JOURNAL OF QUATERNARY SCIENCE (2023) **38**(4) 597–607 ISSN 0267-8179. DOI: 10.1002/jqs.3500

JQS Journal of Quaternary Science QRA Quaternary Research Association

Plant–insect interactions in the Quaternary fossil record of the Azores Archipelago (Portugal)

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Received 4 August 2022; Revised 2 December 2022; Accepted 23 December 2022

ABSTRACT: The fossil record of the Azores still lacks evidence of terrestrial invertebrates. Based on a study of the collections of Quaternary fossil plant imprints from the Azores, located in the depositories of public collections and also newly conducted field research, several samples of fossil leaves with traces of plant–animal interactions were found. These are evidence of marginal feeding (*Phagophytichnus ekowskii*) and anophionome mine (*Cuniculonomus* isp.). One specimen with traces of boring in fossil wood (*Xylonichnus trypetus*), previously only briefly mentioned in the literature, was also described in detail. In addition to a detailed description of the found traces, the present study also discusses the possible trace-makers, using a comparison with the recent phytophagous fauna in relation to the original vegetation of the Azores (that includes laurisilva forest). It is thus possible to consider butterfly caterpillars (group Macrolepidoptera) or locust larvae (Orthoptera/Caelifera) as possible originators of marginal feeding. The ophionome mine could have been caused by the larvae of leaf-miner flies (Agromyzidae) or moths from the group Microlepidoptera (Gracillariidae). Wood-destroying beetles could be the cause of the boring in fossil wood.
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KEYWORDS: Azores Islands; Macaronesia; plant–animal interactions; Quaternary; trace fossils.

Introduction

Due to its isolation, geological and biological history, oceanic islands are considered ideal natural laboratories to study ecological, evolutionary and biogeographical patterns (Whittaker and Fernández-Palacios, 2007; Warren *et al.*, 2015; Whittaker *et al.*, 2017). Moreover, given the high biota endemicity, many oceanic islands are considered to be biodiversity hotspots (Myers *et al.*, 2000).

In the case of the Macaronesian archipelagos (Azores, Madeira, Canary and Cabo Verde archipelagos, Atlantic Ocean), pristine ecosystems were present until human settlement took place, as late as the 15th century (Fernández-Palacios *et al.*, 2016, and references therein), leading to an inevitable negative anthropic impact on native terrestrial ecosystems (e.g. deforestation, extinctions), a pattern observed on islands worldwide (e.g. Wood *et al.*, 2017). Among one of the most affected Macaronesian archipelagos is the Azores Archipelago, presenting today less than 5% of native forest (Triantis *et al.*, 2010; Norder *et al.*, 2020). The effects of human impact on these islands were recently published based mainly on palaeoecological reconstructions (e.g. Connor *et al.*, 2012; 2013; Raposeiro *et al.*, 2017; Rull *et al.*, 2017). However, there is currently some debate on the presence of humans before the 15th century in the Azores with authors not being in accordance concerning the levels of habitat change prior to Portuguese colonisation (see debate in Raposeiro *et al.*, 2021; Elias *et al.*, 2022). Despite their importance, these studies concentrate mainly on the most recent centuries, and on the human impact. Interesting was also the recent finding that Macaronesian island orography played an important role in habitat destruction on these islands, with more complex islands in terms of orography having a large proportion of native forest preserved nowadays (Norder *et al.*, 2020), with orography also playing a role on the distribution of rare arthropod species (Borges *et al.*, 2006).

Yet, terrestrial palaeontology in the Azores is still poorly studied. Recent palaeobotanical studies in the Azores are still infrequent, although the occurrence of fossil plants is known from almost all the islands of the archipelago, with the exception of the islands of Santa Maria and Corvo. Floral remains were found buried in fine-grained pyroclastic rocks (tuffs) across the archipelago and have the character of coalified wood fragments, leaf imprints and also pollen grains (Góis-Marques and Menezes de Sequeira, 2015; Góis-Marques *et al.*, 2019a; Góis-Marques *et al.*, 2019b; Góis-Marques *et al.*, 2020). Currently, ca. 40 species are known from the fossil record (see Supporting Information Table S1 and references therein). Based on radiocarbon dating, Góis-Marques *et al.* (2019a) dated these fossils to the Late Pleistocene to Holocene (<50 ka). A higher age, up to 70 ka, was admitted only in the case of sites around the town of Angra do Heroísmo (Terceira Island).

The sites with fossil fauna are much more sporadic. The vast majority of existing studies have focused on the description of the most known fossiliferous formations on the Azores, i.e. Pliocene and late Pleistocene marine deposits on Santa Maria island (e.g. Ávila *et al.*, 2018, 2020; Hyžný *et al.*, 2020; Uchman *et al.*, 2020). Terrestrial fossil remains are very rare; only sporadic bones of Holocene birds on the islands of Pico, São Miguel, São Jorge, Terceira, Graciosa and Santa Maria were described (Alcover *et al.*, 2015; Rando *et al.*, 2013, 2017). Records of extinct invertebrates are not yet confirmed, although their presence is very likely and depends only on appropriate preservation conditions (Connor *et al.*, 2016;

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Raposeiro *et al.*, 2017). However, based on inferences from historical and contemporary records, Terzopoulou *et al.* (2015) list seven beetle (Coleoptera) species that are potentially extinct. This hypothesis is also confirmed by the rare finding of fossil insects from Madeira (Heer, 1857; Góis-Marques *et al.*, 2019c) and insect-induced trace fossils from the Canary Islands (*Palmiraichnus castellanosi, Rebuffoichnus guanche* and *R. casamiquelai*; Genise *et al.*, 2013; La Roche *et al.*, 2014 and literature therein). In the Canary Islands, also taxonomically unspecified galls and domatia on Holocene leaves have recently been described (Álvarez *et al.*, 2019). The most updated list of present Azorean arthropods was given by Borges *et al.* (2010) and further discussed by Rego *et al.* (2015).

The study of museum collections with finds of fossil flora from the Azores identified several exceptional specimens showing feeding marks from phytophagous insects, not yet found in this archipelago. Locations of the finds are imprecise – with a few exceptions – and, as such, do not allow a precise description of specific sites. This is why only general characteristics are given in the description of sampling sites.

Geological setting

The Azores Archipelago is located in the central North Atlantic, bounded by parallels 39°50 and 36°50′ N and the meridians 25°0′ and 31°20′ W. This archipelago is the result of a complex tectonic setting, corresponding to the triple junction between the north American, Eurasian and Nubian tectonic plates. The archipelago comprises nine islands, geographically divided into three groups. The western group comprises Corvo (17.1 km^2; 720 m a.s.l.) and Flores (143 km^2; 915 m a.s.l.) islands, the central group includes Faial (170 km^2; 1043 m a.s.l.), Pico (448 km^2; 2351 m a.s.l.), São Jorge (246 km^2; 1.053 m a.s.l.), Terceira (400 km^2; 1.021 m a.s.l.) and Graciosa (61.6 km^2; 402 m a.s.l.) islands and the eastern group is formed by São Miguel (742 km^2; 874 m a.s.l.) and Santa Maria (97 km^2; 587 m a.s.l.) islands and the Formigas islets (Fig. 1) (Miranda *et al.*, 2018).

Unlike Hawaii or the Canaries, the age of the Azores islands is still a matter of discussion. Recently, a study by Ramalho *et al.* (2016) supported a complex evolutionary history of Santa Maria with a first emergence in the Late Miocene (6–5.8 Ma), followed by subsidence (5.3–4.1 Ma), renewed volcanic activity (4.1–2.8 Ma) and uplift (3.5 Ma to the present). Concerning arthropods, the phylogeny of the genus *Tarphius* (Amorim *et al.*, 2012) revealed that Azorean *Tarphius* is an old group and that the most recent intra-island speciation event on Santa Maria occurred between 6.1 and 3.7 Ma. Besides, phylogeography of six arthropod species (Parmakelis *et al.*, 2015) showed that active volcanism on young islands may have promoted processes of extinction and that most of the studied species diversified in the last 2 My. All these biological data are more consistent with the Santa Maria–São Miguel–Terceira sequence of island formation. Currently accepted island geological ages can be consulted at Florencio *et al.* (2021) in their table 1.

The detailed stratigraphy of Santa Maria was described by Serralheiro (2003). The island lies on the edge of the Azores Plateau, which means that it is a volcanically extinct island, with the youngest magmatic rocks dated to ca. 4 Ma (Beier *et al.*, 2018). Santa Maria is known especially for its rich palaeontological finds of marine fauna, preserved in limestones of shallow-water character (Ávila *et al.*, 2018).

The island of São Miguel, the largest of the whole archipelago, also belongs to the eastern group, is formed by four large stratovolcanoes active from the Pleistocene (ca. 880 ka) to the present (1880), see Fig. 2.

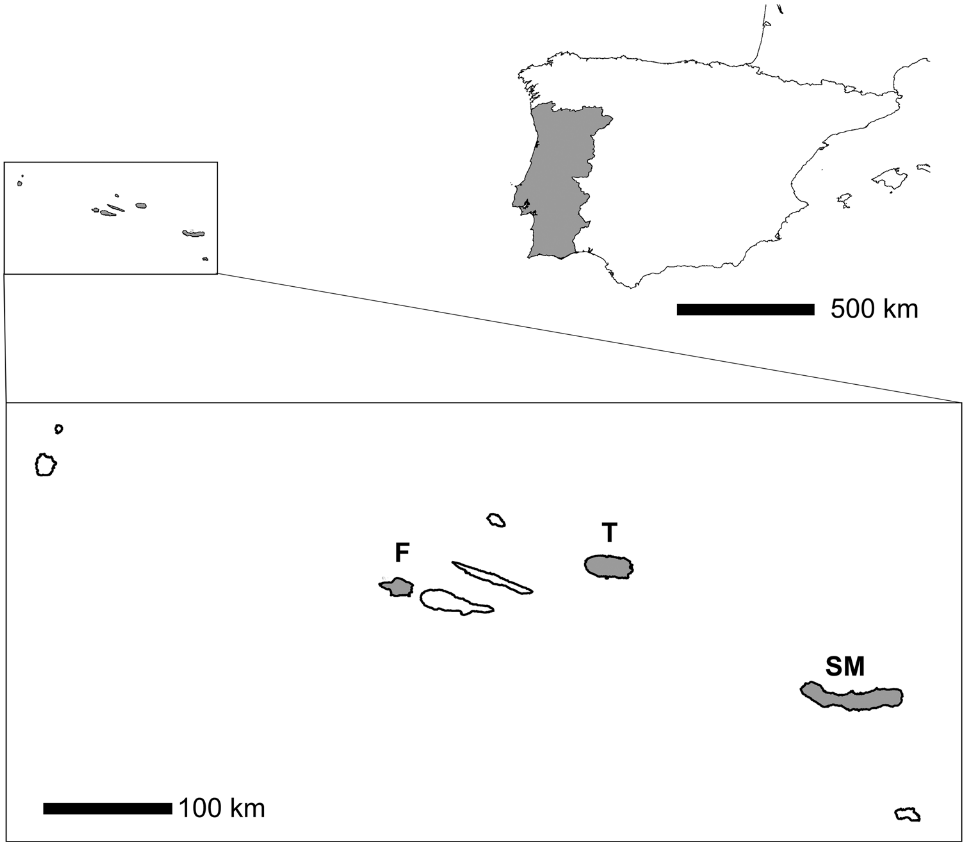

Figure 1. Localisation of the Azores Archipelago. Islands mentioned in this paper are highlighted in grey (F – Faial, SM – São Miguel, T – Terceira).

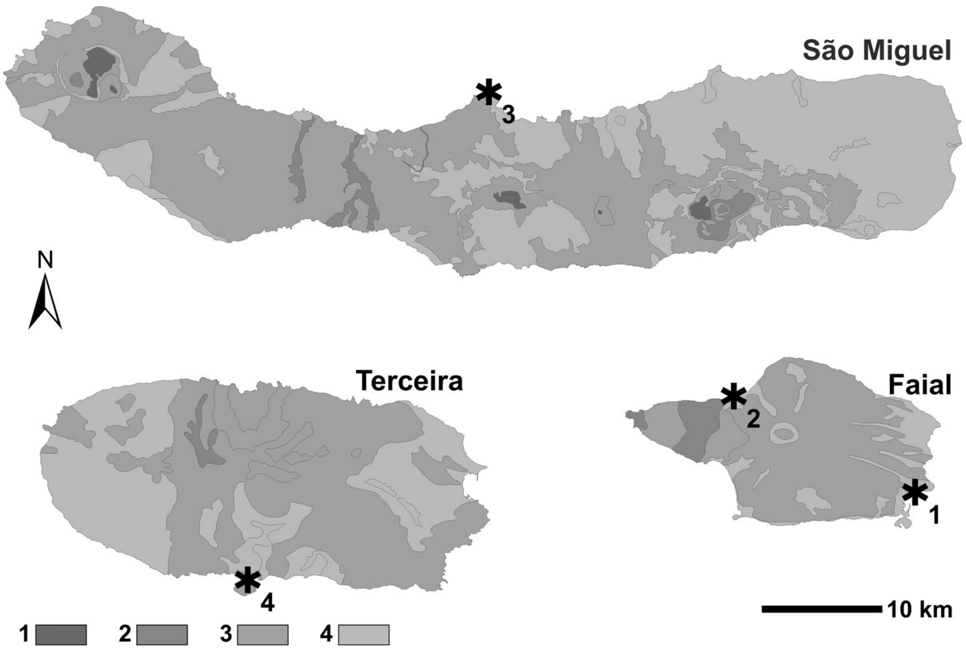

Figure 2. Geological setting of the described islands. 1 – Quaternary sediments, 2 – Quaternary volcanics (recent/subrecent), 3 – Quaternary volcanics (Holocene), 4 – Pliocene/Pleistocene volcanics. Fossiliferous sites are marked with an asterisk. 1 – Espalamaca, 2 – Fajã da Praia do Norte, 3 – Ponta do Cintrão, Ribeirinha, 4 – Angra do Heroísmo.

Islands of the central group were formed in the Pleistocene with a continued volcanic activity till the recent/subrecent: Terceira from >370 ka to 1761, São Jorge from ca. 1.8 Ma to 1907, Graciosa from ca. 1.0–0.7 Ma to 10 ka, Faial from ca. 850 ka to 1958 and Pico from 300 ka to 1720. Islands of the eastern group, Flores and Corvo, lie on the American Plate, and the local volcanic products date to the Pleistocene to Holocene (ca. 2.2–3 ka). Mafic volcanics including pyroclastics represent the dominant rock type on all islands (Calvert *et al.*, 2006; Hildenbrand *et al.*, 2012; Sibrant *et al.*, 2015; Larrea *et al.*, 2018), see Fig. 2.

Material and methods

For the purpose of this study, we used collections of fossil plant imprints from the Azores, located in the depositories of several museums and universities, and also some that were newly collected during fieldwork. These are collections from the Geological Museum in Lisbon, Portugal (77 samples, indicated in the text by abbreviation MG_L), the Volcanospeleological Museum in Angra do Heroísmo 'Os Montanheiros', Azores, Portugal (30 samples, abbreviation MV-AdH), the University of the Azores in Angra do Heroísmo, Azores, Portugal (28 samples) and eight samples, collected in 2019 at the site Fanal Bay, Terceira Island, Azores.

After the initial taxonomic determination of the fossil plant species (or revision in the case that the samples had been already identified), a detailed analysis was made to recognise all possible types of damage caused by animals with the aim of defining the main functional feeding groups. In a generalised approach, these include marginal and non-marginal excisions, skeletonisation, mines (Labandeira, 2002; Genise, 2017) and also traces after oviposition (ecdysichnia, *sensu* Vallon *et al.*, 2016). Plants galls – cecidotaxa *sensu* Vallon *et al.* (2016), were not included in the research. In the ethological concept of their genesis, galls usually provide only the reaction tissue of a given plant, with no specific life manifestation of the trace-maker (Bertling *et al.*, 2006).

Several approaches are applied to the description of the damage. The systematic part of the present study employs identification in the sense of a descriptive morphological point of view, the so-called damage types according to Labandeira *et al.* (2007). The concept of systematic ichnology, i.e. classification in the relevant ichnogenus, is applied as well.

In addition to the ichnological and palaeoecological analysis, the study also includes a brief geological description of localities with documented remains of fossil plant–animal interactions. Where possible, the available published information on the dating of fossiliferous strata is also provided. At most places, however, the necessary data are missing and therefore only approximate dating is mentioned.

The Canon EOS 6D camera and an OLYMPUS SZX12 binocular microscope with photocell (Olympus E-410) were used for photo documentation.

Sampling sites

Imprints of fossil flora with insect traces have been identified in samples from the islands of Faial, São Miguel and Terceira (Angra do Heroísmo).

Faial Island

Four volcanostratigraphic stages contributing to the present geological setting are distinguished on Faial Island. The oldest of these is the Ribeirinha Volcanic Complex, the development of which was started at ca. 850 ka by the formation of a shield volcano. It is composed of a series of lava flows and also beds formed by pumice, scoria and basaltic pyroclastics. It is overlain by the Cedros Volcanic Complex, a polygenetic volcano originated at ca. 450 ka. Its basal part is composed of effusions of Hawaiian/Strombolian type, overlain by products of eruptive explosions and trachytic pyroclasts. The above mentioned two complexes are penetrated by two Fissural Systems: the Horta-Caldeira System with products of mostly basaltic character up to 11 ka in age and the Caldeira-Capelo Fissural System composed of young, Holocene eruptions of basaltic lavas (Pacheco 2001, Larrea *et al.*, 2018).

Espalamaca

An exposure in fine-grained pyroclastics lies in the south of the cape of Ponta da Espalamaca in the southeastern part of the island, ca. 2 km from the town of Horta (38.543°N, 28.614°W, see Fig. 2). A section of fine-grained, weakly lithified yellowish tuffs, pumice and palaeosols, dark brown in colour, is exposed here with a total thickness of ca. 3 m over a distance of about 1 km. It is mostly overgrown by vegetation. These rocks, overlying trachyandesites, show abundant imprints of *Laurus azorica*, *Morella faya* and *Hedera azorica* (see Supporting Information Table S1) (Forjaz, 1960, 1970; Forjaz and Monjardino, 1964). The pyroclastics belong to the so-called Horta-Caldeira Fissural System, also referred to as the Almoxarife Formation, which is a low-altitude and smooth-relief platform ca. 11 ka in age (Larrea *et al.*, 2018).

Fajã da Praia do Norte

This is an approximately 500 m long cliff, lying near the community of Praia do Norte in the northwestern tip of the island (38.610°N, 28.755°W). The section is composed of reddish-brown to greyish andesite ignimbrites (tuffs to breccias) of a variable particle size. Its maximum thickness is 25 m. A finer interval in the upper one-third of the section contains rare fragments of coalified wood but no leaf imprints have been found (Forjaz, 1970; Góis-Marques *et al.*, 2020). The pyroclastics pertain to the upper part of a complex produced by the eruption of Caldeira Volcano, the so-called Cedros Member (C11 deposits, 980–1180 cal a BP, see Madeira *et al.*, 1995; Pacheco, 2001; Pimentel *et al.*, 2015).

São Miguel Island

The largest island of the archipelago was formed by volcanic processes, which can be subdivided into six geologically contrasting areas (Moore 1990). Subaerial effusions were initiated during the formation of the Sete Cidades stratovolcano. Its eruptions, which started at 210 ka, were first of basaltic character and later of trachytic composition. Two chains of cinder cones, mainly of Holocene age and largely of basaltic character, are located between the stratovolcanoes Sete Cidades and Água de Pau. The centre of the São Miguel Island is occupied by the Água de Pau stratovolcano, largely consisting of trachytic pumices 180 ka in age or younger. A belt of lava flows of Pleistocene to Holocene age, dominated by basaltic rocks and trachytes, lies east of the Água de Pau volcano, towards the Furnas volcano. The Furnas volcano is the youngest stratovolcano on the island, located in its central to eastern parts. It is mostly composed of products of trachytic explosive volcanism not older than 100 ka. The last separate unit is the Nordeste Complex in the eastern part of the island, represented by an eroded shield volcano. Its mafic volcanics are the oldest volcanic products on the São Miguel Island – max. 880 ka (Pacheco 2001, Larrea *et al.*, 2018).

Ponta do Cintrão, Ribeirinha

Finds of fossil flora were reported by Diniz (1962) with no site specification or stratigraphic description. One can therefore only guess that the locality lies approximately at midpoint of the northern shore of the São Miguel Island, north of the Ribeirinha community (ca. 37.847°N, 25.489°W, see Fig. 2). The local pyroclastic units of acidic, trachytic character, including fine-grained fossiliferous tuffs, are ranked to the complex of the Fogo/Água de Pau Volcano (ca. 150 ka – present). Their exact age cannot be determined with respect to the lack of locality (Sibrant *et al.*, 2015). Eight plant taxa were described from the site by Diniz (1962), see Supporting Information Table S1.

Terceira Island

The easternmost island of the central group lies on the Terceira Rift and features five main volcanic systems (Nunes 2000). The oldest volcanic centre of Cinco Picos, dated to ca. >370 ka, lies in the eastern part of the island. It forms the largest caldera on the Azores, composed of alkali lavas, pumice-falls and ignimbrite sheets. The volcano of Guilherme Moniz is located in the southern part of the island, and its trachytic lavas started to form at ca. 270 ka. The stratovolcano of Santa Bárbara in the western part of the island were initially, at some 100 ka, formed by basaltic lavas, while its younger strata are formed by rhyolite and trachyte. The young cone of the Pico Alto volcano lies on the western slope of the older Guilherme Moniz volcano; production of ignimbrites of trachytic type started here at the break of the Pleistocene and Holocene. The fissural zone in the central and southeastern part of the island is formed by a line of monogenetic basaltic scoria and spatter cones and associated lava flows, active in the last 50 ky (Larrea *et al.*, 2018).

Angra do Heroísmo

Many finds of fossil flora come from the vicinity of the town of Angra do Heroísmo in the middle part of the southern shore of the Terceira Island; see Fig. 2. Their exact location is, however, usually missing. Leaf imprints were repeatedly found during construction works in the town itself: a large, as yet unpublished collection is deposited in the local *Museo volcanospeleologico*, other finds were reported by Agostinho (1949) and Krejci-Graf *et al.* (1958). Cliffs on the southern edge of the Fanal Bay in the suburbs of São Pedro were a well-known locality, now almost vanished (Forjaz, 1970; Góis-Marques *et al.*, 2019b). Pyroclastic sediments of this area are represented by ignimbrites and tuffs of the fissural basaltic volcanic complex (ca. 70 ka – present) with the dominant Surtseyan volcanic cone of Monte Brazil. Their stratigraphy was described in detail by Gertisser *et al.* (2010).

Results

Systematic ichnology

Ichnoclassis INSECTOPHAGICHNATA (Vialov) Enushchenko et Frolov, 2020

Ichnoordo Phagophytichnida Vialov 1975

Ichnofamily Phagophytichnidae Vialov 1975

Ichnogenus *Phagophytichnus* van Amerom, 1966

Diagnosis: Excisions on the edge of the leaf margin, semicircular to rounded quadrangular. The outer wall of different colour or thickening can be developed around the excision. Plant tissue is missing inside the cut; the rest of the venation may be visible as the short protrusion (van Amerom, 1966; Sarzetti, 2010).

Remarks: Sarzetti (2010) made a detailed revision of the ichnogenus *Phagophytichnus* and she identified four valid ichnotaxa: *P. ekowskii* van Amerom, 1966, *P. pseudocircus* Sarzetti *et al.*, 2008, *P. rectus* Vasilenko, 2007 and *P. regularis* Vasilenko, 2006. Zherikin (2003) published an illustration of the marginal excision in the form of the long cuts following the direction of the leaf veins, named as *P. feistmanteli*. The same characteristics also show *P. sinitsae* and *P. farcimeniformis*, published by Vassilenko in Aristov *et al.* (2013), which is why we consider both of them as the junior synonyms of *P. feistmanteli*. Three other identified forms remained unnamed

(*Phagophytichnus* isp. A, *P.* isp. B and *P.* isp. C), although Sarzetti (2010) made an extensive diagnosis.

***Phagophytichnus ekowskii* van** Amerom, 1966

Material: five marginal feeding, deposited in Museo geológico, Lisbon (MG-L_8526, MG-L_ 8538, MG-L_8558 + one unnumbered sample)

Figures: 3A–C, F; 4A–C

Host plants: *Laurus azorica* (Seub.) Franco (MG-L_8526), *Morella faya* (Aiton) Wilbur (MG-L_8538), Lauraceae indet. (MG-L_8558), *Viburnum tinus* L. (MG-L_unnumbered)

Locality: Azores, Faial Island, Espalamaca (MG-L_8526), Azores, São Miguel Island, Ponta do Cintrão, Ribeirinha (MG-L_8538, MG-L_8558, MG-L_unnumbered)

Damage type *sensu* Labandeira *et al.* (2007): DT 12

Amended diagnosis: Separate excisions at the leaf blade margin, except its apex, semicircular, oval to elliptical in outline, forming a section of less than 270°. The area of the excision does not touch the midrib. All affected venation is missing and can be present only in the form of the short protrusions from the edge of the cut outwards (after van Amerom, 1966; Sarzetti 2010).

Description: Single marginal excisions penetrating the margin of the leaf blade. The outline is approximately hyperbolic (MG-L_8526), broadly oval (MG-L_8538, MG-L_unnumbered), or deeply oval to rounded rectangular (MG-L_8558), 4.2–11.8 mm wide and 3.5–6.2 mm deep. The reaction tissue or the thickened outer wall is not developed, with the exception of sample MG-L_8558, where the outer thickened wall of a lighter colour is visible around both excisions.

Ichnofamily Paleominidae Vialov, 1975

Ichnogenus *Cuniculonomus* isp. Straus, 1977

Material: one ophionome mine, deposited in the Museo volcanospeleologico (Angra do Heroísmo), MV-AdH_190

Figures: 3D; 4D

Host plant: *Laurus azorica* (Seub.) Franco

Locality: Azores, Terceira Island

Damage type *sensu* Labandeira *et al.* (2007): DT not specified, cf. DT41 (but without frass)

Diagnosis: A linear, undulating to sinuous (=ophionome) mine with approximately constant width throughout the whole length, or slightly widening at the terminal end, but without the terminal chamber. The frass or faecal pellets are missing (Sarzetti, 2010; Robledo *et al.*, 2016).

Description: Thin, slightly sinuous mine at the lower part of the leaf blade. In the juvenile part, it runs parallel to the veins, then intersects the midrib and continues perpendicular to the direction of venation. The trace is very thin – 0.25 mm in the beginning and 0.35–0.40 mm at the termination – the total length is 27.5 mm.

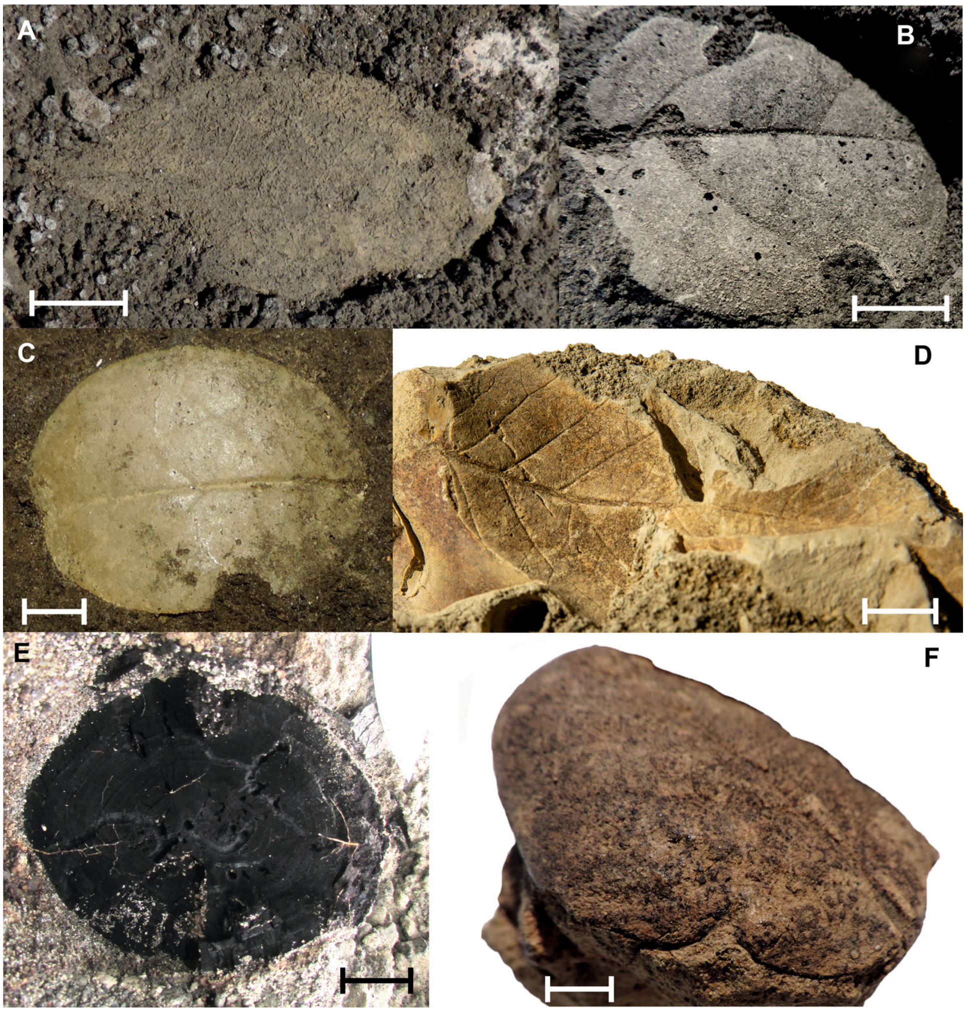

Figure 3. A – *Phagophytichnus ekowskii*, single marginal excision on *Morella faya*, M-GL_8538, B – *P. ekowskii*, two excisions on Lauraceae indet. with the light-coloured outer thickened wall, M-GL_8558, C – *P. ekowskii* – single marginal excision on *Viburnum tinus* subsp. *subcordatum*, MG-L_unnumbered, D – *Cuniculonomus* isp., ophionome mine on *Laurus azorica*, MV-AdH_190, E – *Xylonichus trypetus*, burrows in *Laurus azorica*, unnumbered sample, mentioned in Góis-Marques *et al.*, 2019a, Fig. 6A, F – *Phagophytichnus ekowskii*, single marginal excision on *Laurus azorica*, MG-L_8526. Measurement = 10 mm. Photos A–C, F – authors, D – Museo volcanospeleologico, E – C. Góis-Marques. [Color figure can be viewed at wileyonlinelibrary.com]

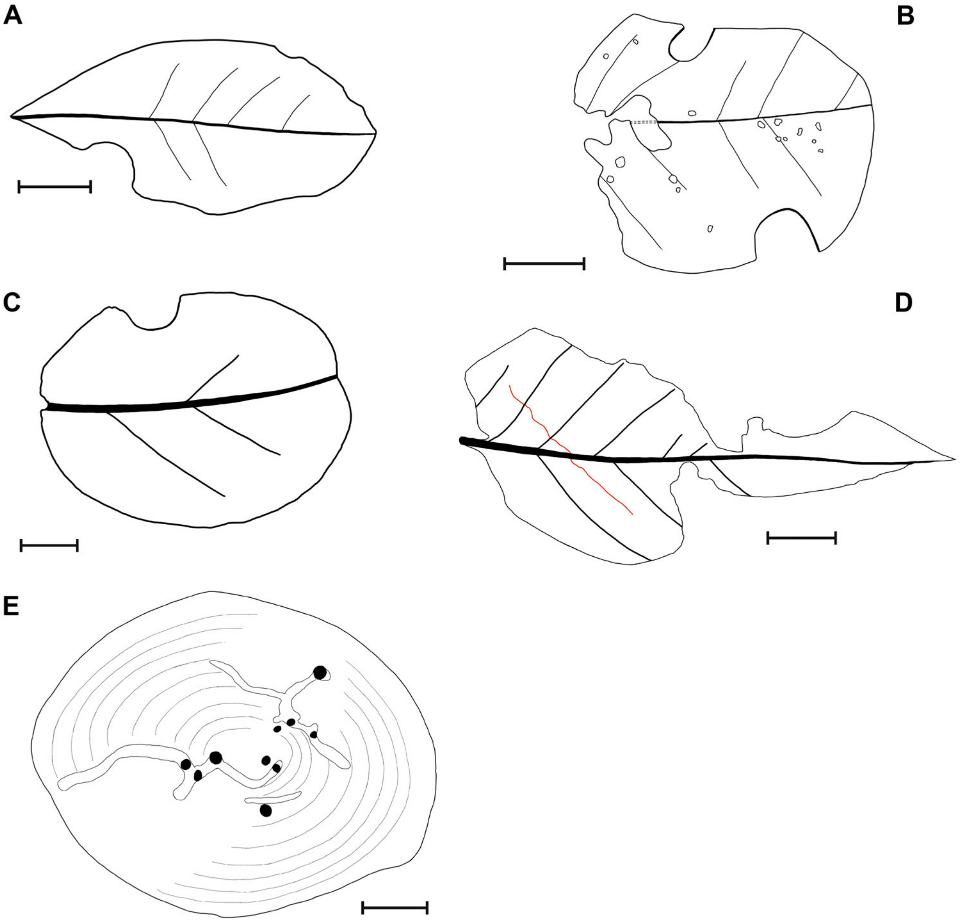

Figure 4. A – *Phagophytichnus ekowskii*, single marginal excision on *Morella faya*, M-GL_8538, B – *P. ekowskii*, two excisions on Lauraceae indet. with the light-coloured outer thickened wall, M-GL_8558, C – *P. ekowskii* – single marginal excision on *Viburnum tinus* subsp. *subcordatum*, MG-L_unnumbered, D – *Cuniculonomus* isp., ophionome mine on *Laurus azorica*, MV-AdH_190, E – *Xylonichus trypetus*, burrows in *Laurus azorica*, unnumbered sample, mentioned in Góis-Marques *et al.*, 2019a, Fig. 6A. Measurement = 10 mm. [Color figure can be viewed at wileyonlinelibrary.com]

Only the negative of the leaf imprint was examined, on which the trace is preserved as the concave groove, partly with a passive fill of the same colour as the surrounding rock.

Ichnofamily Talpidinae Wisshak *et al.*, 2019

Ichnogenus *Xylonichnus* Genise, 1995

Amended diagnosis: Longitudinal, tangential and radial borings interconnected into the boxwork in different depths in the xylem. Cross-section is flat-oval, rectangular to circular. The infill of frass or faecal pellets may be developed (after Genise, 1995; Genise and Hazeldine, 1995).

Remarks: Genise (1995) distinguished two new, separate ichnogenera, *Xylonichnus* and *Cycalichnus*. Both of them are very similar in shape – 3D boxwork of rectangular to rounded burrows, located in the heartwood, filled by the frass, as the main differences are defined as the host plant (*X.* – conifers, *C.* – cycads), trace-maker (*X.* – buprestid beetles, *C.* – termites) and the diameter of the traces. However, in the light of the ichnological principles, the producer-related criterion is the characteristic which must be rejected as the valid ichnotaxobase; information about the host plant is useful only with reservation. The need to review the use of ichnotaxobases is also suggested in Buatois *et al.* (2017).

Based on the abovementioned similarity between both ichnogenera, we consider *Cycalichnus* to be a synonym for *Xylonichnus*, which is listed as the first in the article by Genise (1995). In accordance with this postulate, three valid ichnospecies can be distinguished: *X. trypetus* Genise, 1995, *X. meniscatus* (Genise and Hazeldine 1995) with frass packed in backfill menisci and *X. garciorum* (Genise, 1995) comb. nov. without the outer wall.

Xylonichus trypetus Genise, 1995

Material: one system of burrows in the charcoalified tree trunk

Figures: 3E; 4E

Host plant: *Laurus azorica*

Locality: Azores, Faial Island, Fajã da Praia do Norte

Damage type *sensu* Labandeira *et al.* (2007): —(Applied only to leaves and seeds)

Amended diagnosis: A boxwork of anastomosed longitudinal, tangential and radial borings at different depths in the xylem. Cross-section is rectangular to circular. Borings have an outer layer and can be filled with frass (after Genise, 1995).

Description: A three-dimensional boxwork of narrow, cylindrical longitudinal borings, connected with slightly sinuous to curved tangential and radial ones, having a constant diameter over the entire length (2–3 mm). The surface of the tunnels is smooth, with a distinct outer wall of a lighter colour than the surrounding charcoalified trunk. The borings are partly filled with a frass without a distinct structure. The sample was previously described and published as 'trace of xylophage' in Góis-Marques *et al.*, 2019a (Fig. 6E).

Discussion

From Macaronesia, the only known occurrence of fossil flora with evidence of invertebrate activity has so far been that of

Álvarez *et al.* (2019). The authors described leaf imprints in hydrothermal carbonate sediments around the foothills of the Rambla de Castro (Tenerife, Canary Islands), pointing to possible plant–animal interactions (galls on leaves of *Salix* cf. *canariensis* and axillary domatia along the main veins of leaves *Laurus* cf. *novocanariensis*). No mechanical damage in the form of feeding marks on fossil leaves was found here. Therefore, the fossil record of the Azores and the wider environment lacks comparative material. However, due to the relatively young age of trace fossils from the islands of Faial, São Miguel and Terceira (Late Pleistocene to Holocene), possible alternatives can be discussed with recent herbivorous groups of invertebrates, either on the basis of food specialisation or traces of morphometric similarity.

However, studies on Azorean phytophagous and their food specialisation are also scarce and point to low levels of specialisation (Ribeiro *et al.*, 2005; Rego *et al.*, 2019). The most specialised phytophagous insects are associated with *Erica azorica*, *Laurus azorica* and *Ilex azorica*. Moth caterpillars of the endemic species *Ascotis fortunata azorica* and *Cyclophora azorensis* are currently the most abundant in the canopies of Azorean endemic trees. Thus, morphometric comparison to identify a possible trace-maker appears to be a more suitable method.

In terms of the whole area of Macaronesia, Machado (2003) describes in detail the biting shapes of beetles belonging to the genus *Laparocerus* (Curculionidae) on the Canary Islands and Madeira. In the Azores the equivalent genus is the endemic *Drouetius* (Curculionidae), which also leaves traces of biting (Machado, 2009). He describes traces of leaf infestation by *Laparocerus*/*Drouetius* beetles as numerous small excisions around the perimeter of the leaf blade, pointing perpendicular-to-oblique to the leaf edge, usually of the same width, with an irregular to serrated margin, often irregularly branched. *Drouetius* currently includes several species and subspecies, most of them very rare due to major land-use changes at lower elevations. Only the several subspecies of *Drouetius borgesis* are common, since this species occurs at higher elevations in the still extant native laurel forest (laurisilva). It is, however, a generalist species that feeds on the endemic leaves of *Laurus azorica*, but also on the leaves of the invasive plant *Hedychium gardnerianum*.

Traces of *Phagophytichnus ekowskii* found in the Azores have a significantly different morphology – they are typical for their individual occurrence on the leaf blade and an oval to elliptical shape with a smooth margin (Fig. 3A–C, 3F; 4A–C). According to the morphometric study by Machado (2003), this corresponds more to traces of butterfly caterpillars (group Macrolepidoptera) or locust larvae (Orthoptera/Caelifera) biting the leaves. The endemic Azorean cone-head *Conocephalus chavesi* (Bolivar, 1905) (Orthoptera, Tettigoniidae) occurs in coastal areas and can potentially be related to leaf biting. This species is now restricted to small areas due to habitat destruction (see Borges *et al.*, 2017).

Geyer and Kelber (1987), Kelber and Geyer (1989) and Iannuzzi and Labandeira (2008) also associate insects of the orders Lepidoptera and Orthoptera with the genus *Phagophytichnus*, and it is therefore possible that they are related to this type of trace even in the case of the Azores fossil record.

Similarly, the question of the mine of *Cuniculonomus* isp. is uncertain (Fig. 3D; 4D). In their list of linear mines, Robledo *et al.* (2016) considers the dipterans (Agromyzidae), occasionally also moths from the group Microlepidoptera (Gracillariidae), as the possible trace-makers of this ichnogenus. Azorean Diptera are poorly studied and efforts should be made to revise their taxonomy and biology (Lobo and Borges, 2010).

The Agromyzidae of the Azores and Madeira have been described by Spencer (1965a), recently, as the checklist for Portugal, including the Azores and Madeira by Černý *et al.* (2018). Occurrences from the Canary Islands were summarised by Spencer (1965b). However, none of these publications shows images of mines and a comparison can be made only with the compendium of leaf miners (Hering, 1927) and moths of the family Gracillariidae (Klimesch, 1979) from the Canary Islands.

The genus *Caloptilia* (Lepidoptera, Gracillariidae) is the only one within the group Microlepidoptera described in the publications above, which has a confirmed area of occurrence in the Azores and at the same time corresponds to the shape of mines of the genus *Cuniculonomus*. These moths characteristically feed on the tree leaves of the family Lauraceae. However, the relevant species with an appropriate shape of mine (*Caloptilia laurifoliae*, *C. staintoni*) do not occur in the Azores, according to Borges *et al.* (2010). Similarly, it is not possible to identify with certainty a closer relationship of any genus within Agromyzidae and *Cuniculonomus* isp. from the fossil record of the island of Terceira (e.g. Spencer, 1987).

Finally, the genus *Xylonichnus* (Fig. 3E, 4E) is associated with the wood-destroying activity of beetles, especially the group Buprestidae. Within the genera found in the Azores, very similar burrows in the shape of 3D box work form species from the genus *Buprestis* (Coleoptera, Buprestidae) (e.g. Bolu *et al.*, 2020). According to Borges *et al.* (2010), however, this genus is reported to have been introduced to the archipelago, so its relationship to newly found fossil traces is uncertain.

Ichnological characteristics of trace fossils are undoubtedly of great importance for the palaeoecological reconstruction of ecosystems, deciphering of food relations and ethological behavioural patterns of the trace-makers without the need for their *in situ* identification in the form of a documented body fossil. To demonstrate this benefit, let us name, for example, the first indirect evidence of the presence of animals in the fossil record of the Faroe Islands (*Helminthoidichnites* isp. and *Palaeophycus* isp.; Pokorný *et al.*, 2015), or a similar description of the endemic assemblage composed exclusively of soft-bodied invertebrates (Pokorný *et al.*, 2017).

Speaking specifically of plant–animal interactions in the fossil record of the European Cenozoic, facts from the fields of Palaeobotany (Denk *et al.*, 2011), invertebrate palaeozoology (Wappler *et al.*, 2014; Skartveit *et al.*, 2017) and ichnology (Wappler and Grímsson, 2016) have been very well correlated and integrated into the Neogene of Iceland. Feeding traces on leaves have also been analysed in detail from freshwater sediments of similar age in the Bohemian Massif (Czech Republic). Here, large numbers of ‘damage types’ *sensu* Labandeira *et al.* (2007) have been identified and their relationships with possible trace-makers have been thoroughly discussed (Knor *et al.*, 2012, 2013, 2015).

Conclusion

Confirmed traces in Quaternary leaf impressions and fossil wood of the Azores (marginal feeding – *Phagophytichnus ekowskii*, ophionome mine – *Cuniculonomus* isp. and borings – *Xylonichnus trypetus*) represent the first documented fossil remains of invertebrate activity in the entire archipelago. Due to the small number of collected samples, it is not possible to identify the exact species or genera of the trace-makers. However, it is considered that it could be the result of the activity of insects (Lepidoptera, Orthoptera and Coleoptera).

Acknowledgements. The research was supported by the J. E. Purkyně University Internal Grant Agency [UJEP-IGA-JR-2021-44-004-2] *Ichnological research of island regions – a case study Macaronesia*. Miguel Ramalho (Laboratório Nacional de Energia e Geologia, I.P., Museu Geológico, Lisbon, Portugal), Fernando Pereira, Susana Ázera (Associação Os Montanheiros, Angra do Heroísmo, Azores, Portugal) and António Félix Flores Rodrigues (Faculdade de Ciências Agrárias e do Ambiente da Universidade dos Açores) are thanked for being willing to allow access to collections and depositories with fossil plants from the Azores and providing detailed photos; Carlos Góis-Marques (Madeira Botanical Group (GBM), Faculdade de Ciências da Vida, Universidade da Madeira, Campus da Penteada, 9000-390, Funchal, Portugal) for the extensive and worthwhile discussion of the manuscript and the valuable advice and recommendations.

Author contributions—**Richard Pokorný**: Conceptualization; Investigation; Funding acquisition; Writing - original draft; Methodology; Validation; Visualization; Writing - review & editing; Formal analysis; Project administration; Data curation; Supervision; Resources. **Paulo A V Borges**: Writing - original draft; Writing - review & editing; Data curation.

Conflict of interest statement—The authors declare no conflicts of interest.

Data availability statement

All data that support the findings are available in the main text or in referenced literature. The fossils mentioned and described herein have been incorporated into a public collection at the Geological Museum in Lisbon, Portugal, and the Volcanospeleological Museum in Angra do Heroísmo 'Os Montanheiros', Azores, Portugal, where they are available for study.

Supporting information

Additional supporting information can be found in the online version of this article.

Table S1. Summary list of fossil plants, described in Azores (Hartung, 1860; Drouet, 1866; Goeze, 1867a, b; Berthois, 1948; Agostinho, 1949; Krejci-Graf et al., 1958; Forjaz, 1960; Diniz, 1962; Forjaz and Monjardino, 1964; Fries, 1968; Forjaz et al., 1970; Zbyszewski et al., 1971; Arruda, 2002; Jorge et al., 2011; Góis-Marques and Menzes de Sequeira, 2015; Góis-Marques et al., 2019a, b; 2020). The sites with occurrence of trace fossils are highlighted in gray.

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