# Inventory and review of the Mio–Pleistocene São Jorge flora (Madeira Island, Portugal): palaeoecological and biogeographical implications

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The occurrence of plant fossils on Madeira Island has been known since the mid-nineteenth century. Charles Lyell and George Hartung discovered a leaf bed rich in Lauraceae and fern fossils at São Jorge in 1854. The determinations were controversial but a full review was never performed. Here we propose possible geological settings for the fossiliferous outcrop, and present an inventory and a systematic review of the surviving specimens of the São Jorge macroflora. The São Jorge leaf bed no longer outcrops due to a landslide in 1865. It was possible to establish the two alternative volcano-stratigraphical settings in the sedimentary intercalations from the Middle Volcanic Complex, ranging in age from 7 to 1.8 Ma. The descriptions of Heer (1857), Bunbury (1859) and Hartung & Mayer (1864) are reviewed based on 82 surviving specimens. From the initial 37 taxa, we recognize only 20: *Osmunda* sp., *Pteridium aquilinum*, *Asplenium* cf. *onopteris*, aff. *Asplenium*, cf. *Polystichum*, cf. *Davallia*, *Woodwardia radicans*, Filicopsida gen. et sp. indet. 1 and 2, *Ocotea foetens*, *Salix* sp., *Erica arborea*, cf. *Vaccinium*, *Rubus* sp, cf. *Myrtus*, Magnoliopsida gen. et sp. indet. 1 to 3, Liliopsida gen. et sp. indet. 1. Magnoliopsida gen. et sp. indet. 4 is based on one previously undescribed flower or fruit. The floristic composition of the São Jorge fossils resembles the current floristic association of temperate stink laurel (*Ocotea foetens*) forest, suggesting a warm and humid palaeoclimate and indicating that laurel forests were present in Macaronesia at least since the Gelasian, a time when the palaeotropical geofloral elements were almost extinct in Europe.

**Keywords**: Macaronesia; Madeira Island; São Jorge; historical collections; leaf macrofossils; laurel forest

## Introduction

During the mid-nineteenth century Sir Charles Lyell and George Hartung explored the geology of Madeira Island, seeking evidence for a subaerial formation of oceanic islands (e.g. C. Lyell 1854). The purpose was to falsify Buch's catastrophist theory of craters of elevation (Wilson 1998, 2007). On 18 January 1854, Lyell and Hartung found a leaf bed at the base of a 300 m deep ravine on the north side of the island at São Jorge (C. Lyell & Hartung 1856). These fossils represented some of the first and most important evidence in support of a gradual build-up of oceanic islands above sea level (e.g. C. Lyell 1855). The collections gathered from this site were studied by two palaeobotanists – Oswald Heer (1809–1883) and Charles Bunbury (1809–1886) – between 1855 and 1859 (Heer 1856a, c, 1857; Bunbury 1858, 1859). Their papers described 36 species based on leaf fossils, establishing the existence of a flora similar to that presently occurring on the island, but also including a few extinct forms (e.g. *Ilex hartungi*). Moreover, Heer (1857) was the first to pinpoint the remarkable similarities between the present-day flora of Madeira and the Tertiary fossil flora from Europe. Later, in 1864, Hartung published the identifications, made by Heer, of leaf fossils from another Madeira locality at Porto da Cruz (Hartung & Mayer 1864), and described a new fern from the São Jorge outcrop. A full historical account of Madeiran palaeobotany has been given by Góis-Marques *et al.* (2014).

Recently, there has been a renewed interest in the nineteenth century studies of Macaronesian palaeobotany, with special reference to the identified taxa and their geological setting. The main reason is the potential of plant fossils as age constraints in molecular phylogenetics and in elucidating biogeographical patterns (Anderson *et al.* 2009; Fernández-Palacios *et al.* 2011; Fernández-Palacios 2013; Góis-Marques & Menezes de Sequeira 2015; Kondraskov *et al.* 2015). Anderson *et al.* (2009) challenged the assumption that oceanic islands have a low potential for informative plant fossil preservation. Indeed, prospecting in Gran Canaria revealed evidence of several Miocene–Pliocene macrofloras. Moreover, Anderson *et al.* (2009) presented a

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preliminary bibliographical survey on Macaronesian localities bearing plant fossils, where the São Jorge macroflora is presented as the "most widely known fossil flora from a Macaronesian island" (Anderson *et al.* 2009, appendix s1, p. 1). An attempt to frame geologically and discuss this macroflora is presented in the same paper, but no further details are given. Fernández-Palacios *et al.* (2011, p. 236) considered the São Jorge macroflora *"the most important site analysed to date."* Their paper presented a model for the biogeographical dispersion of the laurel forest through the palaeo-Macaronesia, using the inferred age and species list of the São Jorge macroflora to prove the long existence, or extinction, of some plant taxa in Macaronesia (e.g. *Ulmus*, *Corylus*).

Despite the importance of the São Jorge flora, a full revision has never been attempted. Historically, the São Jorge fossil identifications were disputed by several authors as being dubious due to their fragmentary state, or misinterpretation with extant plants (e.g. Darwin Correspondence Project; Lowe 1857–1872; Starkie Gardner 1881, 1882). Additionally, some authors (e.g. Hickey 1973; Dilcher 1974; Hickey & Wolfe 1975) have pointed out inaccurate identifications made in several nineteenth century palaeobotanical studies. More recently there has been a trend favouring the study of Madeiran sedimentary deposits containing fossil faunas, either from a biostratigraphical point of view or as palaeogeographical markers, such as the Miocene marine deposits of São Vicente (Ramalho *et al.* 2015 and references therein), and the Holocene aeolian deposits of Caniçal (Goodfriend *et al.* 1996) and its palaeozoology (e.g. Cook *et al.* 1993; Rando *et al.* 2012, 2014; Alcover *et al.* 2015). This bias resulted in the stagnation of palaeobotanical studies, and the continuous citation of the earlier nineteenth century works (e.g. Vahl 1904; Teixeira 1948; Mitchell-Thomé 1974, 1976; Zbyszewski *et al.* 1975; Teixeira & Pais 1976; Nóbrega 1999; Sziemer 2010; Fernández-Palacios *et al.* 2011). Recent research on the palaeobotany of Madeira Island resulted in the reconstruction of an historical perspective, and in the relocation of the nineteenth century collections (Góis-Marques 2013; Góis-Marques *et al.* 2014).

This paper aims to frame stratigraphically the São Jorge macroflora, to review the taxonomy of the surviving specimens from two historical collections described by Heer (1857) and Bunbury (1859), and to discuss the palaeoecological and biogeographical implications for Madeiran and Macaronesian floras.

## Institutional abbreviations

**NHMUK**: Natural History Museum, London, UK; **SMC**: Sedgwick Museum of Earth Sciences, Cambridge, UK; **ETH-Z-ERDW**: Departement Erdwissenschaften-Eidgenössische Technische Hochschule, Zurich, Switzerland.

## Geological setting

### Madeira Island

The geology of Madeira presented in this work follows the volcanic stratigraphy developed for the production of the most recent geological map of Madeira Island (Brum da Silveira *et al.* 2010a, b, c). Madeira Island is the largest island of the Madeira archipelago, which includes the islands of Madeira and Porto Santo, and the Desertas and Selvagens islets (Fig. 1B). It is located in the Central Atlantic Ocean, 700 km west of the north-west coast of Africa and 850 km south-west of mainland Portugal, being geographically bounded by the parallels 32°38' and 32°52' N, and the meridians 16°39' and 17°16' W (Fig. 1A). The island is 58 km long in the E–W direction and 28 km wide in the N–S direction, corresponding to an area of 736 km$^2$ (Brum da Silveira *et al.* 2010a).

Madeira, Desertas and Porto Santo are considered to represent a hotspot track extending in a NNE–SSW direction from the south of mainland Portugal, which also includes a line of seamounts of decreasing age to the SSE (Seine, Unicorn, Ampere, Coral Patch and Gorringe; Geldmacher *et al.* 2005). Additionally, the build-up of Madeira's volcanic edifice may be associated with a volcano-tectonic interaction between the mantle plume and a set of WNW–ESE to EW trending structures marked in the bathymetry by the alignment of the island itself and submarine reliefs immediately to the west (Brum da Silveira *et al.* 2010a).

According to Brum da Silveira *et al.* (2010a) and Ramalho *et al.* (2015), the island of Madeira corresponds to the emergent part of a Miocene to Holocene shield volcano. The construction of the Madeira shield volcano occurred during three major eruptive periods materialized by three volcano-stratigraphic units separated by major unconformities that represent prolonged quiescence periods. The Lower Volcanic Complex (LVC) represents the submarine (LVC1) and emergent (LVC2) phases (>7.0 Ma), the Middle Volcanic Complex (MVC) marks the main subaerial shield-building phases (MVC1, 2 and 3) developed between 7.0 and 1.8 Ma, while the Upper Volcanic Complex (UVC) corresponds to capping (UVC1) and post-erosional (UVC2) volcanism (1.8 Ma to present). Besides the volcanic products, the three volcanic complexes include frequent interlayered sedimentary deposits composed of various facies, usually associated with debris flows or mud flows (lahars), and hyperconcentrated flows.

### Historical accounts of the São Jorge leaf bed

According to the nineteenth century descriptions, the fossiliferous sediments cropped out on the right side of the floodplain of the stream named 'Ribeira do Meio', a tributary of the 'Ribeira Grande de São Jorge' stream, on the north-east flank of the island (Fig. 1B, C). The outcrop
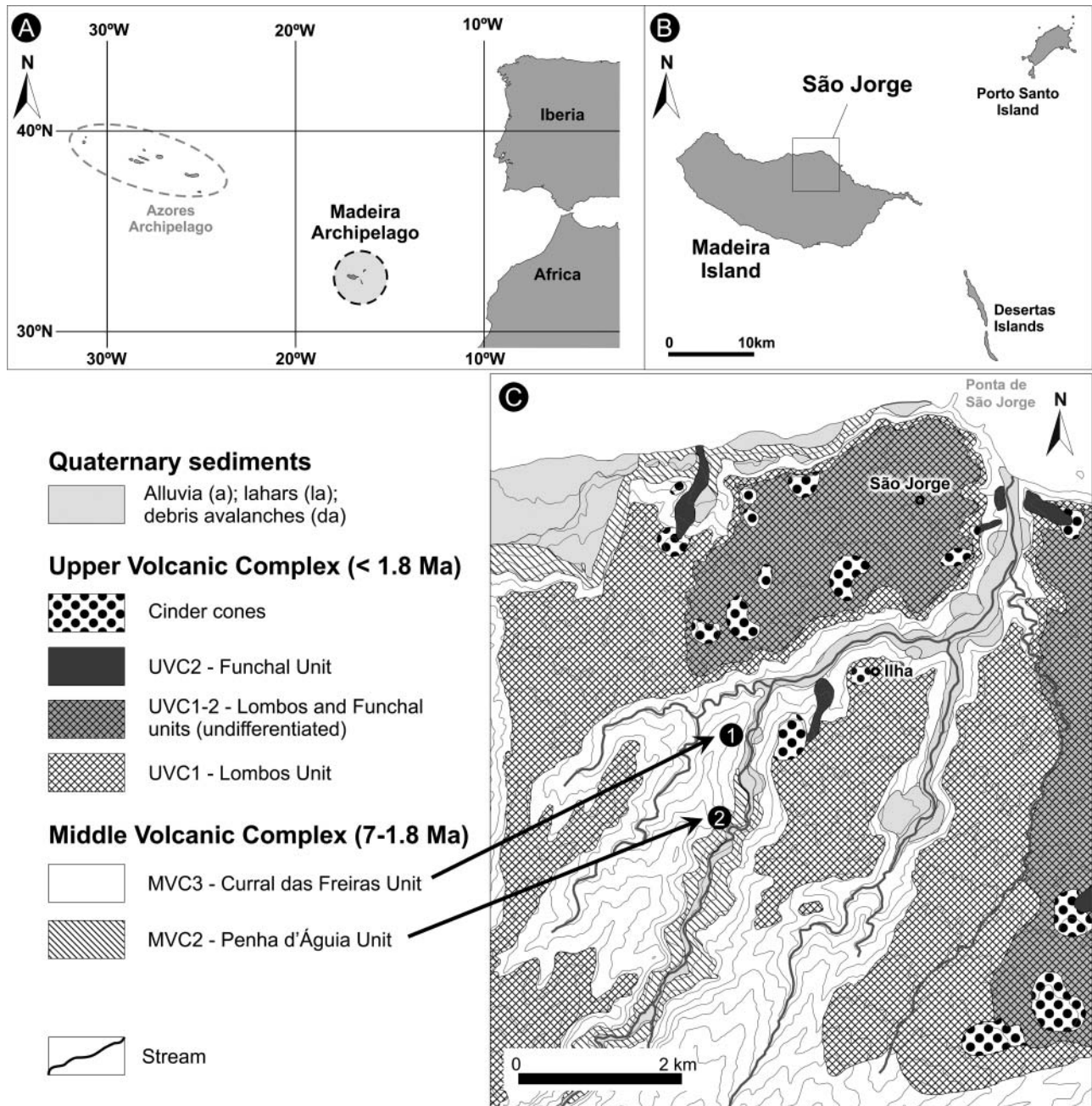
**Figure 1.** Geographical location of Madeira Island and the São Jorge outcrop. **A,** Madeira Archipelago relative to Iberia, Africa and the Azores; **B,** Madeira Island and the location of the São the Jorge area; **C,** simplified geological map of the São Jorge area showing the possible locations of the 'Ribeira do Meio', now called 'Ribeira Grande de São Jorge' outcrop: (1) possible downstream location of the outcrop included in the Curral das Freiras Unit (MVC3); (2) alternative upstream position included in the Penha d'Águia Unit (MVC2) (modified from Brum da Silveira *et al*. 2010c).

was located SW of the present parish of Ilha (municipality of Santana) at an elevation of 300 m (Fig. 1C) (e.g. C. Lyell 1855; Heer 1857). Lyell and Heer referred to it as being located in São Jorge. This is because the site of Ilha was only elevated to the status of a parish in 1989, having belonged to the parish of São Jorge until that date.

We have adopted the old name of São Jorge in order to avoid toponymic confusion.

Lyell and Hartung studied the outcrop during the winter of 1853–1854 (C. Lyell 1854) and the stratigraphical setting was later published by Heer (1857) and Hartung & Mayer (1864). The original description of the local

stratigraphical succession includes (from base to top): (1) a lower lignite layer ('unterster lignit') of indeterminate thickness, whose base is located below the stream bed; (2) a basalt lava flow, 4.5 to 5 m thick; (3) a thin (0.25 m thick) clay level ('sogenannter underclay'); (4) the Superior Lignite, a lignite deposit 0.10 m thick; (5) a 0.90 m thick 'Tuffaceous breccia'; (6) a 'mass of hardened mud', 0.10 to 0.90 m thick; and (7) a layer of 'Tuffaceous breccia' partially covered by an indeterminate thickness of soil. Overlying the sequence is a volcanic pile more than 300 m thick.

According to the description, the fossils were observed and collected in the two tuffaceous breccia layers (layers 5 and 7). The analysis of the fossil matrix reveals that the lithology of these layers corresponds to a breccia with a silty-clay matrix, containing leaf impressions and compressions. The volcanic clasts are angular to sub-angular in shape, with rare rounded clasts and showing variable degrees of alteration. Starkie Gardner (1882, p. 279) published a different stratigraphical description, where he did not observe lignite, but instead "7 feet of blackish shales, with well-preserved twigs and branches." He had most probably visited a lateral outcrop of this sedimentary sequence because the originally described site had been covered by a landslide (Starkie Gardner 1882).

## Material and methods

Góis-Marques *et al.* (2014) published a bibliographical and biographical analysis, which allowed the search for the fossiliferous outcrop at São Jorge to be narrowed and the historical collections to be re-located. The study also examined nineteenth century maps of Madeira Island, descriptions and field sketches (i.e. C. Lyell's unpublished field notes, 1853–1854; C. Lyell & Hartung 1856; Ziegler 1856, 1858; Heer 1857). Based on these documents, fieldwork was performed in order to try to re-locate the outcrop.

The institutions with São Jorge collections were visited and the specimens studied. The NHMUK specimens were photographed and drawn using a camera lucida, with low illumination by a fibre-optic lamp to enhance the venation. The SMC and ETH-Z-ERDW specimens were studied under a stereomicroscope and specimens were photographed with low light and later redrawn from the photographs; additionally, the ETH-Z-ERDW specimens were compared with the plates published by Heer (1857) and Hartung & Mayer (1864).

The leaf fossils were described according to Tryon (1960), Ellis *et al.* (2009) and Press & Short (1994). Extant leaf morphology descriptions from Macaronesian taxa (e.g. Rasche & Kovar-Eder 2009) and extant leaf material were used for comparison with the fossil material. Systematic taxonomy follows the criteria of Jardim &

Menezes de Sequeira (2008). Open nomenclature follows the recommendations given by Bengtson (1988). Synonymies are limited to the publications describing or attempting to review taxa from the São Jorge macroflora.

## São Jorge leaf bed location and geological setting

The fossiliferous site of the São Jorge leaf bed described in the original nineteenth century studies was not found despite several attempts using available descriptions from the nineteenth century publications. The valley associated with the 'Ribeira Grande de S. Jorge' stream is steep orographically and densely vegetated, which obstructs the access to and visibility of some potential outcrops. There are several references in the literature to slope instability in the valley (Starkie Gardner 1882; Johnson 1885; Brown 1901), and according to later descriptions, the outcrop was covered by a landslide after 1917 (Silva & Meneses 1940). Additionally, there have been toponymic changes in the (almost) two centuries following the discovery of the leaf bed, which complicates determining the exact location of the outcrop (Góis-Marques 2013). Three different formations belonging to MVC2, MVC3 and UVC1 stratigraphical units crop out on the valley slopes (Fig. 1C). The São Jorge outcrop could either belong to the Penha d'Águia (MVC2) or to the Curral das Freiras (MVC3) units, the formations exposed in the lower slopes of the valley, corresponding to epiclastic sediments (conglomerates and sandstone breccia facies associated with debris flows, mudflows and hyperconcentrated flows) intercalated in these volcanic sequences (Brum da Silveira *et al.* 2010a). According to the most recent geological map (Brum da Silveira *et al.* 2010c) and comparison with the map and plates of Ziegler (1856) published in the nineteenth century, the fossiliferous sediments of São Jorge probably correspond to an outcrop of MVC3 or MVC2 (>1.8 Ma; Fig. 1C).

## Collections and specimens

The historical collections comprise two main sets of fossils: the Lyell and Heer collections, totalling 82 specimens (Supplemental Table 1). The Lyell Collection is kept at the NHMUK, and originally comprised 140 specimens (Bunbury 1859; K. M. Lyell 1881), but is now reduced to 32 specimens. Additionally, six uncatalogued specimens from this collection were found at SMC associated with the Charles Bunbury Collection. These fossils were obtained for Lyell in 1854 and entrusted to Bunbury for study (Bunbury 1859). The Heer Collection is located at ETH-Z-ERDW and comprises 44 specimens. These specimens were collected by Hartung and sent in two collections to Heer between 1854 and 1855 (Heer 1857). Another small collection comprising an unknown number of specimens was sent to Heer by Johnson in 1860 (Heer

1861a). Additionally, Heer studied a collection gathered before 1861 by Dr Mittermeyer (probably Carl Mittermaier (1823–1917)) (Heer 1861a, b), and the results were published in Hartung & Mayer (1864).

The São Jorge macroflora consists of impressions and compressions of leaves with no cuticles preserved (Fig. 2). In addition, a small fruit or flower was found in the Bunbury material (Fig. 2L), which is described here for the first time (Heer 1857 also described a flower, but the specimen is missing). The fossils are preserved in a breccia with a siltstone matrix, or in siltstone. Most are incomplete leaves in which the third or higher order venation is not preserved, or when present is difficult to interpret. The conchoidal fractures in the sediment also contribute to the incompleteness of the specimens.

## Systematic palaeontology

Division **Pteridophyta** Schimper, 1879
Class **Filicopsida** Pichi-Sermolli, 1958
Order **Osmundales** Link, 1833
Family **Osmundaceae** Martynov, 1820
Genus *Osmunda* Linnaeus, 1753
***Osmunda* sp.**
(Fig. 3A; Supplemental 2, Fig. 1)

1857 *Osmunda regalis* L.; Heer: 26, pl. 1, fig. 13.
1861a *Osmunda regalis* L.; Heer: 315.

**Material.** ETH-Z-ERDW 2392, 3704, 3704.

**Description.** Fragmentary impressions of sterile pinnae. Costa sinuous towards the apex. Secondary veins open and bifurcate at least twice, terminating at the margin. Margin apparently toothed.

**Remarks.** The fossils have a morphology, venation pattern and margin concordant with *Osmunda* sp. Heer (1857) identified this based on one specimen, but in the ETH-Z-ERDW collection there are two specimens that can be attributed to *Osmunda* (possibly as a result of specimen fragmentation). Presently, *Osmunda regalis* is extinct on Madeira Island (Jardim & Menezes de Sequeira 2008), but herbarium specimens collected in 1850 and 1914 indicate that it is a native species (Gibby & Paul 1994).

Order **Dennstaedtiales** Doweld, 2001
Family **Hypolepidaceae** Pichi-Sermolli, 1970
Genus *Pteridium* Gleditsch ex Scopoli, 1760
***Pteridium aquilinum*** (Linnaeus) Kuhn, 1879
(Figs 2A, 3B, C; Supplemental 2, Figs 2, 3)

1857 *Pteris aquilina* L.; Heer: 26, pl. 1, figs 1–10b.
1859 *Pteris aquilina* L.; Bunbury: 53.
1861a *Pteris aquilina* L.; Heer: 315.

**Material.** NHMUK V19891, V19892, V19893, V19894, V19896, V19897, V19912. ETH-Z-ERDW 2381, 3709, 3709, 5473, 3709, 5741.

**Description.** Several fragments of sterile pinnae. Pinnae pinnatifid; some specimens become entire at apex; ultimate segments convex. Venation open and bifurcate, ending at the margin. Margin entire. Some specimens show ultimate segments apparently revolute.

**Remarks.** This is the most abundant fossil fern in the São Jorge flora, represented by several fragments of pinnules that are consistent in size, shape and venation with living specimens of *Pteridium aquilinum* (L.) Kuhn [ = *Pteris aquilina* L.]. The pinnatifid pinna with a terminal apex entire is distinct from other endemic or native ferns living in Madeira. Some fragments show revolute ultimate segments possibly related to fertile fronds. Heer (1857) pointed to the possibility that some fragments could be attributed to a distinct morphotype corresponding to *'Nephrodium molle'* Swartz [ = *Christella dentata* (Forsskål) Brownsey & Jermy], but the venation of the ultimate segments is not consistent with the latter. Other fern species may be present in the diversity of fragments attributed to *P. aquilinum* but the preservation and fragmentary state does not allow further discrimination. The extant species *P. aquilinum* is common throughout Madeira Island and occupies open habitats (Gibby & Paul 1994).

Order **Aspidiales** Pichi-Sermolli, 1958
Family **Aspleniaceae** Newman, 1840
Genus *Asplenium* Linnaeus, 1753
***Asplenium* cf. *onopteris*** Linnaeus, 1753
(Supplemental 2, Fig. 4)

1857 *Trichomanes radicans* Swartz; Heer: 25, pl. 1, fig. 11a, b.

**Material.** ETH-Z-ERDW 5463.

**Description.** Penultimate segment with a petiolate insertion; ultimate segments acute. Venation does not extend to the margin. Texture membranaceous.

**Remarks.** The fossil exhibits a membranous texture, resembling the thin and translucent fronds of the family Hymenophyllaceae (Gibby & Paul 1994). However, the apices of the terminal teeth of the living species *Vasdenboschia speciosa* (Willdenow) G. Kunkel [ = *Trichomanes radicans* Swartz] are round, which does not match the acute apices of this fossil. *Asplenium onopteris* is closer in size, venation and shape of the ultimate segments and has long acuminate teeth. According to Gibby & Paul (1994), this species is frequent in the north of Madeira Island, occurring at altitudes between 600 and 1000 m.
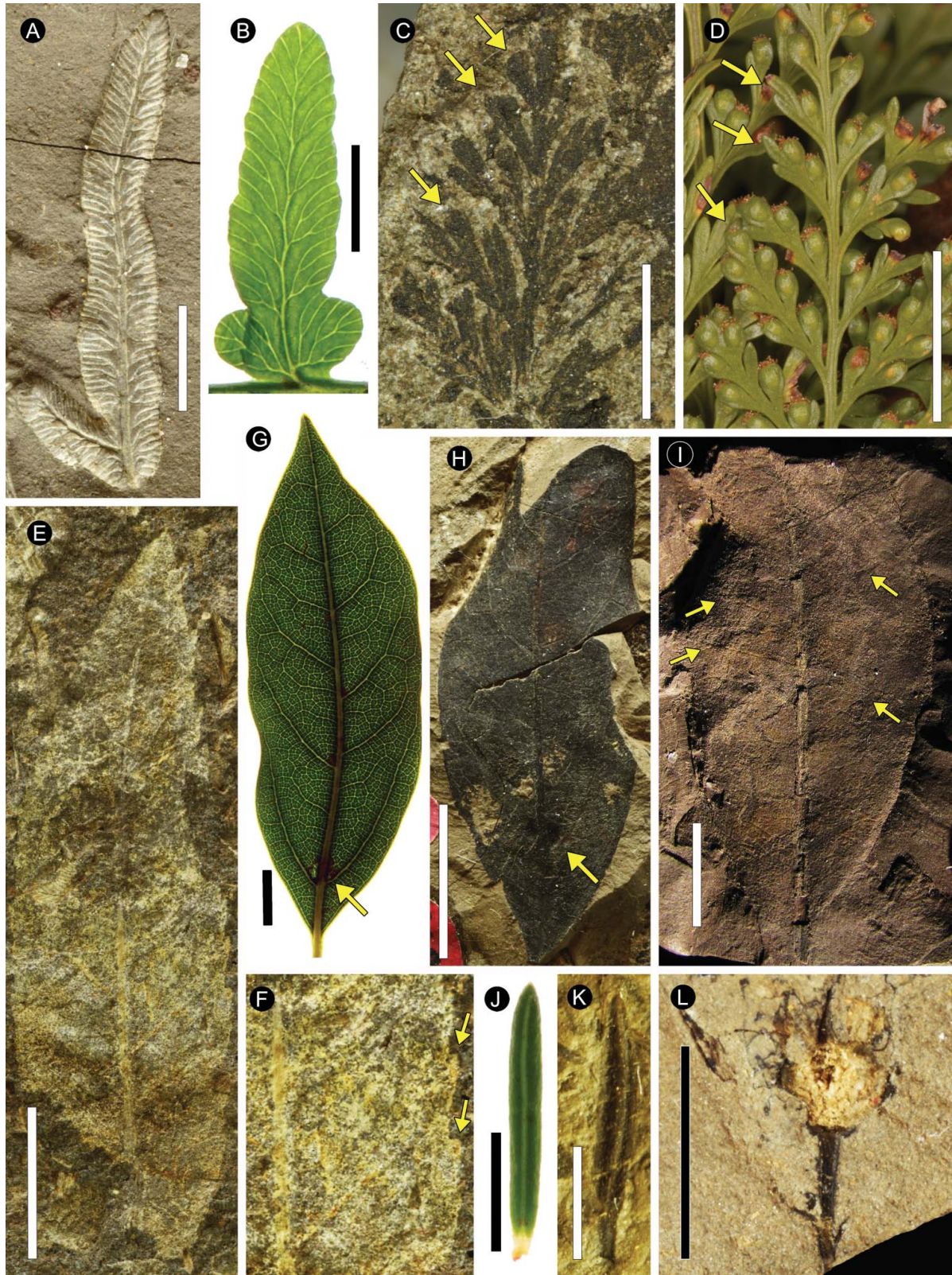
**Figure 2.** Preservational state and comparison with modern leaves of selected leaf fossils from the São Jorge fossil flora. **A,** *Pteridium aquilinum* (NHMUK V19893); **B,** ultimate sterile segment of *P. aquilinum*; **C,** cf. *Davallia* (NHMUK V19890) compared with D; **D,** *Davallia canariensis* ultimate fertile segments with terminal indusia (arrows); **E,** Magnoliopsida gen. et sp. indet. 1 (NHMUK V19907) preserved in a coarse matrix and **F,** detail of craspedodromous secondary venation and toothed margin (arrows); **G,** leaf of *Ocotea foetens* showing the leaf architecture and domatia in the axils of the acute sub-basal secondary veins (arrow); **H,** *O. foetens* (NHMUK V19906) showing the basal domatia (arrow); **I,** cf. *Myrtus* (ETH-Z-ERDW 5456) showing fade secondary venation like extant *Myrtus communis*; **J,** leaf of *Erica arborea* compared with K; **K,** *Erica arborea* fossil (NHMUK V 19912); **L,** Magnoliopsida gen. et sp. indet. 4, a probable flower or fruit. Scale bars: A–D, L = 5 mm; E–I = 10 mm; J, K = 2.5 mm.

**Figure 3.** Line drawings of selected Filicopsida from the São Jorge fossil flora. **A,** *Osmunda* sp. (ETH-Z-ERDW 3704); **B, C,** *Pteridium aquilinum*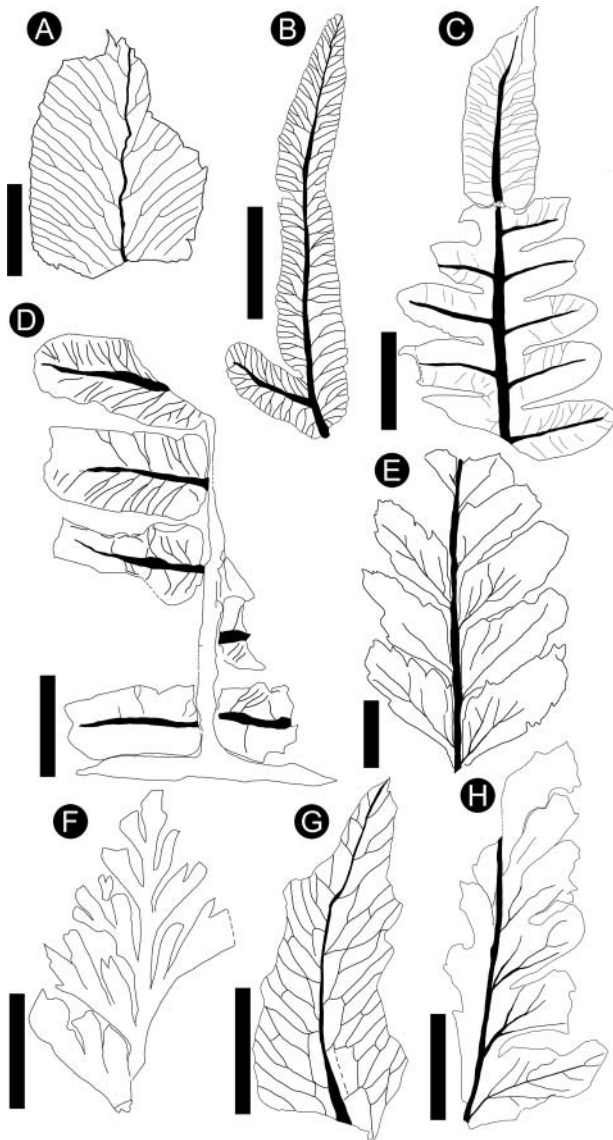 (NHMUK V19893 and V19894 respectively); **D,** aff. *Asplenium* (NHMUK V19895); **E,** cf. *Polystichum* (NHMUK V19901); **F,** cf. *Davallia* (NHMUK V19890); **G,** *Woodwardia radicans* (NHMUK V19898); **H,** Filicopsida gen. et sp. indet. 2 (NHMUK V19899). Scale bars = 5 mm.

### aff. *Asplenium*
(Fig. 3D; Supplemental 2, Fig. 5)

1859 *Pteris aquilina* L.; Bunbury: 53.

**Material.** NHMUK V19895.

**Description.** Fragment of a penultimate segment, apparently 2-pinnate. Costa with opposite ultimate segments; insertion sessile. Costule well defined, with open venation; margin entire to crenate.

**Remarks.** The sessile insertion of the ultimate segments is not consistent with *Pteridium aquilinum* (L.) Kuhn [ = *Pteris aquilina* L]. The morphology resembles that of *Asplenium*, especially *A. trichomanes* or *A. anceps*, although these fern fronds are 1-pinnate. The fragmentary state does not allow further determination.

### cf. *Polystichum*
(Fig. 3E; Supplemental 2, Fig. 6)

1859 ?*Aspidium*; Bunbury: 54.

**Material.** NHMUK V19901.

**Description.** Fragment of a penultimate segment; ultimate segments sub-opposed with petiolate insertion; costules asymmetrical with insertion on the basiscopic side. Venation open to forked. Margin regularly serrate.

**Reamrks.** Bunbury (1859) compared this morphotype with the living species *Polystichum setiferum* (Forsskål) Woynar. Although the fossil material is not well preserved, the shape, the venation of the ultimate segments and the regularly serrate margin resemble those of this genus.

### cf. *Davallia*
(Fig. 2C, F; Supplemental 2, Fig. 7)

1859 ?*Davallia canariensis* (J. E. Smith); Bunbury: 53.

**Material.** NHMUK V19890. SMC, not numbered.

**Description.** Pinna fragment. Pinnae pinnatifid. Ultimate segments resemble the terminal indusium with the pouch-shaped segments from extant plants.

**Remarks.** The shape of the ultimate segments resembling the pouch-shaped indusial is the character that makes this fossil similar to *Davallia canariensis* (L.) Smith. However, the preservation as a compression fossil in a coarse matrix does not preserve additional characters. A curious fact is the presence of part and counterpart housed in different institutions (SMC and NHMUK). *Davallia canariensis* is a common epiphyte in the laurel forest and grows on rocks and walls along Madeira Island (Gibby & Paul 1994).

Order **Blechnales** Pichi-Sermolli ex Reveal, 1993
Family **Blechnaceae** Newman, 1844
Genus ***Woodwardia*** Smith, 1739
***Woodwardia radicans*** (Linnaeus) Smith, 1739
(Fig. 3G; Supplemental 2, Fig. 8)

1857 ?*Woodwardia radicans* Cavanilles; Heer: 26, pl. 1, fig. 12.
1859 *Woodwardia radicans*; Bunbury: 53.
1861a *Woodwardia radicans*; Heer: 315.
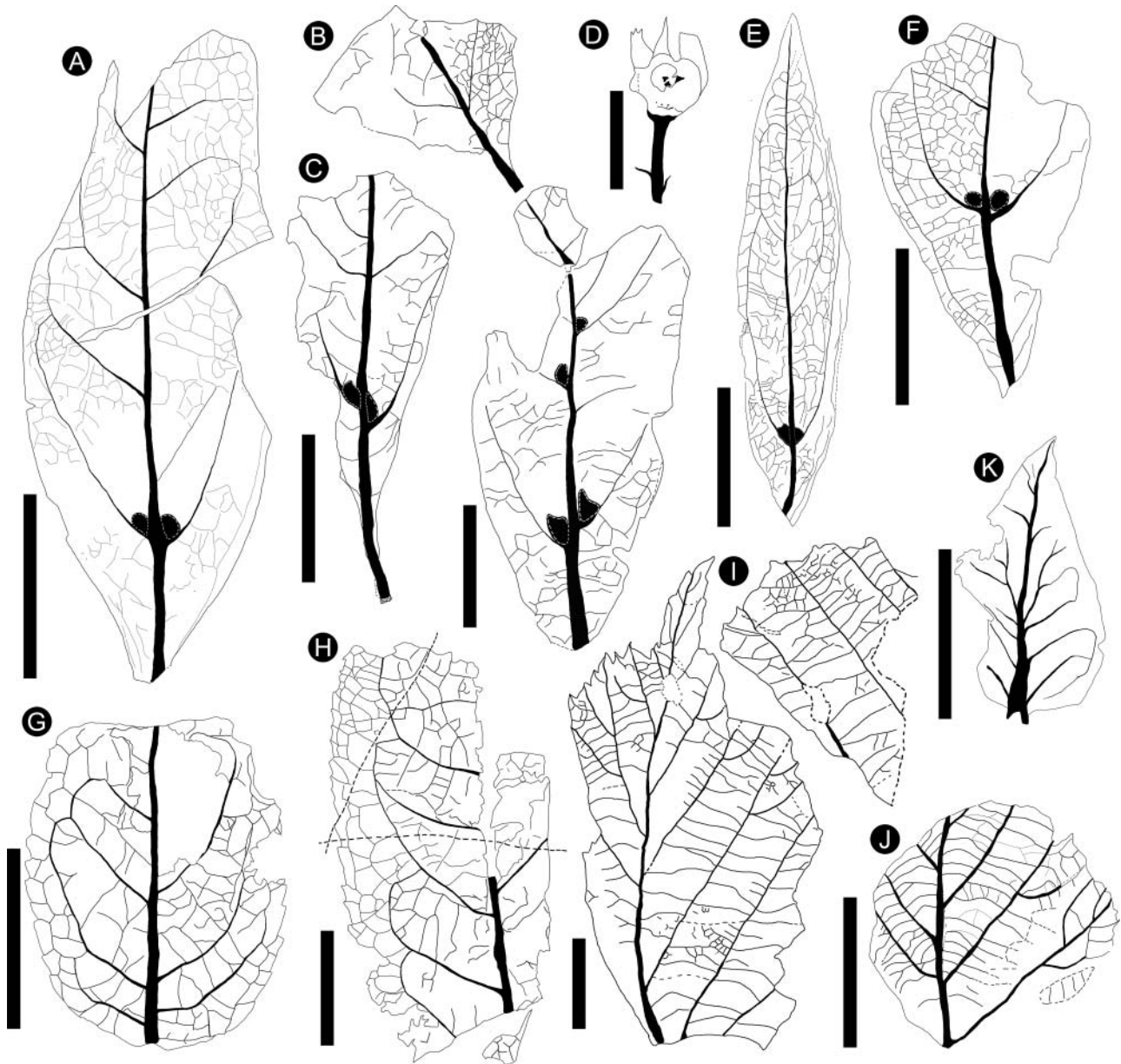
**Figure 4.** Line drawings of selected Magnoliopsida from the São Jorge fossil flora. **A,** *Ocotea foetens* (NHMUK V19906); **B,** *O. foetens* (NHMUK V19903); **C,** *O. foetens* (NHMUK V19907); **D,** flower? fruit? (NHMUK V19898); **E,** *O. foetens* (NHMUK V19919); **F,** *O. foetens* (NHMUK V19904); **G,** cf. *Vaccinium* (NHMUK V19911); **H,** cf. *Vaccinium* (NHMUK V19910) **I,** *Rubus* sp. (ETH-Z-ERDW 3708); **J,** *Rubus* sp. (NHMUK V19902); **K,** Magnoliopsida gen. et sp. indet. (NHMUK V19918). Scale bars = 10 mm, except D = 2.5 mm.

**Material.** NHMUK V19898.

**Description.** Pinnule fragment with anastomosed venation; costa prominent; sori oblong and localized parallel to the costa. Margin not preserved.

**Remarks.** Although fragmentary, the specimen shows the characteristic anastomosed venation and position of the sori of *W. radicans*. This species is native and frequent in Madeira (Gibby & Paul 1994).

**Filicopsida** gen. et sp. indet. 1
(Supplemental 2, Fig. 9)

1857 *Asplenium bunburyanum* Heer: 27, pl. 1, fig. 14.

**Material.** ETH-Z-ERDW 2841.

**Description.** Penultimate segment pinnatifid. Ultimate segments venation open and simple to bifurcate. Margin entire, except the apex of the ultimate segment with spiky teeth, oriented towards the apex.

**Remarks.** Heer (1857) compared this species to 'Asplenium lanceolatum' Hudson [ = A. billotii F. W. Schultz], a native of Madeira Island (Jardim & Menezes de Sequeira 2008). However, this fragment is comparable to other taxa such as *Dryopteris* or *Asplenium*. Although morphologically distinct, the incompleteness and lack of a more complete or a fertile frond prevents further determination.

**Filicopsida** gen. et sp. indet. 2
(Fig. 3H; Supplemental 2, Fig. 10)

1857 *Aspidium lyelli* Heer: 27, pl. 1, fig. 15, 15a–c.
1859 *Aspidium lyelli* Heer; Bunbury: 53.

**Material.** NHMUK V19899a, b. ETH- Z-ERDW 5740.

**Description.** Fertile and sterile pinnatifid penultimate segments. Ultimate segments venation open and simple. Fertile specimen (ETH-Z-ERDW 5740) with dispersed sori, connected to the ultimate venation. Sori apparently peltate, with between four and six sori for each lobe. Margin dentate; tooth not well preserved, but present in both fertile and sterile pinnae.

**Remarks.** Heer (1857) compared this morphotype to 'Aspidium frondosum' Lowe [ = Arachniodes webbiana (A. Braun) Schelpe]. Though the venation, arrangement of pinnules and sori between the two genera are similar, other fern taxa can also show a similar morphology (e.g. Thelypteridaceae: *Christella dentata*, *Lastrea limbosperma*).

**Filicopsida** *incertae sedis* 1
(Supplemental 3, Fig. 1)

1857 *Asplenium marinum* L.; Heer: 26, pl. 1, figs 16, 17.

**Material.** ETH-Z-ERDW 2840.

**Remarks.** Described from an incomplete ultimate segment impression with no margin preserved. Heer (1859) based his identification on an acroscopic lobe which is not well preserved. This fossil could fit several taxa present in the modern flora of Madeira Island.

Division **Spermatophyta** Willkomm, 1854
Subdivision **Magnoliophytina** Frohne & U. Jensen ex Reveal, 1995
Class **Magnoliopsida** Brongniart, 1843
Order **Laurales** Perleb, 1826
Family **Lauraceae** Jussieu, 1789
Genus *Ocotea* Aublet, 1775
*Ocotea foetens* (Aiton) Baillon, 1870
(Figs 2H, 4A–C, E, F; Supplemental 2, Figs 11–15)

1857 *Oreodaphne foetens* Aiton; Heer: 29, pl. 2, figs 4–13.

1859 ?*Laurus canariensis* Webb & Berthelot; Bunbury: 54.
1859 *Oreodaphne foetens* Aiton; Bunbury: 55.
1861a *Oreodaphne foetens*; Heer: 315.

**Material.** NHMUK V19903, V19905, V19904, V19906, V19907, V19919. ETH-Z-ERDW 3705, 3710a, b, 2842b, 5416, 2401, 3701, 2380.

**Description.** Leaf attachment petiolate, leaf organization simple. Blade attachment marginal, laminar size nanophyll to microphyll with L:W ratio 2.5:1 to 3:1, laminar shape elliptical with medial symmetry and basal symmetry symmetrical to asymmetrical. Margin entire with acute apex angle, convex apex shape, acute base angle and decurrent base shape. Lamina with two large superficial laminar glands in the axil of the most basal secondary veins. Primary venation pinnate, one basal vein, and no agrophic veins. Major secondaries simple brochidodromous, some apparently eucamptodromous with irregular spacing that abruptly increases proximally, forming one pair of acute suprabasal secondaries and excurrent attachment to midvein. Minor secondary simple brochidodromous, with irregular spacing. Intersecondaries span more than 50% of the length of the subjacent secondary, occur less than one per intercostal area, and proximal course is parallel to major secondaries. Intercostal tertiary vein fabric regular to irregular reticulate, epimedial tertiary fabric mixed percurrent, exterior tertiary curse looped. Quaternary vein fabric in some specimens apparently regular.

**Remarks.** Bunbury was the first to recognize Lauraceae leaves in the São Jorge macroflora (C. Lyell 1854). Later, Heer (1857) identified 'Oreodaphne foetens Aiton' [ = Ocotea foetens (Aiton) Baillon]. Bunbury (1859) compared his specimens with the figures given by Heer (1857), identifying all of his specimens as 'Laurus canariensis Webb and Berthelot?' [ = Laurus novocanariensis Rivas Martinez, Lousã, Fernández Prieto, E. Dias, J.C. Costa & C. Aguiar]. Bunbury (1859) recognized only one specimen as 'Oreodaphne foetens' [ = Ocotea foetens (Aiton) Baillon].

The comparison of all fossil specimens with extant *O. foetens* leaves led us to conclude that all specimens of 'L. canariensis' and 'Oreodaphne foetens' identified by Bunbury (1859) are attributable to *O. foetens* (Aiton) Baillon. The fossil leaves and the extant leaves of *O. foetens* are comparable in the presence of one pair of acute sub-basal secondary veins, with a pair of protruding glands or domatia in the axils, sometimes appearing in the superior veins (e.g. Schimper 1870–1872; Press & Short 1994; Rasche & Kovar-Eder 2009) and the tertiary venation being regular polygonal reticulate (Rasche & Kovar-Eder 2009). This tree is a significant constituent of Madeira Island temperate laurel forest (Stink-laurel forest) flora, occurring between altitudes of 800 and 1450 m

above sea level (asl) in the south of Madeira, and between 300 and 1400 m asl in the north face (Capelo *et al.* 2005). Specimen NHMUK V19919, determined as *Phyllites*, most probably is the '*Salix*' described by Bunbury (1859), which is now revised as *O. foetens* (Fig. 4E).

Order **Salicales** Lindley, 1833
Family **Salicaceae** Mirbel, 1815
Genus *Salix* Linnaeus, 1753
***Salix* sp.**
(Supplemental 2, Fig. 16)

1857 *Salix lowei* Heer: 27, pl. 1, fig. 18.
1859 ?*Salix*; Bunbury: 55.

**Material.** Missing from the Heer and Lyell collections, but figured in Heer (1857).

**Description.** Leaf attachment petiolate, leaf organization simple. Blade attachment marginal, laminar microphyll with L:W ratio > 3.3:1, laminar shape lanceolate with medial symmetry and basal symmetry symmetrical. Margin entire, apex missing, acute base angle, and convex base shape. Primary venation pinnate. Major secondary vein framework brochidodromous. Irregular major secondary spacing with uniform variation of the major secondary angle to the midvein. Proximal secondaries decurrent to major secondary attachment. Intersecondary veins parallel to major secondaries, more than 50% of subjacent are secondary. Higher venation is not preserved.

**Remarks.** Although the specimen is missing, it was described and illustrated by Heer (1857) and doubtfully identified by Bunbury (1859) in Lyell's collection. The illustration given by Heer of an entire, lanceolate leaf, a base with convex shape, secondary venation brochidodromous, and intersecondary veins agrees with the extant leaves of *S. canariensis* (Rasche & Kovar-Eder 2009). This species is native and common along streams throughout Madeira Island (Press & Short 1994).

Order **Ericales** Dumortier, 1829
Family **Ericaceae** Jussieu, 1789
Genus *Erica* Linnaeus, 1753
***Erica arborea*** Linnaeus, 1753
(Fig. 2K; Supplemental 2, Fig. 17)

1857 *Erica arborea* L.; Heer: 27, pl. 1, fig. 18.
1859 *Erica arborea* L.; Bunbury: 55.

**Material.** NHMUK V19912, V19913. ETH-Z-ERDW 5464.

**Description.** Leaf attachment petiolate, leaf organization simple. Blade attachment marginal, laminar size leptophyll with L:W ratio > 9:1, laminar shape oblong to linear with medial symmetry. Margin entire and apparently revolute with acute apex angle, straight apex shape, and base not preserved. Primary venation pinnate, one basal vein. Higher venation is not preserved.

**Remarks.** The genus *Erica* is the only known Madeiran taxon with simple leaves, which are linear and leptophyll sized. The fossils observed are closer to the species *E. arborea* in size; *E. platycodon* subsp. *maderincola* differs mainly because of the larger leaf size, and the margin is irregularly toothed. *Erica arborea* is native to Madeira, being distributed from sea level to the highest peaks. This species is geographically distributed all over Macaronesia, the Mediterranean and eastern Africa (Désamoré *et al.* 2011).

Genus *Vaccinium* Linnaeus, 1753
**cf. *Vaccinium***
(Fig. 4G, H; Supplemental 2, Figs 18, 19)

1857 *Vaccinium maderense* Link; Heer: 30, pl. 2, figs 15, 16.
1857 *Ilex hartungi* Heer: 31, pl. 1, figs 23, 24.
1857 *Rosa canina* L.; Heer: 32, pl. 2, fig. 26.
1859 *Vaccinium maderense* Link; Bunbury: 56.
1859 ?*Vaccinium myrtillus*; Bunbury: 56.
1868 *Vaccinium maderense* Link; Lowe: 582.

**Material.** ETH-Z-ERDW 2393, 5472, 5419, 3702. NHMUK V19910, V19911, V19908. SMC: two specimens not numbered.

**Description.** Leaf attachment petiolate. Blade attachment marginal, laminar size nanophyll to microphyll with approximate L:W ratio 2:1. Laminar shape elliptical with medial symmetry and basal symmetry symmetrical to asymmetrical. Margin with serrate teeth. Apex angle apparently acute, with an obtuse base angle and base shape straight to convex. Primary venation pinnate, one basal vein, and absent agrophic veins. Major secondaries festooned semicraspedodromous with irregular spacing. Minor secondary course semicraspedodromous, with major secondary spacing irregular, variation of secondary angle smoothly increasing proximally and secondary attachment excurrent. Intercostal tertiary veins mixed opposite-alternate, epimedial tertiaries alternate percurrent. Exterior tertiary terminating at margin. Tooth spacing irregular, with one order of teeth, 6–10 teeth per cm. Sinus shape angular and tooth shape convex/concave to convex/straight. Principal vein present, terminating marginally at the apex of the tooth.

**Remarks.** Leaf architecture is reminiscent of the living species *Vaccinium padifolium* Smith, with irregular serrate teeth and the major secondaries festooned semicraspedodromous with irregular spacing, although the state of preservation does not allow a full determination. The

extant species *V. padifolium* is a very common shrub or a small tree growing at altitudes from 800 to 1700 m (Press 1994).

Order **Rosales** Perleb, 1826
Family **Rosaceae** Jussieu, 1789
Genus **Rubus** Linnaeus, 1753
*Rubus* **sp.**
(Fig. 4I, J; Supplemental 2, Figs 20, 21)

1857 *Corylus australis* Heer: 28, pl. 2, figs 1–3.
1857 *Ulmus suberosa* Moench?; Heer: 28, pl. 2, fig. 24.
1857 *Psoralea dentata* de Candolle?; Heer: 33, pl. 2, fig. 28.
1859 *Corylus australis* Heer; Bunbury: 55.
1861a *Rubus* sp.; Heer: 315.
1861b *Rubus fruticosus* L.; Heer: 179.
1862 *Rubus discolor* Weihe & Nees; Lowe: 249.
1862 *Rubus grandifolius* Lowe; Lowe: 249.
1864 ?*Corylus australis* Heer; Hartung & Mayer: 134.

**Material.** ETH-Z-ERDW 5739, 5742, 3708, 3740, 2379. NHMUK V19902.

**Description.** Leaf attachment petiolate. Blade attachment marginal, laminar size microphyll to notophyll with L:W ratio 1.5:1 to 1.8:1, laminar shape oblong with medial symmetry and basal asymmetry. Margin serrate with acute apex angle, acuminate apex shape, obtuse base angle and rounded base shape. Primary venation pinnate, five basal veins, with compound agrophic veins. Major secondaries craspedodromous with regular spacing, regular angle to the midvein and excurrent attachment to the midvein. Minor secondary craspedodromous. Intercostal tertiary veins opposite straight to convex with obtuse angles to midvein. Epimedial tertiaries alternate percurrent, with proximal course of the epimedial tertiaries perpendicular to the midvein; distal course of the epimedial tertiaries parallel to intercostal tertiaries. Exterior tertiary course terminates at the margin. Tooth spacing irregular, with at least two orders of teeth; 4–6 teeth/cm; sinus shape angular, and tooth shapes concave/flexuous and concave/straight. Principal vein terminates at the apex of the tooth.

**Remarks.** The identification of these fossils as *Ulmus*, *Corylus* and *Psoralea* gave rise to some controversy and introduced discredit to the results of Heer (1857). Lowe (1862) was the first to criticize the identifications of Heer, and revised them as belonging to the genus *Rubus*. However, Heer had already identified the genus *Rubus* in the São Jorge Flora (Heer 1861a), and published that *Ulmus* resembled *R. fruticosus* L. (Heer 1861b). In his correspondence, Heer also stated that he did not know of the existence of Lowe's flora (Lowe 1857–1872). He stated that James Yates Johnson (1820–1900) probably told Lowe about the revision of *Ulmus* as *Rubus* leaflets (Leu 2013,

p. 36), as Johnson and Heer exchanged correspondence and fossils from São Jorge. Later, Hartung & Mayer (1864) cited Heer, where he pointed out the uncertainty of the identification of *Corylus australis*. Heer's (1857) determinations were influenced by the Atlantis theory, in which the Atlantic islands were at one time connected to the continent (Heer 1856b). The presence of European taxa in Madeira Island became the proof of this theory. However, the revisions by Heer (Heer 1861a, b) and Lowe (Lowe 1862), and subsequent citations of these revisions (e.g. Starkie Gardner 1881, 1882; Cockerell 1928), were forgotten, and Heer's (1857) identifications were not cited until recently (e.g. Fernández-Palacios *et al.* 2011). In the ETH-Z-ERDW collection, two specimens not figured in Heer (1857) were found and identified as *Rubus* sp. Their provenance from São Jorge was initially considered dubious (Góis-Marques *et al.* 2014), but a later reappraisal showed that the fossil matrix is consistent with other specimens. Most probably these are the additional specimens that were sent by Johnson (Heer 1861a, b).

Morphologically, *Rubus* leaflets concur with the fossils, sharing the same laminar shape, margin type and venation. Other fossil localities in Madeira Island (Porto da Cruz) have also produced fossils of compound leaves associated with stems with prickles and endocarps attributable to the genus *Rubus* (Hartung & Mayer 1864; Góis-Marques in prep.). This genus is distributed throughout Europe and Macaronesia, with at least two endemic taxa on Madeira Island (Jardim & Menezes de Sequeira 2008).

**cf.** *Myrtus*
(Fig. 2I; Supplemental 2, Fig. 22)

1857 *Myrtus communis* L.; Heer: 30, pl. 2, figs 21, 22.
1859 ?*Myrtus*; Bunbury: 56.
1862 *Myrtus communis* L.; Lowe: 113.
1864 *Myrtus communis* L.; Lowe: 268.

**Material.** ETH-Z-ERDW 5465, 3701, 2400. NHMUK V19909.

**Description.** Leaf attachment petiolate. Blade attachment marginal, laminar size microphyll to notophyll; L:W > 2:1. Laminar shape elliptical with medial symmetry and basal symmetry symmetrical. Margin untoothed, apex angle acute, apex shape straight; base angle acute and convex base shape variable from straight, convex to concave. Primary venation pinnate with major secondary veins brochidodromous. Regular to irregular major secondary spacing. Variation of the major secondary angle to midvein uniform. Tertiary vein fabric poorly preserved but apparently percurrent. Higher venation not preserved.

**Remarks.** The figures given by Heer (1857) seem to show the characteristic intramarginal secondary veins

characteristic of *Myrtus communis*. However, in the surviving specimens this character is not preserved. Lowe (1862, 1864) considered the fossil '*Pistacea phaeacum*' as *Myrtus*. We agree with Lowe as the specimen does not differ from the ones described as *Myrtus*, nor do they resemble *Pistacea* leaflets.

### Magnoliopsida gen. et sp. indet. 1
### (Fig. 2E, F; Supplemental 2: Fig. 23)

1857 *Phyllites* (*Rhus*) *ziegleri* Heer: 33, pl. 2, figs 29–32.

**Material.** ETH-Z-ERDW 5482, 3706. NHMUK V19907.

**Description.** Leaf attachment petiolate. Blade attachment marginal, laminar size microphyll, L:W ratio approximately 3:1, laminar shape elliptical with medial symmetry and base apparently asymmetrical. Margin with serrate teeth. Apex angle apparently acute with convex apex. Base angle acute with a straight base. Primary venation pinnate. Major secondaries craspedodromous, with regular spacing, uniform angle to midvein and excurrent attachment to midvein. Intercostal tertiary veins regular reticulate. Tooth spacing regular, with one order of teeth and 4 teeth/cm. Sinus shape angular and tooth shape convex/straight. Principal vein terminating at tooth apex.

**Remarks.** Described by Heer (1857) based on four specimens. Currently there are only three specimens, one not previously reported in Lyell's collection (NHMUK V19907). This leaf is identified as *Phyllites*, and compared to *Rhus coriaria* L., an introduced plant (Jardim & Menezes de Sequeira 2008). Morphologically, the fossils resemble *Marcetella maderensis* (Bornmüller) Sventenius leaflets, sharing the toothed margin, craspedodromous venation and laminar shape elliptical with asymmetrical base; the intercostal tertiary veins are regular reticulate. However, the fossils are poorly preserved and display considerable differences such as the number of secondary veins and less spaced and asymmetrical cordate base, hindering further interpretation.

### Magnoliopsida gen. et sp. indet. 2
### (Fig. 4K; Supplemental 2: Fig. 24)

1859 *Phyllites* Bunbury: 55.

**Specimen.** NHMUK V19918.

**Description.** Leaf attachment petiolate. Blade attachment marginal, laminar size nanophyll; L:W ratio 1.8:1. Laminar shape ovate, with medial symmetry and basal asymmetry. Margin entire with acute apex, acute apex angle, concavo-convex base and shape, obtuse base angle. Pinnate primary venation. Major secondaries brochidodromous, with some apparently cladrodromous, possibly due to the preservation. Secondary spacing irregular, with

irregular angle and excurrent attachment. Intercostal tertiary veins regular reticulate.

**Remarks.** The specimen is well preserved, but the absence of distinctive characters makes a determination impossible, although it could resemble young leaves of *Hedera*.

### Magnoliopsida gen. et sp. indet. 3
### (Supplemental 2, Fig. 25)

1857 *Myrica faya* L.; Heer: 28, pl. 1, figs 19–23.
1872 *Ardisia excelsa* Aiton; Lowe: 34.

**Material.** ETH-Z-ERDW 2842a.

**Description.** Leaf attachment petiolate. Blade attachment marginal, laminar size microphyll with L:W ratio 2.4:1, leaf shape apparently obovate, margin entire, medial symmetry and basal symmetry symmetrical; margin entire with acute apex angle, convex apex shape, acute base angle and decurrent base shape. Primary venation pinnate, secondary veins apparently eucamptodromous with regular spacing that abruptly increases proximally, major secondary angle to midvein uniform.

**Remarks.** The original description is based on five leaf fragments figured by Heer (1857). Today only one specimen is present in the ETH-Z-ERDW collection. This morphotype differs from *Myrica faya* Aiton because of the absence of an irregularly toothed margin, although the margin can vary from entire to toothed (Short 1994). The secondary venation seems to differ from the leaves of *M. faya*, which have brochidodromous venation. Lowe (1872) reviewed Heer's fossils as *Ardisia excelsa* Aiton [ = *Heberdenia excelsa* (Aiton) Banks ex de Candole]. The absence of more specimens and better preservation prevents further determination.

### Magnoliopsida gen. et sp. indet. 4
### (Figs 2L, 4D; Supplemental 2, Fig. 26)

**Material.** NHMUK V19891.

**Description.** Flower (?) composed by a pedicel with two bracts, ovary (?) and perianth (?). Pistil incomplete, composed only of the ovary. Ovary attached to the receptacle and part of the locule visible due to fracture of the flower. On top of the pistil there are three structures that resemble a perianth.

**Remarks.** Fossil not observed or described by Bunbury (1859). This flower (?) is found in a composite specimen along with *Woodwardia radicans*. It resembles the fossil flower described by Heer (1857), but differs from it by the presence of bracts and the smaller size. It could also represent a developing fruit.

**Magnoliopsida** *incertae sedis* 1
(Supplemental 3, Fig. 2)

1857 *Clethra arborea* L.; Heer: 29, pl. 2, figs 18, 19.

**Material.** ETH-Z-ERDW 2843.

**Remarks.** The original reference is based on two specimens. Only one specimen is present in the collection, represented by an incomplete leaf with a non-preserved margin and no apex or base. The primary vein is pinnate, secondary veins brochidodromous, and intercostal tertiary veins alternate percurrent. It resembles cf. *Vaccinium*, but the lack of characters does not allow further identification.

**Magnoliopsida** *incertae sedis* 2
(Supplemental 3, Fig. 3)

1857 ?*Pittosporum*; Heer: 32, pl. 2, fig. 27.
1859 *Pittosporum*; Bunbury: 56.

**Material.** ETH-Z-EDRW 5418. NHMUK V19914.

**Remarks.** Based on two leaf apices, with margin entire and primary venation pinnate and secondary venation brochidodromous. The fragments are well preserved and could fit the foliage of several Magnoliopsida taxa present in the modern Madeiran flora.

**Magnoliopsida** *incertae sedis* 3
(Supplemental 3, Fig. 4)

1857 *Rhamnus latifolius* L'Héritier; Heer: 31, pl. 1, fig. 25.
1862 *Rhamnus latifolius* L'Héritier; Lowe: 112.

**Material.** ETH-Z-EDRW 5475.

**Remarks.** The specimen is an incomplete and poorly preserved leaf. Secondary venation architecture is not discernible as the upper half of the leaf is missing. Intercostal tertiary venation is opposite straight to convex. The margin type is not recognizable. The lack of characters does not allow the classification as *Frangula azorica* [ = *Rhamnus latifolius* L'Héritier]; however, the fossil strongly resembles *Rubus* sp.

**Magnoliopsida** *incertae sedis* 4
(Supplemental 3, Fig. 5)

1857 ?*Vinca major* L.: 30, pl. 2, fig. 20.

**Specimens.** ETH-Z-EDRW 3703, 5471.

**Remarks.** Described from a poorly preserved apex, with primary venation pinnate, and superior venation indistinguishable. *Vinca major* is a plant introduced to Madeira Island (Jardim & Menezes de Sequeira 2008).

**Magnoliopsida** *incertae sedis* 5
(Supplementary 3, Figs 6, 7)

1859 *Phyllites hymenaeoides* Bunbury: 56.
1859 *Phyllites lobulata* Bunbury: 56.
1859 *Phyllites* Bunbury: 56.

**Material.** NHMUK V19916, V19915, V19917, V19920.

**Remarks.** Bunbury (1859) assigned some of the specimens to the genus *Phyllites.* According to Schimper (1874), this genus was used to classify foliar organs that have uncertain taxonomic affinity. They represent leaves of leptophyll to nanophyll size with poorly preserved venation and could be growth stages of Lauraceae or other families, but their preservational state does not allow further determination.

Class **Liliopsida** Batsch, 1802
**Liliopsida** gen. et sp. indet. 1
(Supplemental 2, Fig. 27)

1857 Gramineen; Heer: 34, pl. 2, fig. 33.
1859 ?*Cyperus*; Bunbury: 54.
1861b *Carex* (*Carex maxima* Scopoli); Heer: 179.

**Material.** NHMUK V19900, V19892.

**Description.** Blade fragments with parallel venation. Some fragments show a midvein.

**Remarks.** The size and parallel venation is characteristic of monocotyledonous plants. We agree with Heer (1857) and Bunbury (1859) that genera of Poaceae and Cyperales probably exist in this flora as they are common hygrophilous and nemoral plants in the present-day vegetation. The fragmentary state prevents further determination.

**Missing specimens**

**Filicopsida** *incertae sedis*
***Pteris cretica*** L., sensu Heer 1861a

1861a *Pteris cretica* L.; Heer: 315.
1861b *Pteris cretica* L.; Heer: 179
1864 ?*Pteris cretica* L.; Heer in Hartung & Mayer: 133, pl. 8, fig. 12.

**Remarks.** Described from an incomplete and apparently linear ultimate segment with poorly preserved venation. The morphology described could fit several different fern taxa (e.g. *Polypodium*, *Pteridium*).

***Adiantum?*** *psychodes* sensu Bunbury, 1859
***Nephorodium?*** **(no. 6)** sensu Bunbury, 1859
***Nephorodium?*** **(no. 7)** sensu Bunbury, 1859

**Remarks.** Three ferns missing from Lyell's collection and not figured by Bunbury (1859).

**Magnoliopsida** *incertae sedis*

1861a *Laurus canariensis*; Heer: 315.

**Remarks.** The collection gathered by Carl Mittermaier (1823–1917), owned by Heinrich Georg Bronn (1800–1862) and sent for determination to Heer (Heer 1861a, b) had a list which included two Lauraceae (*Laurus canariensis* and *Ocotea foetens*). Most certainly Heer correctly identified *L. canariensis* [ = *Laurus novocanariensis* Rivas Martinez, Lousã, Fernández Prieto, E. Dias, J. C. Costa & C. Aguiar].

## Discussion

### Geological setting and leaf bed location
The age of the São Jorge leaf bed has been discussed in recent literature. Some authors consider the leaf bed to be approximately 2 Ma in age (e.g. Sziemer 2010; Fernández-Palacios *et al*. 2011), or, according to the stratigraphy given by Geldmacher *et al*. (2000), younger than 3.8 Ma, possibly between 3 and 0.7 Ma (Anderson *et al*. 2009). Based on the volcano stratigraphy established by Brum da Silveira *et al*. (2010c) and the nineteenth century descriptions, we suggest that the fossiliferous sediments can be included in the Curral das Freiras (MVC3) or Penha d'Águia (MVC2) units of the Middle Volcanic Complex. The age of the leaf bed must be older than 1.8 Ma, taking into account the upper age limit for the Middle Volcanic Complex. The failure to locate the outcrop precludes a more precise stratigraphical location of this fossil flora.

### Taphonomy
The taphonomical processes are probably related to rapid transport (e.g. mudflow), which is evident from the fragmentary state of the specimens and preservation in a silty-clay breccia. São Jorge fossiliferous sediments most likely represent flood deposits inside a naturally dammed fluvial valley, a frequent process in the valleys of Madeira as a result of landslides or lava flowing down the slopes (Brum da Silveira *et al*. 2010a). The overall leaf size of the flora ranges from nanophyll to microphyll, which differs from the extant plants which can range from notophyll to mesophyll (e.g. *Ocotea foetens*). Spicer (1989) suggested that leaf size constrains transport and deposition for fossilization. However, other factors could be involved, such as differential size separation during deposition, the conchoidal fractures of the sediment, and biased sampling as the fossils were collected by a peasant (K. M. Lyell 1881).

The historical account describes the presence of two lignite layers in the São Jorge outcrop. The occurrence of lower rank coal is unique in Madeira Island, and is most probably associated with a large accumulation of plant material from the forest that covered the island, or possibly the *in situ* accumulation of bryophytes (e.g. *Sphagnum* sp.) forming a bog. The infill of the basin with volcanic material from latter eruptions provided sufficient lithostatic pressure and temperature to produce lignite.

### Collections, specimens and review
Through more than 160 years the São Jorge collections have suffered considerable losses, e.g. the Lyell collection was composed of 140 specimens, of which only 32 specimens have survived. However, it is worth mentioning that this reduction did not involve a major reduction of the taxa described by Heer (1857) and Bunbury (1859). From the 25 taxa described by Heer (1857), we found 23 taxa represented by 44 specimens; Bunbury (1859) described 23 taxa, and in the present collection there are 19 taxa represented by 36 specimens (NHMUK and SMC). Most probably there was an attempt by the curators to retain the most important specimens.

The total number of taxa recognized by Heer (1857), Bunbury (1857) and Heer in Hartung & Mayer (1864) is 37. In the present paper we recognize 20 taxa, taking into account the dispersed reviews made by several authors, and the analysis of the surviving specimens. Nine Filicopsida taxa are proposed in this review, of which two taxa are identified at species level (*Pteridium aquilinum* and *Woodwardia radicans*), one taxon identified at genus level (*Osmunda* sp.), one comparable at species level (*Asplenium* cf. *onopteris*), three taxa comparable or with affinities at genus level (cf. *Polystichum*, cf. *Davallia*, aff. *Asplenium*) and two fern taxa identified at class level (Filicopsida gen. et sp. indet. 1 and 2). Ten Magnoliopsida are proposed, of which two taxa were identified at species level (*Ocotea foetens* and *E. arborea*), two determined at genus level (*Salix* sp. and *Rubus* sp.), two taxa comparable at genus level (cf. *Vaccinium* and cf. *Myrtus*), and four taxa identified at class level (Magnoliopsida gen. et sp. indet. 1 to 4), which includes a flower or fruit (Magnoliopsida gen. et sp. indet. 4). Finally, one taxon at class level is proposed for Liliopsida (Liliopsida gen. et sp. indet. 1). We also propose the demotion of several taxa suggested by Heer (1857), Bunbury (1859) and Hartung & Mayer (1864) to *incertae sedis*: *Asplenium marinum*, *Clethra arborea*, *Pittosporum*, *Rhamnus latifolius* [ = *Frangula azorica*], *Vinca major*, *Phyllites hymenaeoides*, *Phyllites lobulata* and *Phyllites* (no. 22 in Bunbury's 1859 list).

The 82 specimens studied indicate a flora dominated by penultimate or ultimate fern segments (27 fossils studied, though several unidentifiable fragments are present in almost all specimens), untoothed (entire)-margined Magnoliopsida leaves (37 fossils studied), less common

toothed-margined Magnoliopsida (18 fossils studied) and rare Liliopsida leaves (two fossils studied).

## Palaeoecology of the São Jorge flora

The São Jorge fossil flora shows similarities with the modern vegetation of Madeira Island, especially with the laurel forest, as already noted by Heer (1857) and Bunbury (1859). However, the fossil association when compared with the present-day vegetation of Madeira Island suggests that the São Jorge macroflora is, although species impoverished, homologous to the climax stink-laurel temperate forest community (*Clethro arboreae-Ocoteetum foetentis*) proposed by Capelo *et al.* (2005). This evergreen broad-leaved forest is dominated by *O. foetens* and other lauroid leaf species (e.g. *Laurus novocanariensis*, *Picconia excelsa*, *Heberdenia excelsa*) that are represented in the São Jorge leaf bed by *O. foetens* leaf fossils and other undetermined lauroid leaves (e.g. Magnoliopsida gen. and sp. indet. 3). The understory vegetation is characterized by abundant ferns such as *Diplazium caudatum*, *Pteris incompleta*, *A. onopteris*, *Dryopteris maderensis*, *W. radicans* and *C. macrocarpa*, some of which are represented in the São Jorge flora (e.g. *W. radicans*, *A.* cf. *onopteris*); herbs like *Festuca donax* and *Carex lowei* are probably represented by Liliopsida gen. et sp. indet. 1.; climbers are also common in the extant community and are represented in the fossil association by *Rubus* sp.; and epiphyte species are represented by *D. canariensis* (cf. *Davallia*). The natural hedge and first substitution stage (*Vaccinio padifoli-Ericetum maderincolae*; Capelo *et al.* 2005) could be represented by *E. arborea* and *V. padifolium* (cf. *Vaccinium*). Companion species common in this series are represented by *P. aquilinum* and *S. canariensis.* It is our view that the São Jorge flora most probably represents a fully developed laurel forest, which is in contrast with the opinion of Kondraskov *et al.* (2015) who suggested that the Macaronesian plant fossil record does not show a vegetational type. Other plant communities could also be present, as *Myrtus communis* (cf. *Myrtus*) is associated with the high-scrub succession community of the barbuzano tree (*Apollonias barbujana*), and the Mediterranean forest is a vegetational belt that grows below the stink laurel community (see Capelo *et al*. 2005). Unfortunately, a specific determination is not possible.

The São Jorge flora seems to indicate that the palaeoclimate in which these taxa evolved was very similar to that of the present day. A multivariate statistical analysis like CLAMP was excluded as it needs more than 20 dicot morphotypes for robust results (e.g. Spicer 2008; CLAMP online). However, the comparability of the São Jorge fossil flora to an extant vegetation type leads us to suspect that it developed in similar morphoclimatic conditions (infra- to mesotemperate, humid to hyperhumid; see Capelo *et al.* 2005).

## Biogeographical implications

Macaronesian vegetation, especially the laurel forests, are considered an impoverished 'Tertiary relict' of the Palaeotropical geoflora, a vegetation belt that once dominated the margins of the Tethys Sea, from the Late Cretaceous to the late Miocene (Fernández-Palacios *et al.* 2011 and references therein). As the climate deteriorated through the Pliocene and Pleistocene, the surviving elements of the Palaeotropical geoflora were filtered due to pre-adaptation or non-adaptation to drier and/or colder climates (Martinetto *et al.* in press). This culminated in the extinction in Europe of several taxa that today are still found in other geographical areas (e.g. East Asia, Macaronesia; Martinetto *et al.* in press). The existence of a Palaeo-Macaronesia, where several islands were built up and eroded below sea level during a 60 myr interval, coexisting with the 'Palaeotropical geoflora' is one of keys to understanding the origin of Macaronesian floras (Fernández-Palacios *et al.* 2011). However, plant fossils from Macaronesia are the prerequisite to understanding the biogeography of the Macaronesian flora (Anderson *et al.* 2009). Reports of fossil floras with lauraceous leaves dating from the Pliocene to the Holocene in Macaronesian islands are known, but these are seldom described in stratigraphical, systematic and taxonomic detail. In the Canary Islands, Lauraceae leaf fossils have been found in Barranco de La Virgen in Gran Canaria (Pliocene, 5.5 to 2.7 Ma) (Suárez-Rodrígues 2013). Other undescribed macrofloras from Gran Canaria come from Las Cuevas del Guincho (4.5 to 4 Ma) and Berrazales (< 3.9 Ma), but a formal description is lacking (Anderson *et al.* 2009 and references therein). In La Palma Island a Late Pleistocene macroflora and microflora has been described, sharing some genera (i.e. *Salix* and cyperaceous leaves) with the São Jorge site (Vegas *et al.* 2013 and references therein). Holocene pollen also supports the presence of laurel forests in Tenerife (La Laguna), La Gomera (Laguna Grande) and Gran Canaria (Laguna de Valleseco) (de Nascimento *et al.* 2009, 2015, 2016; Nogué *et al.* 2013). In the Azores Islands, several reports of Pleistocene or younger plant macrofossils indicate the existence of a laurel forest type vegetation on at least five islands (Góis-Marques & Menezes de Sequeira 2015 and references therein). Holocene fossil pollen was also studied in the Azores by Connor *et al.* (2012) from Pico (Lagoa do Carvoeiro) and Flores (Lagoa Rasa). In the Madeira archipelago, the only fossil flora with lauraceous elements is the São Jorge flora. Unfortunately, Macaronesian fossil macrofloras, although abundant, lack formal descriptions, and consequently comparisons with the São Jorge flora are not possible.

Cautiously, due to identification problems, Fernández-Palacios *et al.* (2011) proposed that the São Jorge macroflora could represent two main groups of vegetation: one extant example of laurel forest in Macaronesia, and the

second composed of extinct taxa such as *Ulmus minor*, *Corylus australis* and *Pistacia phaecum*. The presence of extinct taxa in Tenerife (Canary archipelago), such as *Carpinus* and *Quercus*, is recognized in fossil pollen (de Nascimento *et al.* 2009). The presence of these putative extinct taxa in the São Jorge flora is in our view not supported by the reappraisal presented in this work, and the most parsimonious explanation is the presence of other native taxa with similar leaf architecture (e.g. see *Rubus* sp.) as part of the past vegetation community. However, the presence of extinct taxa in the São Jorge macroflora cannot be ruled out, as many of the distinct morphotypes described here have no direct correspondence with actual plants (e.g. Magnoliopsida gen. et sp. indet. 1). Moreover, non-destructive micro-sampling from selected São Jorge specimens for palynological study could help reconstruct the palaeoecology and to ascertain the possible presence of extinct taxa (e.g. Massamba N'siala & Mercuri 2010).

Recently, Kondraskov *et al.* (2015) tested the 'Tertiary relict' theory of the laurel forest through a molecular clock approach. Their results suggested that most taxa were not 'Tertiary relicts' but rather Plio–Pleistocene in origin. The only taxon analysed by Kondraskov *et al.* (2015) shared with the present São Jorge flora is *Ocotea foetens*, in which the mean stem age is 1.83 Ma; this is coincident with the proposed São Jorge macroflora age of ≥1.8 Ma, although they propose that *O. foetens* could have diverged at 3.15 Ma. Our results show that Madeira Island was already colonized by a laurel forest since at least 1.8 Ma, or possibly earlier.

## Conclusions

The São Jorge macroflora is still to date the best-known fossil flora from Macaronesia, but unfortunately is no longer available due to a landslide prior to 1865. The combination of historical documents and fieldwork make it possible to establish the approximate lithostratigraphical setting within the sedimentary intercalations of the MVC with an age ≥1.8 Ma.

The descriptions of Heer (1857), Bunbury (1859) and Hartung & Mayer (1864) are reviewed based on 82 surviving specimens and published illustrations. From the initial 37 taxa presented by those authors, we recognize only 20: *Osmunda* sp., *Pteridium aquilinum*, *Asplenium* cf. *onopteris*, aff. *Asplenium*, cf. *Polystichum*, cf. *Davallia*, *Woodwardia radicans*, Filicopsida gen. et sp. indet. 1 and 2, *Ocotea foetens*, *Salix sp.*, *Erica arborea*, cf. *Vaccinium*, *Rubus* sp., cf. *Myrtus*, Magnoliopsida gen. et sp. indet. 1 to 3, Liliopsida gen. et sp. indet. 1. Magnoliopsida gen. et sp. indet. 4 is based on one undescribed flower (?) or fruit (?). Due to insufficient taxonomic characters, we consider as *incertae sedis* the following: *Asplenium marinum*, *Clethra arborea*, *Pittosporum*, *Rhamnus latifolius*,

*Vinca major*, *Phyllites hymenaeoides*, *Phyllites lobulata* and *Phyllites* (no. 22).

We propose that the São Jorge flora represents a vegetation type comparable to the extant stink-laurel temperate forest association *sensu* Capelo *et al.* (2005) because of the presence of *O. foetens*, understory and epiphyte ferns and companion species typically found in this community. The palaeoecology implies that the past vegetation was growing in similar climatic conditions to today.

Deciduous trees recognized as extinct taxa in Madeira were reviewed as *Rubus* sp., a typical genus of the laurel forest. The genus *Pistacia* from the São Jorge flora is considered the oldest evidence from the Mediterranean forest (Fernández-Palacios *et al.* 2011), and is here revised as cf. *Myrtus*.

The historical palaeobotanical collections from ephemeral sites such as the São Jorge outcrop, the articles describing them and their plates are extremely important as they are unique sources available to study the past vegetation from that area (Massamba N'siala & Mercuri 2010). One hundred and sixty-two years after the discovery of the São Jorge leaf bed, and 159 years since the first description of the São Jorge macroflora, information can still be retrieved from these old and forgotten collections. The potential and importance of Macaronesian palaeobotany, especially for the understanding of vegetation palaeoecology and plant palaeobiogeography, implies that future research will be fruitful in determining the floristic novelties of these islands.

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## Supplemental material

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