Historical Biology

An International Journal of Paleobiology

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/ghbi20

First evidence of ants (Hymenoptera, Formicidae) in the early Pleistocene of Madeira Island (Portugal)

Carlos A. Góis-Marques, Pedro Correia, Andre Nel, José Madeira & Miguel Menezes de Sequeira

To cite this article: Carlos A. Góis-Marques, Pedro Correia, Andre Nel, José Madeira & Miguel Menezes de Sequeira (05 Dec 2022): First evidence of ants (Hymenoptera, Formicidae) in the early Pleistocene of Madeira Island (Portugal), Historical Biology, DOI: 10.1080/08912963.2022.2152688

To link to this article: https://doi.org/10.1080/08912963.2022.2152688

Published online: 05 Dec 2022.

HISTORICAL BIOLOGY
https://doi.org/10.1080/08912963.2022.2152688

First evidence of ants (Hymenoptera, Formicidae) in the early Pleistocene of Madeira Island (Portugal)

Carlos A. Góis-Marques [a,b], Pedro Correia [c], Andre Nel [d], José Madeira [b,e] and Miguel Menezes de Sequeira [a]

[a]Grupo de Botânica da Madeira (GBM), Faculdade de Ciências da Vida, Universidade da Madeira, Campus da Penteada, Funchal, Portugal; [b]Instituto Dom Luiz (IDL), Laboratório Associado, Universidade de Lisboa, Campo Grande, Lisboa, Portugal; [c]Geosciences Center, Department of Earth Sciences of, University of Coimbra, Coimbra, Portugal; [d]Institut Systématique Evolution Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, Université des Antilles, Paris, France; [e]Departamento de Geologia, Faculdade de Ciências da, Universidade de Lisboa, Campo Grande, Lisboa, Portugal

ABSTRACT

To be successfully established on oceanic islands, native ants (Hymenoptera: Formicidae) have to migrate from the mainland or from nearby islands, crossing the ocean barriers, to find a suitable habitat. Despite the general interest on oceanic islands biotas, nothing is known about the deep-time migration and settling of native ants in these insular ecosystems. Palaeoentomological studies on oceanic islands that could provide palaeobiological information on Formicidae are scarce. Here, we describe and illustrate the first fossil of an ant from the Macaronesian archipelagos (Atlantic Ocean), based on a partial forewing found within 1.3 Ma (Calabrian, Pleistocene) lacustrine sediments from Madeira Island, Portugal. Although unidentifiable beyond the family level, this fossil record provides a minimum age for the presence of ants in the Madeira archipelago. Palaeoecologically, this record indicates the presence of suitable habitats for ants during the early Pleistocene.

ARTICLE HISTORY
Received 7 September 2022
Accepted 24 November 2022

KEYWORDS
Calabrian; dispersal; fossil; macaronesia; oceanic island; palaeomyrmecology

Introduction

Nowadays, ants (Hymenoptera: Formicidae) are a widespread eusocial insect group on oceanic islands (Morrison 2016). Ontogenically, oceanic islands are volcanic subaerial edifices build over oceanic plates and isolated from mainland (e.g. Whittaker and Fernández-Palacios 2007). Yet, it is considered that ants have a limited migration capability. Past colonisation of these islands was dependent on successfully crossing of the ocean barrier, either by female alates or by rafting (Morrison 2016). In fact, isolation of oceanic islands contributed to some archipelagos, such as the Hawaii, to entirely lack native ants (Krushelnycky et al. 2005; Morrison 2016). Today, anthropogenetic dispersal is the main mechanism by which ants arrive to insular ecosystems, many becoming problematic invasive species (e.g. Krushelnycky et al. 2005; Wetterer and Espadaler 2010; Morrison 2016).

In the volcanic Macaronesian archipelagos (i.e. Azores, Madeira, Canary and Cabo Verde archipelagos), arthropods, especially insects, represent a diverse group displaying high endemicity (see Báez and Oromí 2005; Borges et al. 2008, 2010; Oromí and Báez 2009; Triantis et al. 2010). Oddly, this pattern does not apply to ants. The number of endemic Macaronesian Formicidae varies widely within these archipelagos, with the Canary Islands having ca. 28% of endemic ant species (Total = 71; Endemic = 20; Native = 24; Introduced = 27; see Native Biodiversity Data Bank of the Canary Islands: http://www.biodiversidadcanarias.es/biota), Cabo Verde ca. 9–15% (Total = 39; Endemic = 3, possibly up to 6; Native = 24; Introduced = 9; Wetterer and Espadaler 2021), Madeira ca. 3% (Total = 31; Endemic = 1; Macaronesian endemic = 1; Native = 8; Introduced = 21; Wetterer et al. 2007; Guillem and Bensusan 2022) although it could also be 0% (see Guillem and Bensusan 2022) and one shared macaronesian endemic in the Azores (Total = 14; Endemic = 0; Macaronesian endemic = 1; Native = 5; Introduced = 8; Wetterer et al. 2004). The low number or even the possible lack of endemic ant species in the Madeira, the Azores and Cabo Verde archipelagos, when compared to the Canary Islands, could be interpreted due to past failure of natural migration, colonisation and evolution of ants, or the rivalry and elimination of endemic and native ants by exotic ants brought by human settlers (Wetterer et al. 2004, 2006, 2007; Wetterer and Espadaler 2010, 2021; Guillem and Bensusan 2022). However, nothing is known about the deep-time presence of ants in the Macaronesian archipelagos. The continental ant fossil record is abundant and well preserved (e.g. LaPolla et al. 2013; Barden 2017), but on oceanic islands, ant fossils are extremely rare and to date the only example come from the late Holocene of Easter Island (Horrocks et al. 2013). The discovery and description of well-dated and informative insect fossils from oceanic islands can provide minimum arrival ages and add valuable palaeobiological information on their taxonomy, evolution, ecology and biogeography (Morrison 2016; Góis-Marques et al. 2019d).

Insect fossils found in Macaronesian islands are rare in part due to a lack of active palaeoentomological research (Góis-Marques et al. 2019d). According to a brief overview given by Góis-Marques et al. (2019d), to date Macaronesian insect somatofossils are only known from Madeira Island: one Coleoptera (Heer 1857; Machado 2006) from São Jorge Mio-Pleistocene deposits (Góis-Marques et al. 2018) and a recently described Ichneumonidae hind wing found in the 1.3 Ma Porto da Cruz sediments (Góis-Marques et al. 2019d). From other Macaronesian archipelagos, until now, only insect ichnofossils were described for the Canary islands (e.g. Edwards and Meco 2000; Meco et al. 2011; Alonso-Zarza et al. 2012; Genise et al. 2013; La

CONTACT Carlos A. Góis-Marques c.goismarques@gmail.com Unidad de Botánica, Departamento de Biodiversidad, Ecología y Evolución, Universidad Complutense de Madrid Calle José Antonio Novais, 12, Madrid 28040, Spain

Published online 05 Dec 2022

Roche et al. 2014; Genise 2017) and one example for the Azores (Góis-Marques et al. 2019b).

Tafonomically, insect fossils are usually found associated with plant fossils (e.g. Coope 1970; Elias 2010). On Madeira Island, localised lacustrine and fluvial sedimentary deposits can be rich in plant fossils. Within these, occasional insect fossils are found (Heer 1857; Góis-Marques et al. 2019d; Góis-Marques 2020). Here, we describe the first Macaronesian fossil of an ant, providing evidence of the presence of ants in the early Pleistocene of Madeira Island. Furthermore, we briefly discuss the possible biogeographical, evolutionary and palaeoecological implications.

Geological setting

Madeira island is located on the mid-Atlantic Ocean, ca. 850 km SW of mainland Portugal and ca. 700 km NW of Morocco (Figure 1A). The subaerial edifice corresponds to a highly dissected shield volcano (Ramalho et al. 2015) (Figure 1B). Geologically, the island was divided into three volcanic complexes (Figure 1C): the Lower Volcanic Complex (LVC1 and 2), with >7 Ma; the Middle Volcanic Complex (MVC1, 2 and 3) ranging from 7 to 1.8 Ma; and the Upper Volcanic Complex (UVC1 and 2), from 1.8 Ma to Holocene (Brum da Silveira et al. 2010a, 2010b, 2010c; Ramalho et al. 2015).

In the Porto da Cruz, in the NE part of the island (Figure 1 B and C), fluvial and lacustrine sediments crop out intercalated within lava flows from the UVC2. Recently, $^{40}Ar/^{39}Ar$ dating constrained this deposit to ca. 1.3 Ma, Calabrian, Pleistocene (Góis-Marques et al. 2019e). Since the 19th century, plant and insect fossils have been described from the Porto da Cruz sediments (Hartung and Mayer 1864; Starkie Gardner 1882; Góis-Marques 2013; Góis-Marques et al. 2019a, 2019d, 2019e).

Material and methods

A partial forewing fossil was identified under a stereomicroscope on a split piece of finely laminated lacustrine sandstone. Fossil macrophotographs were acquired using a Nikon D5500 attached to a macro extension tube and a 100-mm macrolens employing the software DigiCamControl 2.1.4.0 (http://digicamcontrol.com). Fossil identification was achieved by comparing the specimen to extant insect wings from the data base DrawWing (Tofilski 2004). Additionally, the fossil was compared to illustrations and photographs of extant (e.g. Saunders 1896; Donisthorpe 1915; Emery 1925; Brown and Nutting 1949; Bernard 1968; Barquín 1981; Perfilieva 2000; Cantone 2019) and fossil ant taxa (e.g. Dlussky 2011; Antropov et al. 2013; Perfilieva 2022). When available, the fossil was compared to wings of extant genera or species of Formicidae present on Madeira Island (Wetterer et al. 2007) using data archived in the online database AntWiki (https://www.antwiki.org/). Forewing venation description follows the terminology given in Perfilieva (2000). Open nomenclature follows the recommendation by Bengtson (1988).

Results

Systematic palaeontology

Order **Hymenoptera** Linnaeus, 1758
Family **Formicidae** Latreille, 1802
Genus ***Lasius***? Fabricius, 1804

Diagnosis: see Perfilieva (2022).
Repository: Palaeobotanical collection of the Madeira University Herbarium Richard Thomas Lowe (UMAD).
Fossil specimen studied: P586 (UMad 10973) (Figure 2B).
Locality: Porto da Cruz, Machico, Madeira Island, Portugal.
Stratigraphy and age: UVC2 g, Funchal unit, Upper Volcanic Complex (Brum da Silveira et al. 2010a, b), with an age of ca. 1.3 Ma.
Fossil description: Incomplete forewing, preserved as a coalified compression. Size of fragment 4.5 × 1.1 mm. Pterostigma cell (**Pt**) incomplete, with attached costal (**C**) and radial (**R**) partial veins, the **R** becoming faint towards apex. Second interradial (**2 r-rs**) vein complete, attached to base of **St** forming an angle of ca. 137° in relation to **Pt**, directing to wing apex. **2 r-rs** vein joints to fourth medial abscissa (**4 M**), fifth abscissae of radial sector (**5RS**) and

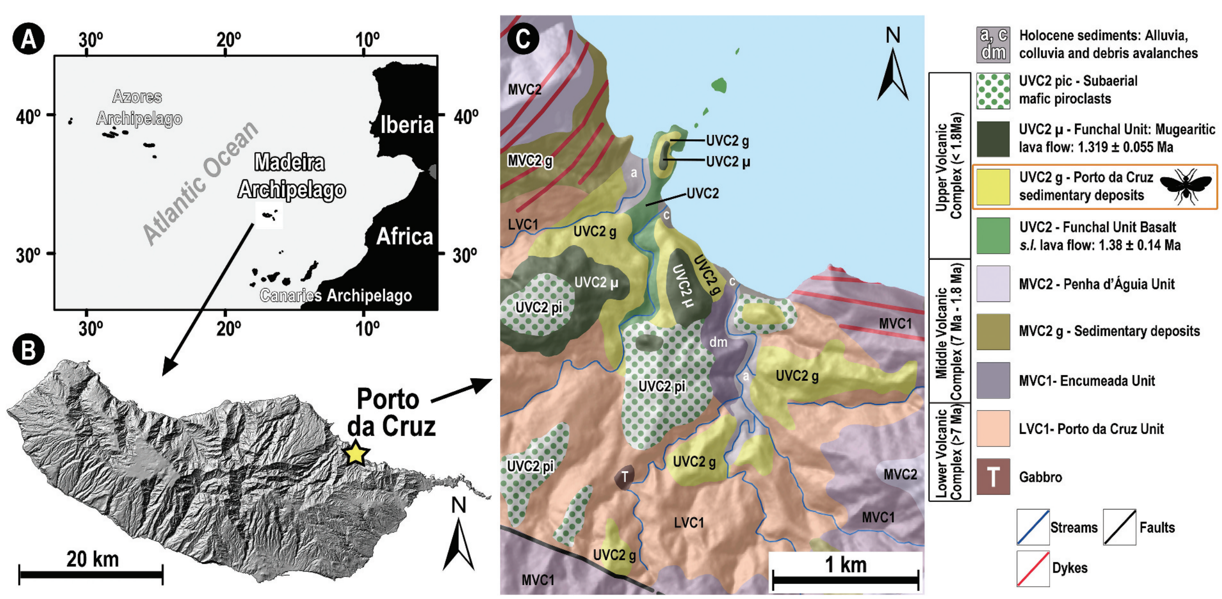

Figure 1. Location of Madeira Island and Porto da Cruz fossiliferous sediments. **A**, Geographical location of Madeira Archipelago; **B**, Digital elevation model of Madeira Island indicating Porto da Cruz locality (star); **C**, Geological map of Porto da Cruz area adapted from Brum da Silveira et al. (2010c). Insect figure indicates the provenance and stratigraphy of specimen P586.

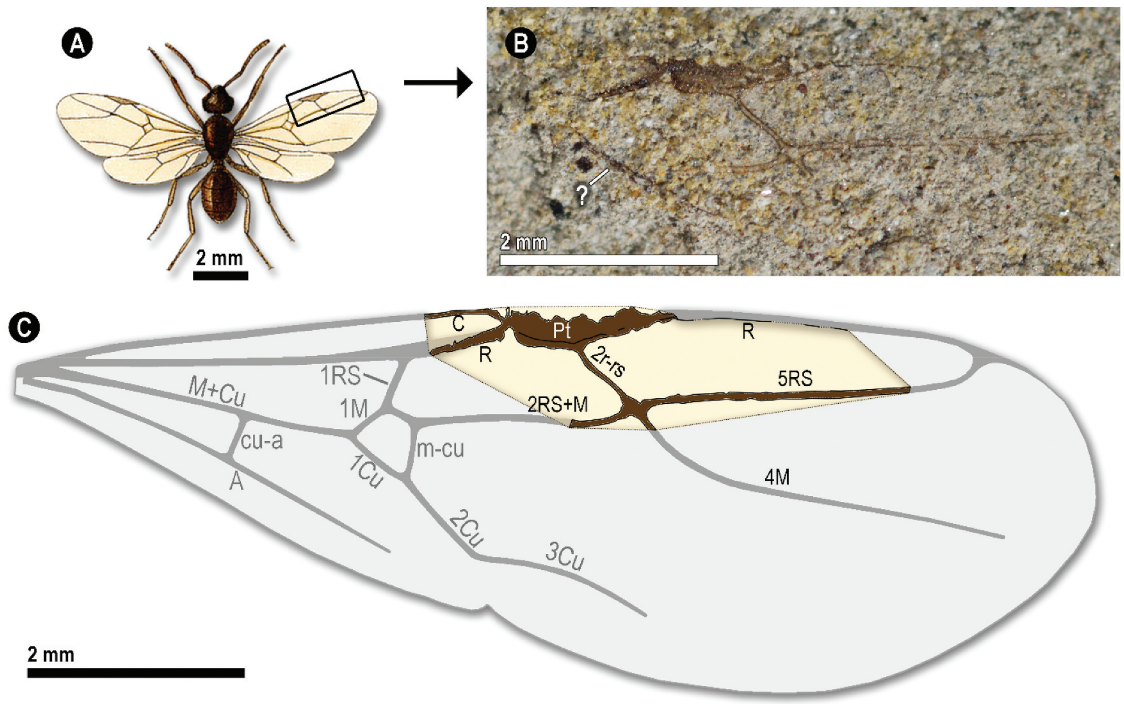

Figure 2. Formicidae forewing fossil and comparison to a typical *Lasius* forewing. **A**, drawing of a typical alate male ant *Lasius alienus* (Foerster, 1850), extracted from Saunders (1896, plate 3, fig. 2) with rectangle indicating the preserved forewing part in the fossil; **B**, specimen P586, a partial Formicidae forewing fossil; question mark indicates unknown parts; **C**, line drawing and reconstruction of the forewing fossil wing adapted over a †*Lasius schiefferdeckeri* Mayr, 1868 forewing (adapted from Dlussky 2011, fig. 2–1). Legend: **A**: anal; **C**: costal; **cu-a**: cubito-anal transverse; **R**: radial; **RS**: radial sector; **M**: medial; **Pt**: pterostigma; **m-cu**: medio-cubital transverse; **Cu**: cubital; **r-rs**: interradial; numbers indicate abscissae order.

third medial abscissa (**3 M**) incomplete veins forming a cross-joint. Further morphology not preserved.

Remarks: Despite its incompleteness, the dimension and venation pattern of the fossil fragment (Figure 2B) agree with the forewing venation of a Formicidae (Figure 2C). The fossil is comparable to the forewing illustrations of extant taxa such as *Tetramorium caespitum* (Linnaeus, 1758) (Donisthorpe 1915, fig. 18), *Formica rufa* Linnaeus, 1761, and *Camponotus ligniperda* (Latreille, 1802) (Emery 1925, plate 1, fig. 13–14), *Opisthopsis* Dalla Torre, 1893 (Brown and Nutting 1949, fig. 20), *Lasius Niger* (Linnaeus, 1758) (Perfilieva 2000, fig. 1a), *Azteca instabilis* (Smith, F., 1862) (Cantone 2019, fig. 2A), and to fossil taxa such as *Lasius schiefferdeckeri* Mayr, 1868 (e.g. Dlussky 2011, fig. 2–1,3 and 4; fig. 3–1) or *Lasius vulgaris* Perfileva (Perfilieva 2022, Plate 10, fig 7–8). The venation of the fossil forewing closely matches the class IIId proposed by Perfilieva (2010), or the forewing typology II, the 'Formica type' by Cantone (2019, Anexo 2). This forewing type is interpreted as an evolutionary vein reduction, being found within the subfamilies Dolichoderinae, Formicinae, and Myrmicinae (Perfilieva 2010, 2015; Cantone 2019). Although the oblique shape of the vein 2 r-rs and the presence of a vein M better corresponds more closely to a Formicinae than to the two other subfamilies, some taxa in the three groups have very similar venations (see Brown and Nutting 1949, pl. 9; Perfilieva 2015, fig. 3). Taxa from these three subfamilies occur today in Madeira Island (Wetterer et al. 2007; Espadaler 2008). Genera such as *Lasius* or *Monomorium*, both including native species on Madeira, have alate forms with similar forewing venations. The venation combined with the forewing reconstruction, with a length of ca. 10 mm (Figure 2C), can be found on extant larger female *Lasius* spp. (wing lengths calculated from Saunders 1896, plate III, fig. 3; Donisthorpe 1915, Plate X) with body lengths of ca. 9 mm (Female *Lasius* body length variation: 6.2–9.5 mm; Bernard 1968). This excludes *Monomorium*, as queens of this genus have a body length half or less of the larger *Lasius* spp. (see Smith 1858; Bernard 1968). According to Wetterer et al. (2007), *Lasius grandis* Forel 1909 is the most common ant species on Madeira. Given the similarity of the fossil to extant and fossil species and its size, we provisionally identify it as *Lasius*. However, the fragmentary nature of the specimen prevents further identification to an extant species, or to evaluate if it belonged to an extinct or extirpated taxon.

Discussion

Where are the macaronesian ant fossils?

Due to a lack of palaeoentomological studies, it is currently not known if ant somatofossils on oceanic islands are likely to be found or even abundant, or, in fact, where to look for them. Expectably, ant fossils should be found in similar sedimentary deposits as those found in the mainland. According to Elias (2010), in the mainland, Quaternary ant fossils are abundant (e.g. head capsules and mandibles) in unconsolidated terrestrial organic deposits, especially in silt-rich lacustrine deposits and in peats and bogs. On oceanic islands, due to their volcanic origin, suitable terrestrial sediments may have a limited expression. Yet, in Macaronesian archipelagos, such sedimentary deposits do occur in all archipelagos, many of them studied to assess the floristic diversity or to perform palaeoecological reconstructions (e.g. Vegas Salamanca et al. 1998; Connor et al. 2012; Nogué et al. 2013; Rull et al. 2017; Castilla-Beltrán et al. 2019; Góis-Marques et al. 2019e). Although the increase in palaeoecological research using sedimentary deposits on Macaronesian islands, to date no ant fossils were reported. Another unexplored possibility to find ant and other arthropods fossils in oceanic islands is to look for them in fossiliferous volcanic ash-tuffs deposits. For example, in the Azores, several islands have a palaeobotanical record preserved within ash-tuffs (Góis-Marques and Menezes de Sequeira 2015; Góis-Marques et al. 2019b, 2019c). Very well-preserved insects are frequent in Pliocene volcanic ash-tuffs in the French Massif Central (A.N. pers. obs). Still, to date no insect fossils were ever found in these tephra layers, although this might be due to a very limited palaeontological exploration of these deposits. Still the questions remain: are ant fossils overlooked in Macaronesia? Or could the lack of reports mean that ants arrived very recently to some archipelagos (e.g. the Azores)?

Biogeographical, ecological and evolutionary considerations

The question of 'when and how did ants arrived to Madeira Island and to other Macaronesian Islands?' is almost impossible to answer, but the finding of fossils in insular context can provide some evidence and trigger further questions about their long-term presence in Madeira Island and on Macaronesian archipelagos.

The finding of ant fossils will certainly be useful to frame a minimum arrival date to these archipelagos. Although fragmentary, the forewing fossil morphology now described clearly fits within the forewing morphology of Formicidae, providing solid evidence of the establishment of an ant taxon on Madeira Island at least since 1.3 Mya. Ant dispersal capability by flight or by colony rafting to oceanic islands was briefly discussed by Morrison (2016 and references therein). Migration by means of flight is somehow reduced (although wind might aid long distance dispersal) and rafting can effectively act as viable mean for colonies to arrive at oceanic islands (Morrison 2016). In the case of the Macaronesian archipelagos, other geological and biological factors might have aided arthropods, including ant taxa, to migrate to extant islands (see Triantis et al. 2010). The bathymetric maps of the Macaronesian region shows the presence in the last 60 Ma of several volcanic paleo-archipelagos, now eroded, many of them having emerged during the Last Glacial Maximum (Fernández-Palacios et al. 2011 and references therein; Triantis et al. 2010). The continuous presence of palaeomacaronesian archipelagos throughout the Cenozoic, could mean that ant dispersal and colonisation of Macaronesian islands from the mainland through stepping-stone might have been facilitated (Triantis et al. 2010; Fernández-Palacios et al. 2011). At an archipelagic scale, Madeira Archipelago is composed of two main large islands, the 7 My-old Madeira Island (Ramalho et al. 2015) and the ca. 14 My-old Porto Santo Island (Geldmacher et al. 2000). This could mean that ants might have first colonised Porto Santo Island during the Miocene via stepping-stones, and later reached Madeira Island as this island is just 50 km distant.

Palaeobotanical evidence demonstrated the presence of the temperate Stink-laurel forest during the Mio-Pleistocene of Madeira Island (Góis-Marques et al. 2018), a complex ecosystem dominated by a multi-stratified evergreen forest down to at least 30 m high (Capelo et al. 2005). This indicates the long-term existence of suitable habitats for ants to colonise and a biota with which they could co-evolve. Today, however, the ecological role of ants in natural Madeiran ecosystems is still unknown. With the presence of ants at least since 1.3 My-ago on Madeira Island, it could be expected that opportunities existed for ant co-evolution (or at least preservation) of myrmecochory (dispersal of seeds), myrmecophily (ant pollination) and myrmecophilous associations with other insect taxa. Yet, literature research shows these subjects are still poorly explored in Madeira Island. For example, many extant mainland plant taxa that produce seeds with elaiosomes have their counterpart endemic taxa on Madeira archipelago (Jardim and Menezes de Sequeira 2008), such as *Boraginaceae, Delphinium, Euphorbiaceae, Luzula, Maytenus, Myrtus, Teucrium*, or *Viola* (see Lengyel et al. 2010 for a complete list of plant taxa that produce elaiosomes). Today, endemic pigeons are considered the main disperser of seeds and fruits of the native and endemic Macaronesian forests (Marrero and Nogales 2021). But what about ants? A possible myrmecochory relation with endemic plants is currently unknown and ant role in disseminating seeds in native forests might have been overlooked.

Ant fossils found in oceanic islands can be also useful to ascertain the debate of whether established ants in these islands are native or introduced, or to detect extinct or extirpated taxa (Horrocks et al. 2013; Morrison 2016). Unfortunately, the specimen found on Madeira is too incomplete for an identification to extant taxa. Still, given the long-term presence of ants on Madeira, a question arises: why does this island has only one endemic taxon [*Temnothorax wollastoni* (Donisthorpe, 1940)]? As already pointed out, the number of endemic ants varies widely among Macaronesian archipelagos, with the Canaries having ca. 28% of endemics, but the other archipelagos ranging from 15% to possibly 0% of endemics (Guillem and Bensusan 2022; Native Biodiversity Data Bank of the Canary Islands www.biodiversidadcanarias.esbiota; Wetterer and Espadaler 2021; Wetterer et al. 2004, 2007). On oceanic islands, speciation depends on several factors such as isolation, number of islands in each archipelago, island geological age, topographical complexity and habitat availability (Whittaker et al. 2008; Triantis et al. 2010). The high ant endemicity in the Canary Islands is most probably due to its proximity to mainland Africa (Morocco), that facilitated ant early migration (Morrison 2016). Moreover, this archipelago is composed of several large and topographically complex islands which certainly contributed to the evolution of endemic taxa. In contrast the Madeira archipelago (excluding the Selvagens archipelago) is composed of fewer and is more isolated islands, possibly contributing to the single endemic taxon currently described. Presently, Madeira archipelago myrmecofauna is composed of 10 native ants (including one single island endemic) and 21 introduced/exotic ants (Guillem and Bensusan 2022). The high number of exotic ants is due to recent human mediated introductions, which certainly shaped extant ant diversity in all Macaronesian archipelagos, with exotic ants possibly replacing native/endemic ants (Wetterer et al. 2004, 2006, 2007; Wetterer and Espadaler 2010, 2021; Guillem and Bensusan 2022).

Conclusions

The finding of the first ant fossils with 1.3 My-old in Macaronesian islands provides evidence of that these eusocial insects were already part of the insular ecosystems since the Calabrian. However, almost nothing is known about their past or present ecological role. The same situation of uncertainty occurs for the antiquity of the Macaronesian termites (Lamb 1980). We expect this research calls the attention for the need of an active palaeoentomological research on oceanic islands, and to trigger further examination of ant research in Macaronesian natural ecosystems and to examine the disparity of endemic ant taxa in Macaronesian archipelagos.

Acknowledgments

We would like to thank AntWiki project contributors (https://www.antwiki.org/) for all information freely available that made this work possible and express our gratitude to the two anonymous reviewers and their comments that improved this manuscript. CAGM would like to acknowledge former financial support from ARDITI – Regional Agency for the Development of Research, Technology and

Innovation, project M1420-09-5369-FSE-000001- PhD grant; JM is funded by Fundação para a Ciência e a Tecnologia, I.P. (Portugal)/MCTES through national funds (PIDDAC)" – UIDB/50019/2020. PC is funded by Fundação para a Ciência e a Tecnologia, I.P. in the frame of the UIDB/00073/2020, UIDP/00073/2020 project of the I&D unit Geosciences Center (CGeo, University of Coimbra).

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This work was supported by the Fundação para a Ciência e a Tecnologia, I.P./ MCTES through national funds (PIDDAC) [UIDB/50019/2020]; ARDITI – Regional Agency for the Development of Research, Technology and Innovation [M1420-09-5369-FSE-000001- PhD grant]; Fundação para a Ciência e a Tecnologia, I.P. [UIDB/00073/2020].

ORCID

Carlos A. Góis-Marques http://orcid.org/0000-0002-0255-7641
Pedro Correia http://orcid.org/0000-0002-0573-7138
Andre Nel http://orcid.org/0000-0002-4241-7651
José Madeira http://orcid.org/0000-0003-4729-8994
Miguel Menezes de Sequeira http://orcid.org/0000-0001-9728-465X

Author contributions

This paper was conceptualised by CAGM. CAG-M and MMdS performed field and laboratorial work. The analysis, writing, and editing were performed by CAGM, PC, AN, JM and MMdS. All authors read and approved the paper.

References

Alonso-Zarza AM, Genise JF, Verde M. 2012. Calcrete and insect trace micromorphology from the pleistocene paleosol profiles of the Canary Islands. Poch RM, Casamitjana M, Francis ML, editors. Proceedings of the 14th international working meeting on soil micromorphology. Lleida, Spain: Departament de Medi Ambient i Ciències del Sòl (UdL); p. 233–235.

Antropov AV, Belokobylskij SA, Compton SG, Dlussky GM, Khalaim AI, Kolyada VA, Kozlov MA, Perfilieva KS, Rasnitsyn AP. 2013. The wasps, bees and ants (insecta: vespida = hymenoptera) from the insect limestone (late eocene) of the isle of Wight, UK. Earth Environ Sci Trans R Soc Edinb. 104(3–4):335–446. doi:10.1017/S1755691014000103.

Báez M, Oromí P. 2005. Arthropoda. In: Arechavaleta M, Zurita N, Marrero MC, Martín JL, editors. Lista preliminar de especies silvestres de Cabo Verde (hongos, plantas y animales terrestres). Santa Cruz de Tenerife: Consejería de Medio Ambiente e Ordenación Territorial, Gobierno de Canarias; p. 60–100.

Barden P. 2017. Fossil ants (Hymenoptera: Formicidae): ancient diversity and the rise of modern lineages. Myrmecol News. 24:1–30. doi:10.25849/myrmecol.news_024:001

Barquín J 1981. Las Hormigas de Canarias: taxonomía, Ecología y Distribución de los Formicidae. Unpublished PhD, Universidad de La Laguna.

Bengtson P. 1988. Open nomenclature. Palaeontology. 31(1):223–227.

Bernard F. 1968. Les fourmis (Hymenoptera Formicidae) d'Europe occidentale et septentrionale. Paris: Centre National de La Recherche Scientifique.

Borges PAV, Aguiar AMF, Boieiro M, Carles-Tolrá M, Serrano ARM. 2008. The arthropods (arthropoda) of the madeira and selvagens archipelagos. In: Borges PAV, Abreu C, Aguiar AMF, Carvalho P, Jardim R, Melo I, Oliveira P, Sérgio C, ARM S, Vieira P, editors. Listagem dos fungos flora e fauna terrestre dos arquipélagos da Madeira e Selvagens. Funchal e Angra do Heroísmo: Direcção Regional do Ambiente da Madeira e Universidade dos Açores; p. 245–262.

Borges PAV, Vieira V, Amorim IR, Bicudo N, Fritzén N, Gaspar C, Heleno R, Hortal J, Ler J, Logunov D, et al. 2010. Lista de Artrópodes (Arthropoda). In: Borges PAV, Costa A, Cunha R, Gabriel R, Gonçalves V, Frias Martins A, Melo I, Parente M, Raposeiro P, Rodrigues P, et al., editors. Listagem dos organismos terrestres e marinhos dos Açores. Cascais: Principia; p. 179–246.

Brown WL, Nutting WL. 1949. Wing venation and the phylogeny of the Formicidae (Hymenoptera). Trans Am Entomol Soc. 75(3/4):113–132.

Brum da Silveira A, Madeira J, Ramalho R, Fonseca P, Prada S. 2010a. Notícia explicativa da carta geológica da ilha da Madeira na escala 1:50.000, Folhas A e B. Funchal: Secretaria Regional do Ambiente e Recursos Naturais, Região Autónoma da Madeira.

Brum da Silveira A, Madeira J, Ramalho R, Fonseca PE, Rodrigues CF, Prada S. 2010b. Carta Geológica da Região Autónoma da Madeira, na escala 1:50.000, Folha A. Funchal: Secretaria Regional do Ambiente e Recursos Naturais, Região Autónoma da Madeira.

Brum da Silveira A, Madeira J, Ramalho R, Fonseca PE, Rodrigues CF, Prada S. 2010c. Carta Geológica da Região Autónoma da Madeira, na escala 1:50.000, Folha B. Funchal: Secretaria Regional do Ambiente e Recursos Naturais, Região Autónoma da Madeira.

Cantone SM 2019. As asas das formigas (Hymenoptera: Formicidae): estudo comparativo e chaves de identificação das castas aladas [dissertation]. São Paulo: Universidade Estadual Paulista "Júlio de Mesquita Filho".

Capelo J, Menezes de Sequeira M, Jardim R, Mesquita S, Costa JC. 2005. The vegetation of Madeira Island (Portugal): a brief overview and excursion guide. Quercetea. 7:95–122.

Castilla-Beltrán A, de Nascimento L, Fernández-Palacios JM, Fonville T, Whittaker RJ, Edwards M, Nogué S. 2019. Late Holocene environmental change and the anthropization of the highlands of Santo Antão Island, Cabo Verde. Palaeogeogr Palaeoclimatol Palaeoecol. 524:101–117. doi:10.1016/j.palaeo.2019.03.033

Connor SE, van Leeuwen JFN, Rittenour TM, WOvd K, Ammann B, Björck S. 2012. The ecological impact of oceanic island colonization – a palaeoecological perspective from the Azores. J Biogeogr. 39 (6):1007–1023. doi:10.1111/j.1365-2699.2011.02671.x.

Coope GR. 1970. Interpretations of Quaternary insect fossils. Annu Rev Entomol. 15(1):97–121. doi:10.1146/annurev.en.15.010170.000525.

Dlussky GM. 2011. The ants of the genus *Lasius* Fabricius (Hymenoptera, Formicidae) from the Late Eocene European ambers. Vestn Zool. 45 (3):209–222.

Donisthorpe HSJK. 1915. British ants, their life-history and classification. Plymouth: William Brendon and Son.

Edwards N, Meco J. 2000. Morphology and palaeoenvironment of brood cells of Quaternary ground-nesting solitary bees (Hymenoptera, Apidae) from Fuerteventura, Canary Islands, Spain. Proc Geol Assoc. 111(2):173–183. doi:10.1016/S0016-7878(00)80007-3.

Elias SA. 2010. Advances in Quaternary Entomology. Amsterdam: Elsevier.

Emery C. 1925. Hymenoptera, Fam. Formicidae, subfam. Formicinae. Genera Insectorum. 183:1–302.

Espadaler X. 2008. Hymenoptera (Formicidae). In: Borges PAV, Abreu C, Aguiar AMF, Carvalho P, Jardim R, Melo I, Oliveira P, Sérgio C, ARM S, Vieira P, editors. Listagem dos fungos, flora e fauna terrestre dos arquipélagos da Madeira e Selvagens. Funchal e Angra do Heroísmo: Direcção Regional do Ambiente da Madeira e Universidade dos Açores; p. 352.

Fernández-Palacios JM, de Nascimento L, Otto R, Delgado JD, García-del-Rey E, Arévalo JR, Whittaker RJ. 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. Journal of Biogeography. 38(2):226–246. doi:10.1016/S0016-7878(00)80007-3.

Geldmacher J, van den Bogaard P, Hoernle K, Schmincke H-U. 2000. The 40 Ar/ 39 Ar age dating of the madeira archipelago and hotspot track (eastern North Atlantic). Geochemistry, Geophysics, Geosystems. 1(2):1–26. doi:10.1029/1999GC000018.

Genise JF. 2017. Ichnoentomology: insect traces in soils and paleosols. Switzerland: Springer.

Genise JF, Alonso-Zarza AM, Verde M, Meléndez A. 2013. Insect trace fossils in aeolian deposits and calcretes from the Canary Islands: their ichnotaxonomy, producers, and palaeoenvironmental significance. Palaeogeography, Palaeoclimatology, Palaeoecology. 377:110–124. doi:10.1016/j.palaeo.2013.03.005

Góis-Marques CA 2013. Paleobotânica da Ilha da Madeira: inventário e Revisão da Macroflora Fóssil de São Jorge e Porto da Cruz [unpublished master's thesis]. Lisbon: Faculdade de Ciências da Universidade de Lisboa.

Góis-Marques CA 2020. The Quaternary palaeobotany of madeira and azores volcanic archipelagos (Portugal): insights into the past diversity, ecology, biogeography and evolution [unpublished dissertation]. Lisbon: Faculdade de Ciências da Universidade de Lisboa.

Góis-Marques CA, de Nascimento L, Fernández-Palacios JM, Madeira J, Menezes de Sequeira M. 2019a. Tracing insular woodiness in giant *Daucus* (s.l.) fruit fossils from the early pleistocene of madeira island (Portugal). Taxon. 68(6):1314–1320. doi:10.1002/tax.12175.

Góis-Marques CA, de Nascimento L, Menezes de Sequeira M, Fernández-Palacios JM, Madeira J. 2019b. The quaternary plant fossil record from the volcanic azores archipelago (Portugal, North Atlantic Ocean): a review. Hist Biol. 31(10):1267–1283. doi:10.1080/08912963.2018.1444761.

Góis-Marques CA, Elias RB, Steinbauer MJ, de Nascimento L, Fernández-Palacios JM, Menezes de Sequeira M, Madeira J. 2019c. The loss of a unique palaeobotanical site in Terceira Island within the Azores

UNESCO global geopark (Portugal). Geoheritage. 11(4):1817–1825. doi:10.1007/s12371-019-00401-1.

Góis-Marques CA, Jesus J, Menezes de Sequeira M, Madeira J. 2019d. The first Ichneumonid fossil from Pleistocene of Madeira Island (Portugal). Zootaxa. 4612(3):447–450. doi:10.11646/zootaxa.4612.3.13.

Góis-Marques CA, Madeira J, Menezes de Sequeira M. 2018. Inventory and review of the Mio-Pleistocene São Jorge flora (Madeira Island, Portugal): palaeoecological and biogeographical implications. J Syst Palaeontol. 16 (2):159–177. doi:10.1080/14772019.2017.1282991.

Góis-Marques CA, Menezes de Sequeira M. 2015. Darwin, Hooker and Arruda Furtado and the palaeobotany of Azores: rediscovering the first collections. Rev Palaeobot Palynol. 221:47–51. doi:10.1016/j.revpalbo.2015.05.010

Góis-Marques CA, Mitchell RL, de Nascimento L, Fernández-Palacios JM, Madeira J, Menezes de Sequeira M. 2019e. *Eurya stigmosa* (Theaceae), a new and extinct record for the Calabrian stage of Madeira Island (Portugal): ^{40}Ar/^{39}Ar dating, palaeoecological and oceanic island palaeobiogeographical implications. Quat Sci Rev. 206:129–140. doi:10.1016/j.quascirev.2019.01.008

Guillem R, Bensusan K. 2022. Three new exotic species of ants (Hymenoptera, Formicidae) for Madeira, with comments on its myrmecofauna. Journal of Hymenoptera Research. 91:321–333. doi:10.3897/jhr.91.81624

Hartung G, Mayer K. 1864. Geologische Beschreibung der Inseln Madeira und Porto Santo. In: Mit dem systematischen Verzeichnisse der fossilen Reste dieser Inseln und der Azoren von Karl Mayer. Leipzig: Engelmann.

Heer O. 1857. Ueber die fossilen Pflanzen von St. Jorge in Madeira. Neue Denkschr Allg Schweiz Ges Gesammten Naturwiss Band. XV:1–40.

Horrocks M, Marra M, Baisden WT, Flenley J, Feek D, González Nualart L, Haoa-Cardinali S, Edmunds Gorman T. 2013. Pollen, phytoliths, arthropods and high-resolution 14C sampling from Rano Kau, Easter Island: evidence for late Quaternary environments, ant (Formicidae) distributions and human activity. Journal of Paleolimnology. 50(4):417–432. doi:10.1007/s10933-013-9735-5.

Jardim R, Menezes de Sequeira M 2008. As plantas vasculares (Pteridophyta e Spermatophyta) dos arquipélagos da Madeira e das Selvagens. In: Borges PAV, Abreu C, Aguiar AMF, Carvalho P, Jardim R, Melo I, Oliveira P, Sérgio C, ARM S, Vieira P, editors. Listagem dos fungos flora e fauna terrestre dos arquipélagos da Madeira e Selvagens. Funchal e Angra do Heroísmo: Direcção Regional do Ambiente da Madeira e Universidade dos Açores; p. 181–207.

Krushelnycky PD, Loope LL, Reimer NJ. 2005. The ecology, policy, and management of ants in Hawaii. Proc Hawaii Entomol Soc. 37:1–25. http://hdl.handle.net/10125/103

Lamb RW. 1980. Termites (Isoptera) of Macaronesia. Bol Mus Munic Funchal. 33:44–66.

LaPolla JS, Dlussky GM, Perrichot V. 2013. Ants and the Fossil Record. Annual Review of Entomology. 58(1):609–630. doi:10.1146/annurev-ento-120710-100600.

La Roche F, Genise JF, Castillo C, Quesada ML, García-Gotera CM, De la Nuez J. 2014. Fossil bee cells from the Canary Islands. Ichnotaxonomy, palaeobiology and palaeoenvironments of *Palmiraichnus castellanosi*. Palaeogeography, Palaeoclimatology, Palaeoecology. 409:249–264. doi:10.1016/j.palaeo.2014.05.012

Lengyel S, Gove AD, Latimer AM, Majer JD, Dunn RR. 2010. Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: a global survey. Perspectives in Plant Ecology, Evolution and Systematics. 12(1):43–55. doi:10.1016/j.ppees.2009.08.001.

Machado A. 2006. The type material of the species of *Laparocerus* Schönherr, 1834 (Coleoptera, Curculionidae, Entiminae). Journal of Natural History. 40 (35–37):2001–2055. doi:10.1080/00222930601046659.

Marrero P, Nogales M. 2021. Trophic strategies of two sympatric endemic pigeons in insular ecosystems: a framework for understanding spatiotemporal frugivory interactions. Journal of Avian Biology. 52(10):e02803. doi:10.1111/jav.02803.

Meco J, Muhs DR, Fontugne M, Ramos AJG, Lomoschitz A, Patterson D. 2011. Late Pliocene and Quaternary Eurasian locust infestations in the Canary Archipelago. Lethaia. 44(4):440–454. doi:10.1111/j.1502-3931.2010.00255.x.

Morrison LW. 2016. The ecology of ants (Hymenoptera: Formicidae) on islands. Myrmecol News. 23:1–14. doi:10.25849/myrmecol.news_023:001

Nogué S, de Nascimento L, Fernández-Palacios JM, Whittaker RJ, Willis KJ, McGlone M. 2013. The ancient forests of La Gomera, Canary Islands, and their sensitivity to environmental change. Journal of Ecology. 101 (2):368–377. doi:10.1111/1365-2745.12051.

Oromí P, Báez M. 2009. Arthropoda. In: Arechavaleta M, Rodríguez S, Zurita N, García A, editors. Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. Santa Cruz de Tenerife (España): Gobierno de Canarias; p. 189–366.

Perfilieva KS. 2000. Wing venation anomalies in sexual individuals of ants (Hymenoptera, Formicidae) with different strategies of mating behavior. Entomol Rev. 80(9):1181–1188.

Perfilieva KS. 2010. Trends in evolution of ant wing venation (Hymenoptera, Formicidae). Entomol Rev. 90(7):857–870. doi:10.1134/S0013873810070043.

Perfilieva KS. 2015. The evolution of diagnostic characters of wing venation in representatives of the subfamily Myrmeciinae (Hymenoptera, Formicidae). Entomol Rev. 95(8):1000–1009. doi:10.1134/S0013873815080072.

Perfilieva KS. 2022. Ants (Hymenoptera: Formicidae) from Localities of the Russian Far East (Amgu, Velikaya Kema). Paleontol J. 56(4):412–425. doi:10.1134/S0031030122040086.

Ramalho RS, Brum da Silveira A, Fonseca PE, Madeira J, Cosca M, Cachão M, Fonseca MM, Prada SN. 2015. The emergence of volcanic oceanic islands on a slow-moving plate: the example of Madeira Island, NE Atlantic. Geochemist Geophys Geosystems. 16(2):522–537. doi:10.1002/2014GC005657.

Rull V, Lara A, Rubio-Inglés MJ, Giralt S, Gonçalves V, Raposeiro P, Hernández A, Sánchez-López G, Vázquez-Loureiro D, Bao R, et al. 2017. Vegetation and landscape dynamics under natural and anthropogenic forcing on the Azores Islands: a 700-year pollen record from the São Miguel Island. Quat Sci Rev. 159:155–168. doi:10.1016/j.quascirev.2017.01.021

Saunders E. 1896. The Hymenoptera Aculeata of the British islands. London: L. Reeve & CO.

Smith F. 1858. Catalogue of hymenopterous insects in the collection of the British Museum. Part VI. Formicidae. London: British Museum.

Starkie Gardner J. 1882. The geology of Madeira. J Geol Soc London. 38:277–281. doi:10.1144/GSL.JGS.1882.038.01-04.30

Tofilski A. 2004. DrawWing, a program for numerical description of insect wings. J Insect Sci. 4(1):17. doi:10.1093/jis/4.1.17.

Triantis KA, Borges PAV, Hortal J, Whittaker RJ. 2010. The Macaronesian province: patterns of species richness and endemism of arthropods. In: Serrano ARM, Borges PAV, Boieiro M, Oromí P, editors. Terrestrial Artrhropods of Macaronesia – biodiversity, Ecology and Evolution. Lisboa: Sociedade Portuguesa de Entomologia; p. 49–71.

Vegas Salamanca J, Alvarez-Ramis MC, Laamarti N. 1998. Reconstrucción de los megarrestos vegetales fósiles encontrados en los sedimentos epiclásticos de la caldera de Taburiente, La Palma (islas Canarias). Comunicación de las XIV Jornadas de Paleontología. 187–189.

Wetterer JK, Espadaler X. 2010. Invasive ants of Macaronesia. In: Serrano ARM, Borges PAV, Boieiro M, Oromí P, editors. Terrestrial arthropods of Macaronesia: biodiversity, ecology and evolution. Lisboa: Sociedade Portuguesa de Entomologia; p. 133–143.

Wetterer JK, Espadaler X. 2021. Ants (Hymenoptera: Formicidae) of the Cabo Verde Islands. Trans Am Entomol Soc. 147:485–502. doi:10.3157/061.147.0203

Wetterer JK, Espadaler X, Wetterer AL, Aguin-Pombo D, Aguiar AMF. 2007. Ants (Hymenoptera: Formicidae) of the Madeiran Archipelago. Sociobiology. 49(2):1–33.

Wetterer JK, Espadaler X, Wetterer AL, Cabral SGM. 2004. Native and exotic ants of the Azores (Hymenoptera: Formicidae). Sociobiology. 44(1):1–19.

Wetterer JK, Espalader X, Wetterer AL, Aguin-Pombo D, Franquinho-Aguiar AM. 2006. Long-term impact of exotic ants on the native ants of Madeira. Ecol Entomol. 31(4):358–368. doi:10.1111/j.1365-2311.2006.00790.x.

Whittaker RJ, Fernández-Palacios JM. 2007. Island Biogeography: ecology, Evolution and Conservation. New York: Oxford University Press.

Whittaker RJ, Triantis KA, Ladle RJ. 2008. A general dynamic theory of oceanic island biogeography. J Biogeogr. 35(6):977–994. doi:10.1111/j.1365-2699.2008.01892.x.