., 2016) found remarkable species-specific chemical profiles. On 2 *Temnothorax* and 2 *Myrmica* species, Sprenger and Menzel (2020) assigned the right species based on HCs with 0% errors. In some cases, cryptic species could be discriminated with CHCs, for example, in *Tetramorium* (Cordonnier et al., 2018) and in tropical arboreal parabiotic species (Hartke et al., 2019). Peña-Carrillo et al. (2021) also found different cryptic species in *Ectatomma ruidum* (Roger, 1860). Colonies from different localities can have different profiles indicating different species. For instance, Dahbi et al. (1996) found distinct CHCs profiles for *Cataglyphis iberica* (Emery, 1906) between Barcelona and Murcia, and the population from Murcia was later described morphologically as a distinct species, called *Cataglyphis gadeai* (De Haro & Collingwood, 2003). The existence of the new species was later confirmed with molecular biology (Villalta et al., 2018). On the contrary, some species like *Lasius niger* do not change their cuticular hydrocarbons profile according to all their European distribution (Lenoir et al., 2009). Cuticular hydrocarbons may be also a good indicator of climate adaptation but we did not present here indices of that point.as we did not studied variations with altitude, which were presented for example by Bujan et al. (2021, 2022).

Dolichoderinae is a large subfamily of ants with approximately 900 described species (Ward et al., 2010). They are commonly referred to as odorous ants, referencing the volatile compounds reminiscent of fermented cheese or rotting fruit emitted from their pygidial (anal) gland (Penick & Smith, 2015 for *Tapinoma sessile* (Say, 1836)). In France, it is called rancid butter odor.


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The taxonomy of the genus *Tapinoma* has been recently reviewed (Seifert, 2012), and the *T. nigerrimum* group was separated into four cryptic species (*T. darioi* Seifert et al., 2017, close to *T. magnum* Mayr, 1861*, T. ibericum* Santschi, 1925*, T. nigerrimum* (Nylander, 1856) *sensu stricto* (Seifert et al., 2017). A chemical analysis of glandular volatiles molecules confirmed the separation between *T. darioi* and *T. magnum* (D'Eustachio et al., 2019). Nevertheless, some subspecies can now be separated into two species using DNA, for example, *Tapinoma atriceps* and *T. atriceps breviscapum* in Brazil (Escárraga et al., 2021).

Cuticular hydrocarbons of *Tapinoma* have been investigated previously only in a few species: *T. erraticum* (Latreille, 1798)*, T. israele* Forel, 1904*, T. madeirense* Forel, 1895*, T. nigerrimum* (in the old large definition) and *T. simrothi* Krausse, 1911 by Berville et al. (2013). We wanted to see if cuticular hydrocarbons can also be used in species discrimination for more species and particularly in the *T. nigerrimum* group. We reported it in the genus *Tapinoma* and some Dolichoderinae species from 11 countries: France, Germany, Switzerland, Belgium, Portugal, Spain, North Africa (Morocco, Algeria, and Tunisia), Greece, and Italy (Suppl. Data Table 1).

## Methods

### Chemical analysis

Ten workers from each of the studied colonies were collected and killed by freezing. All the ants were immersed in 1 ml of hexane for 60 minutes, after which the ants were retrieved from the vials, and the solvent evaporated. The samples were kept frozen at -20 °C until chemical analyses. For chemical studies performed via a GC/MS-TQ Agilent (GC 7890B, MS 7000C, Agilent Technologies, Santa Clara, CA, USA), the samples were re-dissolved in 50 µl of hexane. Two µL of each extract were injected with an autosampler (Gerstel, Mühleim an der Ruhr, Germany) into an injector heated at 280 ºC in splitless mode and then in a column compound of 5% Phenyl -95% Dimethylpolysiloxane (Zebron ZH-5HT inferno, 30 m × 0.25 mm × 0.25 µm, Phenomenex, Torrance, CA, USA). The gas vector was helium at 1.2 ml min-1. The temperature program was 2 min at 150 °C, and then increasing at 5 °C/min to 320 °C, and 5 min hold at 320 °C (Total 41 min). The transfer line was set at 320 ºC. We used an Electron Ionization source at 230 ºC with an electron energy of -70 eV and a scan range of 40 – 600 m/z with 3.7 scans/s. Compounds were identified by their fragmentation pattern, compared to standard alkanes, library data, and Kovats retention indices. All compounds were included in the analyses. When it was impossible to estimate the amount of each co-eluted compound, they were treated as a single compound. Sterols and other contaminants like phthalates were not included.

All the % of CHCs are provided as mean ± SE (Standard Error) in Suppl. Data Table 2. The data were analyzed using cluster analysis on % with Euclidean distances and the Ward method (Statistica 8.0 program). We also calculated the equivalent chain length, which indicates the mean of hydrocarbon length ECL = $(\Sigma(\%C_n x X_n))/100$), where Cn is the x number of carbons and Xn is the % of this category. Martin et al. 2019 called it the Mean chain-length. ECL is not frequently used in chemical discrimination as it is insufficient to discriminate precisely species but is a good indication to classify them into different groups according to the length of hydrocarbons. This index allows to separate easily some different species as it will appear in the *nigerrimum* group.

We did not analyze hydrocarbons under C20 to avoid possible volatile compounds from the glands.

### List of species and samples (suppl data table 1)

A total of four genera and 13 species from 11 countries (513 samples from 299 sites, from sea level to 2 600m in Sierra Nevada). Columns: Genus, species, country, Department, City, Date of collection, latitude, longitude (decimal World Geodetic System WGS 84), altitude, collectors and determinators (person who identified the sample), number of samples, reference if already known**.**

- ***Tapinoma****:* *T. madeirense* (n = 27), *T. simrothi* (n = 49)*, T. erraticum* (n = 76), T. *melanocephalum* (Fabricius, 1793) (invasive tropical from greenhouses, n = 6), *T. pygmaeum* (Dufour, 1857) (n = 11)*, T. nigerrimum* group with the four species: *T. darioi* (n = 23, including samples from Italy, the country of the type), *T. magnum* (n = 193)*, T. ibericum* (n = 37)*,* and *T. nigerrimum s.str.* (n = 26). In this group, a group appeared separated from the others in Spain Mountains, supporting the presence of a possible new species, waiting for morphological and genetic analyses to be formally described (Seifert com. pers.). It was provisionally named *Tapinoma sp. Spain* (n = 34). Unfortunately, we could not find *T. subboreale* Seifert, 2012, from France.
- *Dolichoderus quadripunctatus* (Linnaeus, 1771) (n = 11).
- The Argentine ant *Linepithema humile* (Mayr, 1868) (n = 12).
- *Bothriomyrmex corsicus* Santschi, 1923, a parasite of *Tapinoma* (n = 8).

### Behavioral analyses

We also tested the aggressiveness between colonies of *T. magnum* from different localities to see if this species forms a unique giant colony like the Argentine ant. Ten ants were placed in a Petri dish, and after 10 minutes, we introduced one ant marked with a dot of painting from another colony. The ants' reaction was observed for 10 minutes, but generally, very rapidly, the result was obtained. Either the introduced ant was accepted and was licked by others and exchanged by trophallaxis with them, or it was rejected and aggressed. In this case, it was retrieved to prevent its death. The tests were repeated 10 times.

## Results and discussion

### 1. Cuticular hydrocarbons of the different species

Hydrocarbon profiles were all typical with carbons chains from C23 to C39 (see Suppl data Table 2). We did not analyze hydrocarbons under C20, which are partially volatiles; they are very important in social life but secondary in colonial recognition. There were mainly linear alkanes, di, and trimethyl alkanes. We found very few alkenes (<1%) except in *Bothriomyrmex* (75 ± 19%). Alcohols and other substances were also rare at these extraction temperatures. We found 174 different hydrocarbons across the species studied, with 25 substances having more than 1% of the total cuticular hydrocarbons. Guillem et al. (2016) found 222 HCs across 12 *Myrmica* species. We verified that the hydrocarbon profiles presented by L. Berville et al. (2013) correspond to our results for *T. erraticum, T. madeirense,* and *T. simrothi*. It appeared that *T. nigerrimum* in their analyses was the recently redescribed species *T. magnum*.

Three distinct clusters appear corresponding to ECL <=27, ECL = 29-30, and one intermediate group with ECL = 27-34 (Fig 1). The maximum ECL is for *Linepithema humile* (Lh ECL = 34.26 ± 0.53), and *Bothriomyrmex corsicus* (Bothrio, ECL = 32.62 ± 0.32). These are discussed below.

The first group (ECL < = 27) consists of *Dolichoderus quadripunctatus, Tapinoma erraticum, T. madeirense, and T. simrothi* (see Fig 2). The four species appear to be clearly separated in Fig 2.

*Dolichoderus quadripunctatus* is the only arboricolous species. It is frequent everywhere in Europe and in 60 departments (and probably more) in France (Antarea, accessed on 10 Feb 2022, Blatrix et al. 2013). It has a low ECL (26.26 ± 0.13, n = 11).

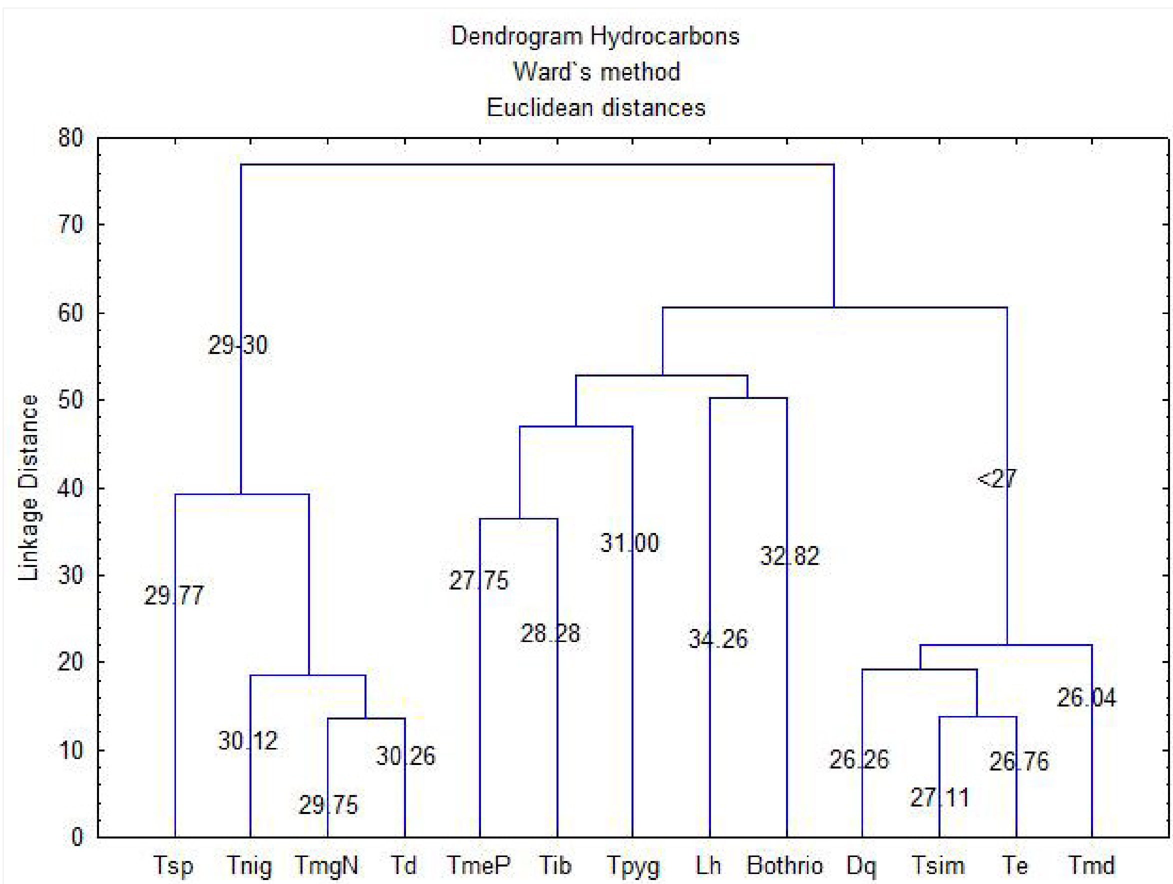


**Fig 1.** Dendrogram with Euclidean distances and Ward method on HCs % for all Dolichoderinae species from left to right: Tsp *T. sp. Spain*, Tn *T. nigerrimum*, TmN *T. magnum* natives, Td *T. darioi*, TmeP *T. melanocephalum* Paris, Tib *T. ibericum*, Tpyg *T. pygmaeum*, Lh *Linepithema humile*, Bothr *Bothriomyrmex corsicus,* Dq *Dolichoderus quadripunctatus*, Tsim *T. simrothi*, Te *T. erraticum*, Tmd *T. madeirense*. ECL are indicated on the figure.

In Figure 3, we analyzed *T. ibericum* and *T. simrothi,* which are difficult to distinguish morphologically. They appear to be well separated based on CHCs profiles.

***Tapinoma ibericum*** is very frequent in South Spain (<41°), according to Seifert et al. (2017): all of Andalusia, also found in Portugal and two places in Corsica (in red Fig 3). ECL is 28.28 ± 0.14. We did not observe differences between Spain, Portugal, and Corsica. It appears to become invasive in France, in a market gardening place near Pau (Meillon, 64), near Bordeaux (Saint-Médard-en-Jalles), and Lyon (Saint-Bonnet de Mure, B. Kaufmann leg). It is rare near Montpellier (1 site only at Mèze) (Centanni et al. 2022). In Pozzuelo de

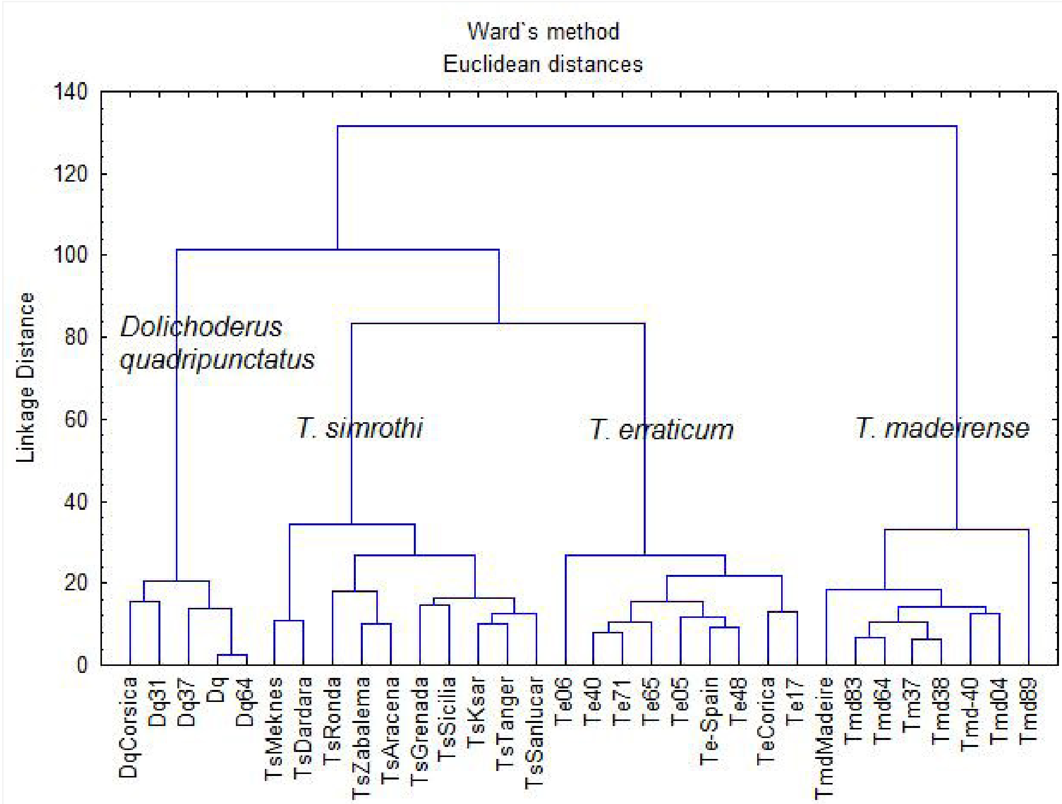


**Fig 2.** Dendrogram with Euclidian distances and Ward method on % for Dq *Dolichoderus quadripuncatus*, Ts *T. simrothi,* Te *T. erraticum, and* Tmd *T. madeirense*. Numbers indicate the department number for France, for example Dq37 id *D. quadripunctatus* Indre-et-Loire, and Corsica.

Calatrava (Spain), where the *T. ibericum* holotypes were described by Santschi (Seifert et al., 2017), only *T. magnum* was found (Ruano and Tinaut, leg). The two species are probably present in the same locality.

*T. ibericum* has to be now considered an invasive species in France. It has the same HCs profile as native ones. It will probably be found in many other places.

***Tapinoma simrothi*** is very frequent in Morocco under 500m (with one exception at 2 125m in Tichka col), frequent in Andalusia, Greece (Salata & Borowiec, 2018), and Sicilia. It has also been found in Corsica in two places (Antarea, accessed on 10 Feb 2022). According to Bernard (1980, 1983), it proliferates in plantations in North Africa, probably introduced from Palestine around 1890 since Forel did not find it in Algeria in 1869. ECL is low (27.11 ± 0.57). The hydrocarbon profiles of this species are more heterogeneous than those of *T. ibericum* (Fig 3). This heterogeneity could reflect geographical structuring, which would indicate the existence of cryptic species. In Lebanon, for example, *T. simrothi phoenicium* is considered a subspecies of *T. simrothi* (Chanine-Hanna, 1981).

### *Tapinoma erraticum and Tapinoma madeirense*

In Figure 4, we analyzed the two species, *T. erraticum, and T. madeirense.* There is a very good separation between *T. erraticum* and *T. madeirense,* as found by Seifert (2012 – morphology and genetics) and Berville et al. (2013 – morphology and HCs), although the two species have very similar ECLs: 26.04 ± 0.08 for *T. madeirense* and 26.76 ± 0.06 for *T. erraticum* (t-test, $P$ = 0.30, NS). Surprisingly, the two species co-exist in some places like Bléré (Fr: Te37 – Tm37 in red Fig 4), which is a calcar dry place (both species confirmed by Xavier Espadaler pers.com.).

We tried to collect neotypes of *T. erraticum* (Latreille, 1798), according to Seifert (2012) in Nespouls, near Brive (19). In fact, they were *T. madeirense* (see Te19 within Tmad in Fig 4). Probably the two species cohabit also in this place.

***T. erraticum*** was found in all departments surveyed in France (05, 06, 17, 34, 37, 40, 48, 56, 64, 65, 71, 20-Corsica), Madrid, and North Spain. This confirms its wide distribution across 85 departments in France (Antarea, accessed on 10 Feb 2022, see also Blatrix et al., 2013). In the French Pyrénées mountains, it can be found up to 1 670m in the Gavarnie circus (65) and 2639m in Eyne (66, Lebas 2021), and at 2 100m according to Bernard (1986, p. 100), and up to 1 470m in Spain (Te-SP). In the Alps, it is signaled until 1 900m (Bernard, 1983, p. 100). We found it at 1 400m (05 - Réallon). *T. erraticum* has been signaled in Algeria, Egypt, and Israel, but these could be misidentifications (Berville et al., 2013). *T. erraticum* appears to extend in the Balkans, with two new sp. (Wagner et al., 2018). It was found in Turkey but could be a cryptic species; more samples are necessary to conclude (Kiran & Karaman, 2020).

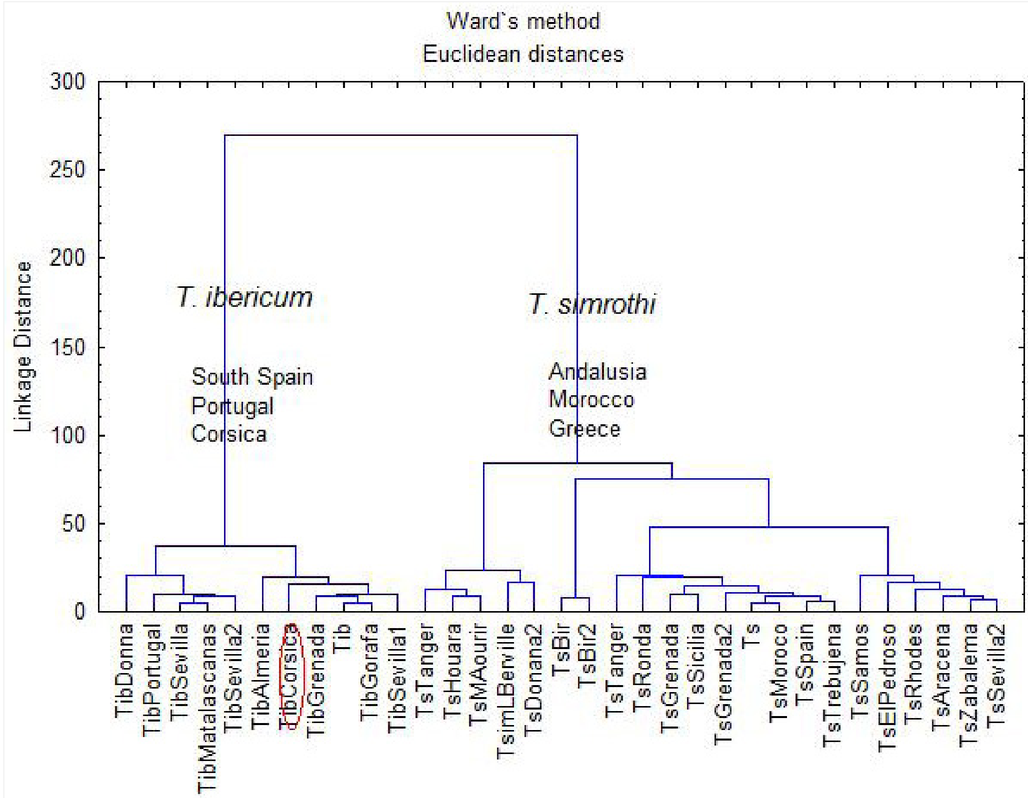


**Fig 3.** Dendrogram with Euclidean distances and Ward method on % for Tib *T. ibericum* (TibCorsica in Corsica in red) and Ts *T. simrothi*. Numbers indicate the department number for France.

***T. madeirense*** was described from Portugal (Madeira island) and our sample confirmed its presence in this island (TmdMad). It is less frequent in France and mainly in the south (04, 11, 30, 40, 56, 64, 37, 38, 83, 89, 20-Corsica, 20 departments in South according to Antarea, accessed on 10 Feb 2022, see also Blatrix et al., 2013), North Spain and Italy.

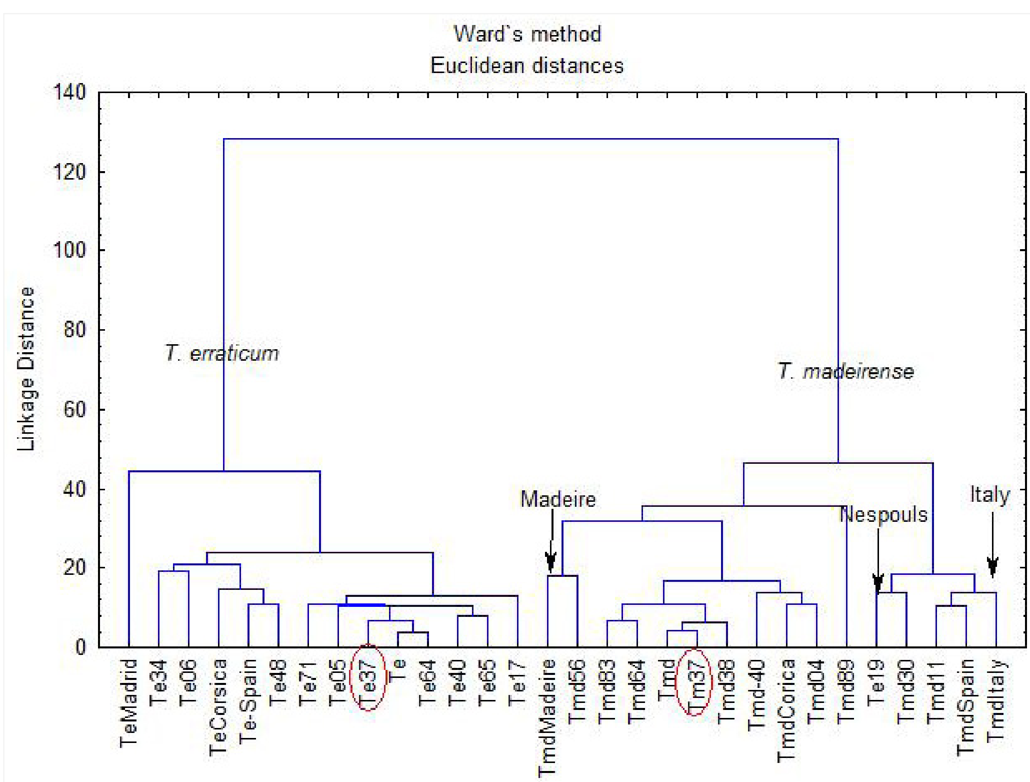


**Fig 4.** Dendrogram with Euclidean distances and Ward method on % for Te *T. erraticum* and Tmd *T. madeirense.* Numbers indicate the department number for France. Te37. *T. erraticum* and Tm37 *T. madeirense* from Bléré (37) in red.

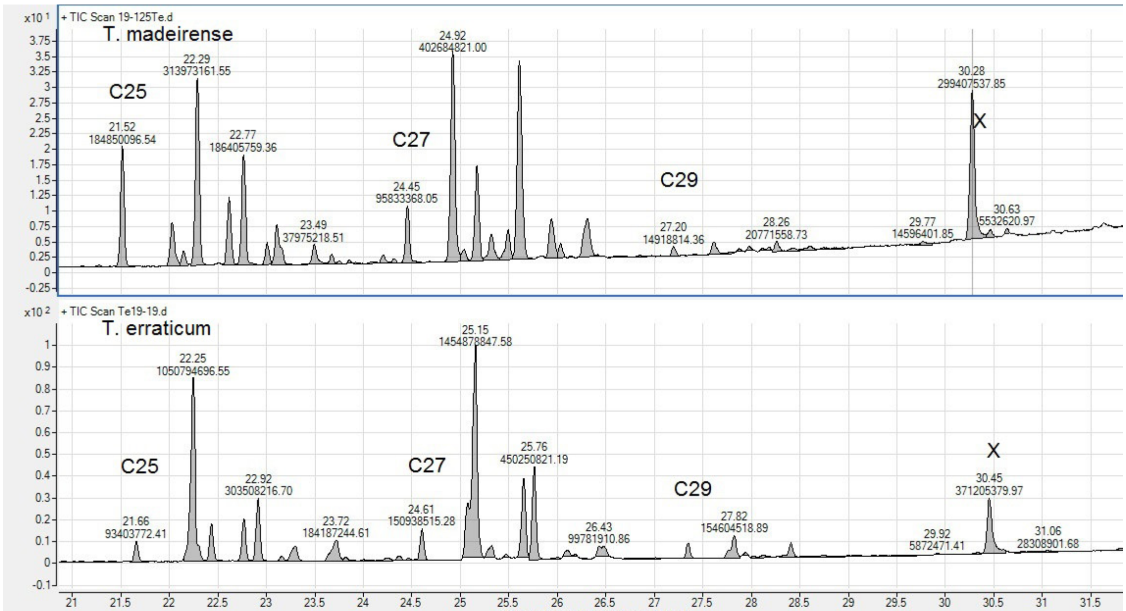


**Fig 4b.** Shows hydrocarbons profiles of the two species *T. erraticum and T. madeirense*, indicating very different CHCs profiles (x = sterol).

In the North of France, it is not found in localities north of Yonne (89) and Indre-et-Loire (37). This species is not found above 900m.

In Figure 5b, it is interesting to see that the profiles are identical for the two species; therefore, the species determination needs precise analysis. Nevertheless, some differences appear clearly; for example, at 38.10 min, it is 8,10+8,14 + 8,16diMeC30 (8,xC30 on the figure) for three species when it changes to 10,12 + 10,14C30 (10,xdiMeC30 on the figure for *T. sp. Spain T. nigerrimum* and *T. darioi* have more hydrocarbons after C31, particularly 5,13+5,15+ 5,17diMeC31 (5,xC31 on the figure). 8,x,xC32 on the figure is not representative due to the variability of the samples.

### The second group of species, with ECL C29 dominant

The second group of species, which is ECL C29 dominant (ECL 29-30), consists of 3 of the 4 known representatives of the *Tapinoma nigerrimum* group (*T. magnum TmgN* natives ECL is 29.74 ± 0.04 - we did not place here invasive ones*, T. darioi* ECL 30.26 ± 0.04*,* and *T. nigerrimum s.st*. ECL 30.12 ± 0.05.),

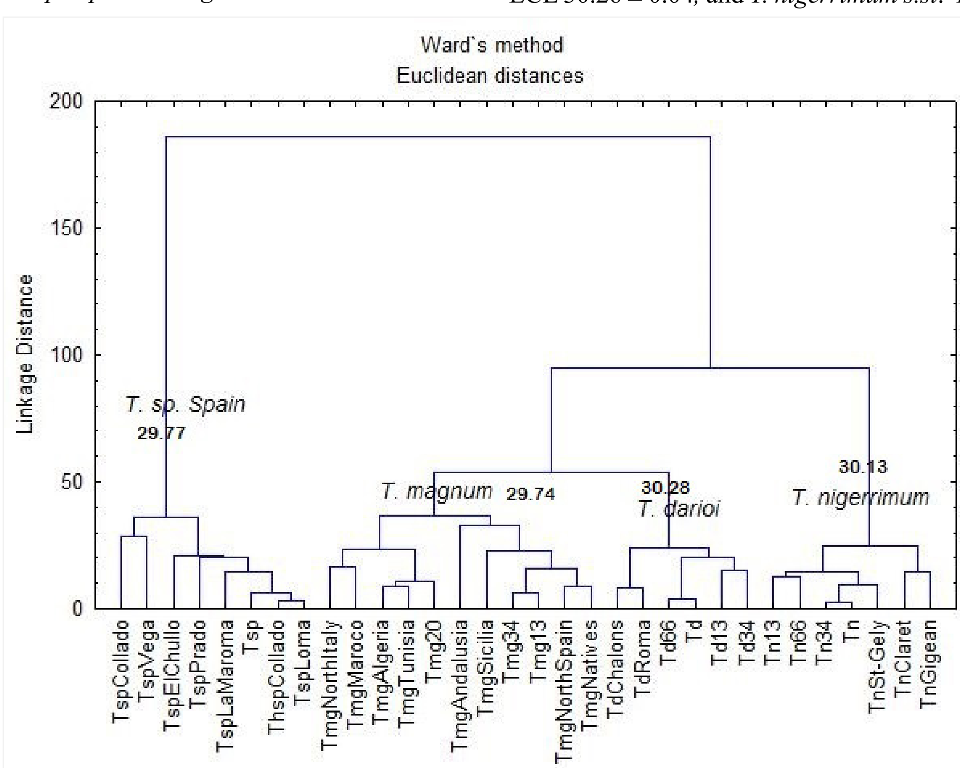


**Fig 5.** Dendrogram with Euclidean distances and Ward method on % for *Tapinoma* species of the *nigerrimum* group (Tsp *T. sp. Spain*, Tm *T. magnum*, Td *T. darioi*, Tn *T. nigerrimum*.

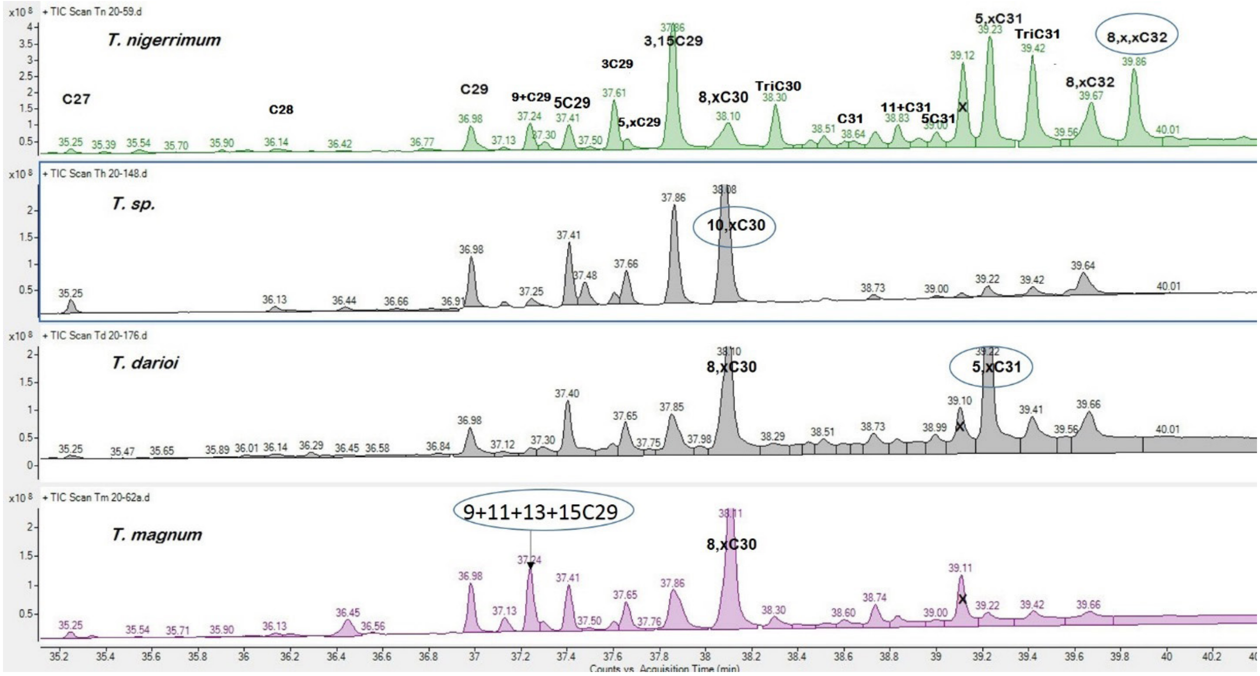


**Fig 5b.** Chromatograms of the *T. nigerrimum* group. x is a sterol.

and the new species (*T. sp. Spain* 29.83 ± 0.05), indicating that it is a complex of very close species. Surprisingly *T. ibericum,* which was included in *T. nigerrimum* group by Seifert et al. (2017) using morphometry and genetic data, falls outside of this group as indicated before.

The 4 species were clearly separated according to their hydrocarbon profiles (Fig 5), but they do not differ according to their ECL, which are very close (Kruskall-Wallis P>0.50). D'Eustachio et al. (2019) analyzed alkaloids and volatiles ketones of *T. magnum and T. darioi* and confirmed the chemical difference between the two species. We did not analyze here volatiles.

***Tapinoma sp. Spain***

This separate cluster, signaling a possible new species, is mainly from mountains in the Sierra Nevada (>2 000m asl). ECL is 29.77 ± 0.04. It was also found in one locality in the mountains North of Madrid at Vega (Castilla) (980m, ECL = 29.42, n=2), but only one point, so it needs to be verified. It is chemically very different from the other species of the *T. nigerrimum* group (Fig 5c). It was considered previously as *T. nigerrimum* and, therefore, maybe one more species to be added to the 72 endemic species for Spain (Tinaut & Ruano, 2021). This needs morphometric and genetic analysis.

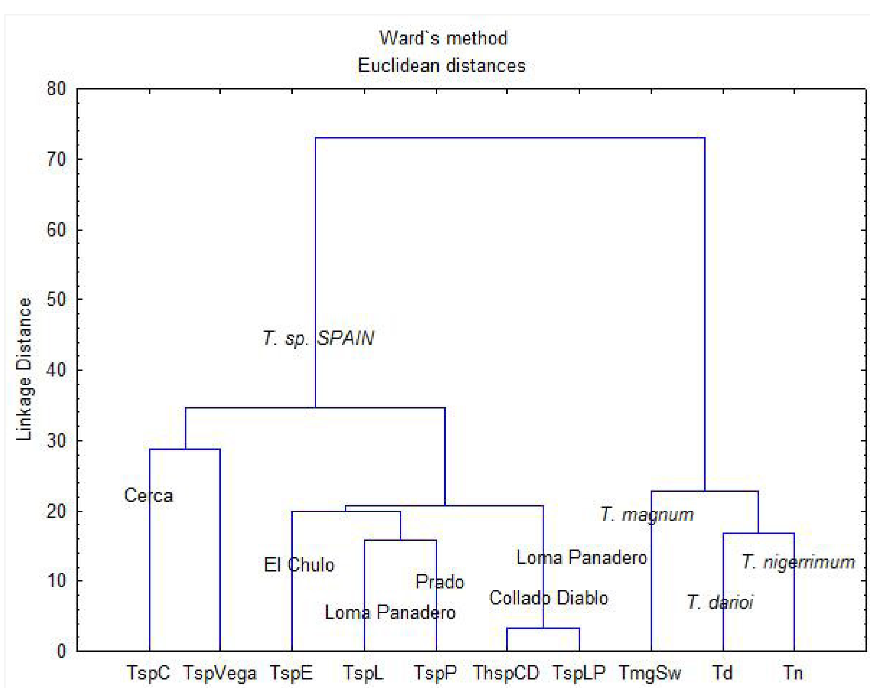


**Fig 5c.** Dendrogram with Euclidean distances and Ward method on % for *Tapinoma sp. Spain* and other members of *T. nigerrimum* group.

***Tapinoma darioi*** is found in France in the Pyrénées-Orientales (66), Hérault (34), Aude (11), Marseille (13), Var (84), and in Italy in Roma (type locality, see Seifert, 2012). *T. darioi* and *T. magnum* are occasionally found in the same localities in their invasive ranges. In Montpellier, *T. darioi* is frequent: in 78 sites (8.42% of the studied sites) (Centanni et al., 2022). It has been recently found in the Loire valley at Saint-Mars-du-Desert (44 - Gouraud & Kaufmann, 2022).

***Tapinoma nigerrimum s.str.*** is found in Europe on the Mediterranean coast from Provence to the Pyrénées-Orientales. It is frequent near the sea but is more generally found in lands up to 350m above sea level. Localities in Prades-Le-Lèzan and Gigean from Seifert are confirmed for this species based on CHCs. In Montpellier, *T. nigerrimum* is frequent: 197 sites (21.17% of the studied sites) and mainly observed on limestone plateaus and hills mostly covered with Mediterranean forests (Centanni et al., 2022). It is also found in the mountains in North Madrid (800-1200m) and Italy (Genova).

### *Tapinoma magnum*

In many papers, the ants called *T. nigerrimum* were probably *T. magnum*, for example, in Fréjus (83-Fr), where colonies had up to 350 queens and 100% of the nests in the Piémanson beach (13-Fr) (Bernard 1983, p.100), which is not the case for the real *T. nigerrimum*. This was confirmed by Seifert et al. (2017), who found, for example, *T. magnum* on Fréjus beach.

*T. magnum* is now an invasive species spreading in many places in Europe and particularly in France and Britany (Gouraud & Kaufmann, 2022; Lenoir et al., 2022a). It has also been found in some areas, like a cemetery in Slovenia. It also probably arrived with plants (Bracko, 2019).

- On the coast everywhere from Six-Fours (83), Cap d'Ail (06), Marseille, Saintes-Marie-de-la-Mer, Fos (13), near Montpellier (34), Girona (Spain), never higher than 20m. The three localities of Seifert (Le Grau du Roi, 2 spots in Saintes-Maries-de-la-Mer) are confirmed.

- Spain in Madrid region (700 to 1350m) and Andalusia (Doñana National Park in sand dunes). Seifert et al. (2017) considered that *T. magnum* is rare in Spain, but the number of samples was insufficient, or it spreads rapidly.

- Corsica on the coast (3-4m) and higher in greenhouses (380-800m). *T. magnum* is becoming a pest in some places like Corsica for market gardening.

- Italy: Roma (57m) and Sicilia (900m).

- Morocco (more than 170m until 1 200m), Algeria (from sea level to 800m), and Tunisia (under 220m). *T. magnum* has been studied in the Algerian National Park, representing 16% of all the ants (Labacci et al., 2020).

- France: in Antarea, it is found only 69 times in 13 departments (accessed 2 November 2022). It is now located in the Southwest around Bordeaux (Galkowski, 2008) and Arcachon (33), Dax (40), Agen (47), Sauvagnon and Arzacq-Arrizet near Pau (64), Bergerac (24), probably Toulouse (31).

It is invasive in the Loire valley, found by Gouraud and Kaufmann (2022): Saumur-49- where it is becoming a veritable plague, Ancenis, and Saint-Germain-sur-Moine,

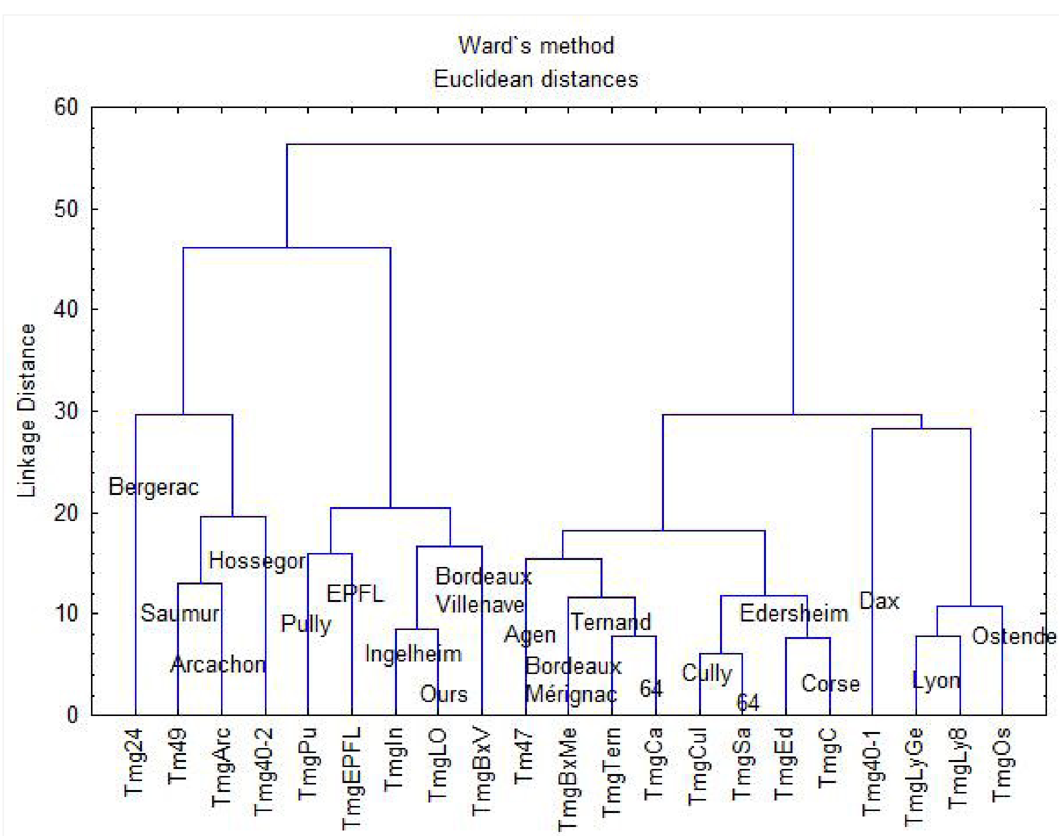


**Fig 6.** Dendrogram with Euclidean distances and Ward method on % for *Tapinoma magnum* of the different localizations.

Ingrandes-Le-Fresne-sur-Loire; in the department 44: Le Croisic, Saint-Mars-du-Désert, La Suze-sur-Sarthe, Saint Nazaire, Batz-sur-Mer and Saint-Lyphard. It is also found in Lyon and Ternand (69), Bourg-en-Bresse (01), and Molières (82) (Lenoir et al., 2022).

- Belgium: Ostende (Dekoninck et al., 2015).
- Switzerland: many places around Lausanne (Freitag & Cherix, 2017).
- Germany: Edersheim, Ginsheim and Ingelheim (Seifert et al., 2017).

Our data confirm Seifert et al. (2012, 2017) results for *T. nigerrimum* group: *T. nigerrimum* s.str. is mainly more distant than 4 km from the coast but can be found near the sea (14% of the places). *T. darioi* is more present near the sea (80% - Siefert et al., 2017). *T. magnum* is very present in degraded areas of human influence, which is typical of invasive species. In Montpellier, *T. magnum* is not frequent: 6 sites (0.65% of the studied sites) are replaced by *T. darioi* (Centanni et al., 2022).

We did not observe chemical differences between native and invasive colonies of *T. magnum*; the profiles are identical (Fig 7). This indicates that no dramatic changes in odor occur with migration. It was verified in colonies maintained in the laboratory for one or two years which kept their chemical profile contrarily to many other invasive species (Lenoir & Perdereau, 2022). Two groups appear within the *T. magnum,* which may correspond to two different genetic groups or origins, but the Euclidian distance is low (=50). This deserves further study.

In Figure 7, we have the imported colonies plus Corsica. They also present two groups. We have yet to find the origins, which can be different. For example, in Bordeaux, there are possibly two origins as the profiles differed between Villenave and Mérignac.

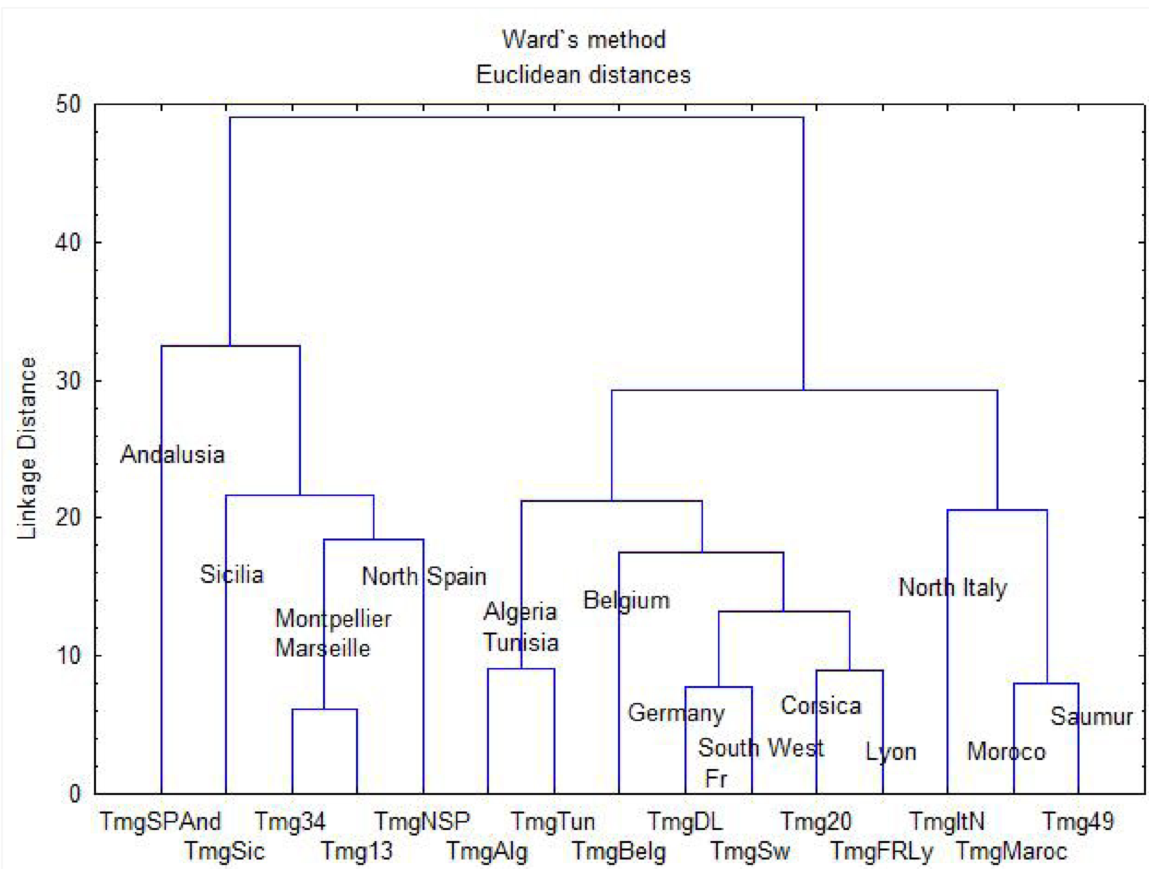


**Fig 7.** Dendrogram with Euclidean distances and Ward method on % for imported *Tapinoma magnum.*

**Aggression tests**

The % of adoptions in aggression tests between two colonies were the following: Sauvagnon/Lausanne 0% adoptions, Sauvagnon/Cully (Sw) 25% indifference and 75% rejections, Lausanne/Cully 100% adoptions, Lausanne/Bordeaux Mérignac 0%, Sauvagnon/Bordeaux Mérignac 0%, Sauvagnon first colony/new colony 100%, Sauvagnon/Caubios (5 km) 100%, Saumur zone A/zone B 100%, Arzaq zone1 (64)/Arzac zone 2 (200m) 100%, Arzacq/Sauvagnon 80% (same origin?).

The aggression between species is always maximum. For example, we tested Sauvagnon / Meillon (*T. magnum / T. ibericum*): 0% adoptions and Sauvagnon *T. magnum / Lasius niger:* 0% adoptions. It indicates that *T. magnum* is very aggressive toward other species and explains probably why they exclude local species.

To summarize, these results on aggression indicate that
- Colonies in large cities like Saumur make a supercolony, and colonies from small distances like Lausanne and Cully are not aggressive, coming probably from the same importation.
- There is no unique giant supercolony as aggression appears between various localities like Bordeaux and Lausanne or Bordeaux and Sauvagnon.

The third group (ECL = 27 to 34; Fig 1) contains the four remaining species studied: *L. humile, T. melanocephalum, T. pygmaeum*, and *B. corsicus*.

**Argentine ant *Linepithema humile***

It is known as an invasive species, found in South France in 13 departments (Antarea accessed 10 Feb 2022), but it seems to expand rapidly. It was found recently in Nantes city (Charrier et al., 2020). Hydrocarbon profiles of the argentine ant are well known, including the queens (see, for example, Blight et al., 2012; Abril et al., 2018; Buellesbach, 2018 for California). Three supercolonies are known: Main European, Corsican and Catalonian, according to Blight et al. (2012). We analyzed ants of the Main European Super colony from Italy and Spain. This species has the higher ECL (34.26 ± 0.53, n = 12) of all studied Dolichoderinae ants with mainly C35 (12.56% ± 2.04), C36 (30.61% ± 3.44) and C37 (26.90% ± 4.07). These long-chain cuticular hydrocarbons protect against desiccation and may allow *L. humile* to support very dry climates. Long-chain compounds are generally thought to enhance desiccation resistance (reviewed, for example, by Gibbs, 1998).

***Tapinoma melanocephalum***

It is a frequent tropical species (see the taxonomic position in Guerrero, 2018) and one of the most invasive ant species in the world. It is also an invasive species found in the greenhouses of many European tropical botanical gardens (Blatrix et al., 2018). We found it in the Jardin des Plantes (Muséum d'Histoire Naturelle Paris) and in the botanical garden in Villers-lès-Nancy. It was also found in the University city of Villeurbanne (69, T. Klaftenberger), in Roubaix (Anaïs Tamelikecht/Agnès Villain), but in this last case, it needs to be verified. According to Antarea, it has been found in 13 departments (accessed 10 Feb 2022). It has been signaled in a building in Liege (Dekoninck et al., 2006) and the Czech Republic (Klimes & Okrouhlik, 2015).

We studied ants from the Jardin des Plantes in Paris. ECL is 27.75 ± 0.04 (n = 6). They have a very simple profile with only 9 HCs >1% (C27 16.31% ± 1.50, 9+11+13C27 9.89±0.59, 3C27 24.61 ± 1.86, C29 13.62 ± 1.14, 9+11+13+ 15C29 21.18 ± 1.35).

This species may be composed of several species, as Siefert (2022) found a new species, *T. pithecorum,* in the Indo-pacific region.

***Tapinoma pygmaeum***

It is a rare *Tapinoma* species described from Saint-Sever (40, Landes, Emery, 1912), rediscovered in France in 1999 (Péru, 1999). It is found in 22 French departments (Antarea, accessed on 10 Feb 2022). We found it near Chartres and near Tours (La Riche and Montlouis). Hydrocarbons have long-chain molecules: ECL = 31.00 ± 0.30 (n = 11).

***Bothriomyrmex corsicus***

It is a rare parasite species found in places with a high density of *Tapinoma* in Pyrénées-Orientales and near Tours (Bléré). Antarea indicated it in 17 departments, mainly in the South (accessed 10 Feb 2022). We found only pure *Bothriomyrmex* colonies. ECL is very high (32.62 ± 0.32, n = 8). It has a very particular hydrocarbon profile with many alkenes (74.99 ± 18.81%). In some individual ants, it was more than 90%, whereas other Dolichoderinae has only very few alkenes. This species has been studied only for volatile compounds. The *Bothriomyrmex* queens can enter the *Tapinoma* colony with a ketone produced only by the queen (Lyod et al., 1986). The abundance of alkenes in workers may also be related to parasitism. The inquiline ant *Myrmica karavajevi*, a parasite of *Myrmica scabrinodis*, used two adaptations to be admitted in the host colony; it smells the host queen odor but also produces sounds similar to the host ants (Casacci et al., 2021). The total quantities of alkenes are more important in the *M. karavajevi* parasite queens (16.68%) compared to *M. scabrinodis* workers (8.58%), but they are very far from the *Bothriomyrmex* quantities.

**Discussion and Conclusion**

Cuticular hydrocarbons of Dolichoderine ants are classical with carbon chains from C23 to C39. All species can be identified with their specific profile, and possibly a new species was identified. The cuticular hydrocarbon profile is an efficient tool to determine Dolichoderine ant species, particularly in the *T. nigerrimum* group, where morphology is very difficult and reserved for good specialists and when genetic data are impossible. The parasite *Bothriomyrmex* is very different from all other species with many alkenes, probably linked to the parasite life, but this inference needs to be discussed.

The four species of the *T. nigerrimum* group described by Seifert et al. (2017) are well-discriminated with hydrocarbon profiles. Surprisingly they were divided into two clearly separated groups: the first group with three species: *T. magnum, T. darioi, T. nigerrimum s.str.* and the new *T. sp Spain. T. ibericum* appears in another different group. *T. magnum and T. darioi* live in different places and form supercolonies (Centanni et al., 2022). It indicates that morphometric plus genetic analyzes versus cuticular hydrocarbons can classify the species differently. It is interesting to note that *T. magnum* forms very large supercolonies in cities but not giant supercolonies like *Linepithema humile*.

*T. ibericum* and *T. simrothi* are well differentiated and have a large distribution in Spain and North Africa. *T. ibericum* is mainly from Spain, while *T. simrothi* is from Morocco (and Corsica).

*T. erraticum* and *T. madeirense* have a very large distribution. They can be present in the same habitat but probably have different microclimatic preferences. According to Claude Lebas (pers. comm.) *T. madeirense* lives only in deadwood.

*T. melanocephalum* is imported into France and found in almost all greenhouses and must be surveyed in city flats as it could become invasive.

*Tapinoma pygmaeum* is a rare species with a particular microhabitat, and it is well separated from all other ones with HCs and morphology.

## Perspectives

More analyses are necessary to analyze relationships between cuticular hydrocarbon composition and adaptations to climate. It is generally accepted that ants can plastically adjust their profile to acclimate to different conditions. Warm-acclimated individuals generally show longer n-alkanes and fewer dimethyl alkanes. Dry conditions result in more n-alkanes and fewer dimethyl alkanes for workers, probably due to better resistance to desiccation (Menzel et al., 2017, 2018). *Aphaenogaster iberica* in the Sierra Nevada mountains also show differences in n-alkanes due to the elevation (Villalta et al., 2020).

It will be interesting to follow the progression of some species, mainly *T. magnum* but also *T. darioi and T. ibericum*. *T. magnum* and *T. darioi* are native to the Southeast of France, but in these regions, they are becoming invasive, for example, in the Montpellier region (Centanni et al., 2022). Two hydrocarbon profiles of *T. magnum* appear, and it will be interesting to see if they have genetic differences.

## Authors' Contribution

AL: conceptualization, methodology, investigation, writing-review & editing.
EP: methodology, writing-original draft.
LB: methodology, writing-review & editing.

## Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

## Ethics

The authors confirm that the manuscript published in bioRxiv: doi: 10.1101/2022.09.28.509850 and has been submitted only to this journal and confirm that all the research meets the ethical guidelines, including adherence to the legal requirements of the study country.

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## Supplementary data

- Map: distribution of the ants collected
- Table 1: List of species and samples
- Table 2: Cuticular hydrocarbons composition of the species.

The supplementary data files are available in the article url: https://periodicos.uefs.br/index.php/sociobiology/article/view/9099

## Websites

- Antarea: http://antarea.fr/fourmi/?

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