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PALAEONTOLOGY

Tracing insular woodiness in giant *Daucus* (s.l.) fruit fossils from the Early Pleistocene of Madeira Island (Portugal)

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Abstract Plants on oceanic islands can evolve insular syndromes such as secondary woodiness, a generalized trend found in island floras worldwide. This phenomenon occurs through evolution *in situ*. It is triggered by ecological and physiological stimuli that transform herbaceous annuals into woody perennials. However, well-dated and informative fossils that could help track and frame the evolution of this syndrome are lacking. Remarkably, in Madeira Island (Portugal), there are good examples of Apiaceae that evolved secondary woodiness, like the giant neoendemic *Melanoselinum* (≡ *Daucus*). Apiaceae has a very scarce fossil record, despite being a cosmopolitan family and an economically important crop. Here we describe the oldest *Daucus* s.l. fossil known to date and the first fossil evidence of a plant with insular woodiness. The fossils are preserved as mummified/compressed mericarps within 1.3-million-year-old fluvio-lacustrine sediments of the Funchal unit, Upper Volcanic complex, near Porto da Cruz. We assign them to the extant neoendemic species *Melanoselinum* (≡ *Daucus*) *decipiens*. The mericarp morphology shows remarkable stasis since the Calabrian stage of the Early Pleistocene. Our results demonstrate that in the Madeiran Daucinae clade, insular woodiness developed at least 1.3 million years ago, indicating a coeval or earlier immigration to Madeira Island of a *Daucus* sp. Our results reinforce the role of palaeobotanical research in oceanic islands, supported by stratigraphy and geochronology studies, as a key element for the understanding of plant palaeobiogeography, ecology and evolution worldwide. We expect this contribution to shed light on the evolutionary origins of carrots, and related plant groups, an important element of human food, and to better comprehend the evolution of plant insular woodiness.

Keywords island syndromes; Macaronesia; *Melanoselinum*; neoendemic; palaeobotany; palaeocarpology

INTRODUCTION

Ever since Darwin (1859) and Wallace (1880), oceanic islands have been recognised as ideal environments to study the evolution, ecology and biogeography of both plants and animals (e.g., Whittaker & Fernández-Palacios, 2007; Whittaker & al., 2017). A generalized trend found in insular floras and equatorial mountains is the autochthonous evolution of woody perennials (i.e., neoendemics) from ancestors that were herbaceous annuals, through the expression of secondary xylem growth showing paedomorphic characters (Carlquist, 1974; Dulin & Kirchoff, 2010). Originally coined as "insular woodiness" by Sherwin Carlquist (Carlquist, 1974), various hypotheses have been proposed to explain the phenomenon and to account for the radical shift in life-form and traits entailed. These were recently reviewed (see Dulin & Kirchoff, 2010; Lens & al., 2013) and include: (i) competition among species resulting in advantageous gigantism; (ii) promotion of plant fitness through shift to perennial habit; (iii) year-round growth enabled by the buffered oceanic climate; (iv) lack of predation by large herbivores permitting perennial growth; and recently, (v) resistance to drought-induced embolism through the development of secondary wood (Dulin & Kirchoff, 2010; Dória & al., 2018).

In Macaronesian archipelagos (Azores, Madeira, Canaries and Cabo Verde; Atlantic Ocean), insular woodiness is found among several plant families, including Apiaceae, Asteraceae, Boraginaceae, Campanulaceae, Euphorbiaceae, Geraniaceae and Scrophulariaceae (Jardim & Menezes de Sequeira, 2008; Lens & al., 2013). Phylogenetic and molecular dating studies of the Macaronesian flora are still infrequent, but their results indicate different timing of arrival and speciation of neoendemics within and between the archipelagos (e.g., Kim & al., 2008; Spalik & al., 2010; Menezes & al., 2018). However, due to the nature of phylogenetic data and analysis, the timing of the triggering of insular woodiness

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is currently impossible to track. In the case of the neoendemic Macaronesian Apiaceae, the phenomenon characterises four main species (Acebes Ginovés & al., 2010; Menezes de Sequeira & al., 2012): *Bupleurum salicifolium* R.Br. ex Buch, distributed in the Canaries and Madeira archipelagos; *Angelica lignescens* Reduron & Danton in the Azores, *Monizia edulis* Lowe and *Melanoselinum decipiens* (Schrad. & J.C. Wendl.) Hoffm. from the Madeira Archipelago. Recent phylogenetic studies of the Madeiran endemic genera *Monizia* Lowe and *Melanoselinum* Hoffm. proposed inclusion within the genus *Daucus* L. (Banasiak & al., 2016). Moreover, a calibrated molecular phylogenetic study that included the Madeiran neoendemic Apiaceae (Spalik & al., 2010) proposed a Gelasian origin of *Daucus* (~2.5 Ma). However, the question remains: when did these giant insular carrots evolve their woody habit? To empirically establish the origins of the insular woody trait in Macaronesian Apiaceae, well-preserved and accurately dated plant fossils are desirable. Nevertheless, using palaeobotanical research to track deep-time plant ecological and evolutionary trends within oceanic islands is still infrequent (Góis-Marques & al., 2019), probably due to the perceived idea of the low probability of discovery of informative plants fossils on volcanic islands (Anderson & al., 2009).

Recent palaeobotanical exploration coupled with geochronological dating of Porto da Cruz sedimentary deposit in Madeira Island led to the discovery of several fruit and seed fossils, constrained to 1.3 Ma by two $^{40}Ar/^{39}Ar$ dates (Góis-Marques & al., 2019). Here we document new fossilised mericarps and compare them to present-day Macaronesian Apiaceae. We also present an overview of the macrofossil record of Apiaceae.

■ GEOLOGICAL SETTING

The geological setting presented here is a summary based on Góis-Marques & al. (2019). Madeira Island is located in the central Atlantic Ocean, at ca. 700 km NW of Marocco and 850 km SW of mainland Portugal (Fig. 1A). Geologically, Madeira corresponds to a highly dissected shield volcano that reaches 1861 m a.s.l. (Fig. 1B). The subaerial part of the island was built by several volcanic events, that were geologically mapped by Brum da Silveira & al. (2010a,b,c) as corresponding to three main volcanic complexes, further divided into units. The Lower Volcanic Complex (LVC1 and 2), with >7 Ma (Ramalho & al., 2015), the Middle Volcanic Complex (MVC1, 2 and 3) ranging from 7 to 1.8 Ma and the Upper Volcanic Complex (UVC1 and 2), from 1.8 Ma to Holocene. In all volcanic complexes there are interlayered sedimentary deposits (Brum da Silveira & al., 2010a).

In the Porto da Cruz area (NE sector of the island; Fig. 1B,C), there are sedimentary outcrops with deposits of fluvio-lacustrine facies (UVC2 g; Fig. 1C), where plant fossils have been discovered since the mid-19th century (Góis-Marques, 2013; Góis-Marques & al., 2014 and references therein). Recently, new explorations yielded new material, and the lava flows underlying (UVC2) and overlying (UVC2 μ) the sedimentary sequence were dated with $^{40}Ar/^{39}Ar$ to 1.38 ± 0.14 Ma and 1.319 ± 0.055 Ma, respectively (Góis-Marques & al., 2019). This constrained the age of the deposit and their fossiliferous content to ~1.3 Ma, Calabrian in age.

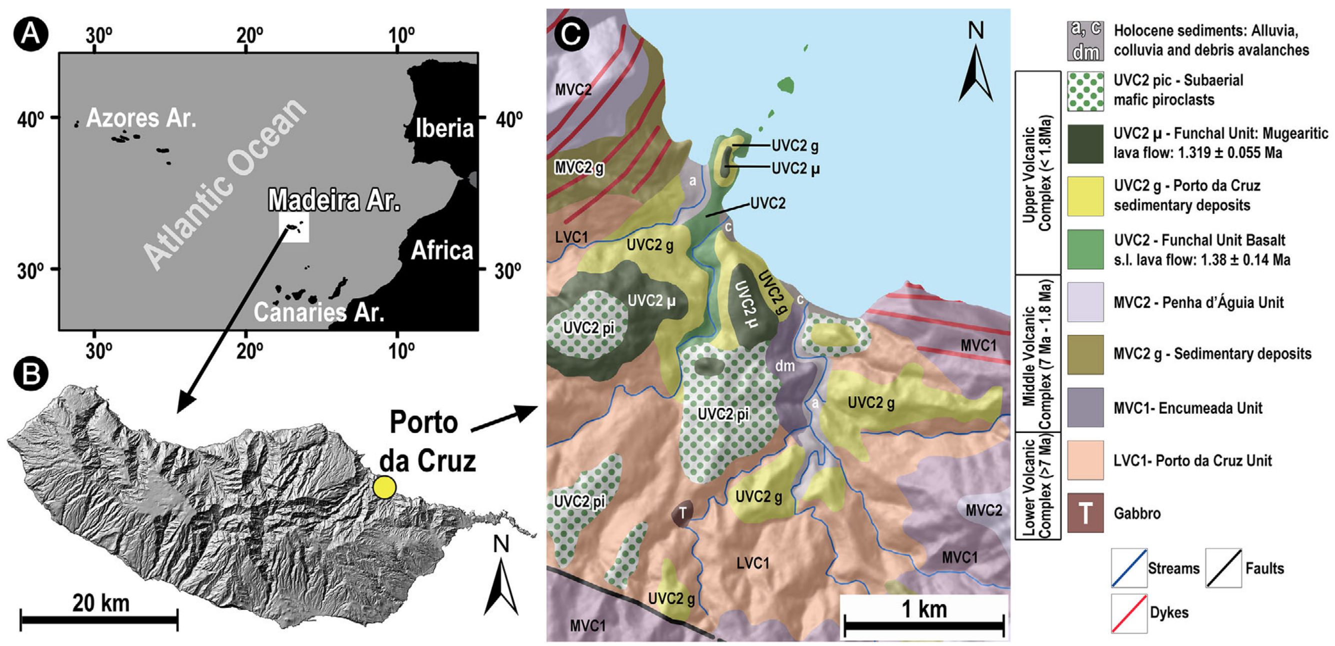

Fig. 1. Geographical location of Madeira Island and the fossiliferous sediments of Porto da Cruz. **A**, Geographical location of the Madeira Archipelago; **B**, Madeira Island indicating the Porto da Cruz locality; **C**, Geological map of Porto da Cruz area adapted from Brum da Silveira & al. (2010c).

■ MATERIALS AND METHODS

Fossils were collected and sampled according to the procedures described in Góis-Marques & al. (2019). In brief, dried, organic rich sediments from Porto da Cruz area (UVC2 g) were collected and deflocculated with H_20_2 3%. Four fossil mericarps were recovered and conserved in 70% ethanol solution. Fossils were examined using a Zeiss Stereomicroscope Stemi SV 11. They were photographed under 70% ethanol using a Nikon D5500 camera equipped with a macro lens. Identification involved comparison with extant herbarium material and selected literature dealing with Macaronesian Apiaceae (e.g., Cannon, 1994; Press & Dias, 1998; Fernandes & Carvalho, 2014). Systematic palaeobotany follows the criteria of Menezes de Sequeira & al. (2012), and Apiaceae fruit description follows various authors (e.g., Cannon, 1994; Hickey & King, 2000; Liu & al., 2006). Fruit fossils were numbered and deposited within the palaeobotanical collection of Madeira University Herbarium (hereafter abbreviated as UMad-P).

■ RESULTS

Systematic Palaeobotany: Apiaceae Lindl. – *Melanoselinum* Hoffm.

Melanoselinum decipiens (Schrad. & J.C.Wendl.) Hoffm., Gen. Pl. Umbell.: 156. 1814 ≡ *Selinum decipiens* Schrad. & J.C.Wendl., Sert. Hannov. 3: 23, t. 13. 1797 ≡ *Daucus decipiens* (Schrad. & J.C.Wendl.) Spalik, Wojew., Banasiak & Reduron in Taxon 65(3): 578. 2016.

Repository. – Palaeobotanical collection of the Madeira University Herbarium (UMad-P): UMad-P501 (Fig. 2E), UMad-P502 (Fig. 2F), UMad-P503 (Fig. 2G) and UMad-P504 (Fig 2H).

Locality. – Porto da Cruz, Machico, Madeira Island, Portugal.

Stratigraphy. – UVC2 g, Funchal unit, Upper Volcanic Complex (Brum da Silveira & al., 2010a,c).

Age. – ~1.3 Ma, Calabrian, Early Pleistocene with ^{40}Ar/^{39}Ar dating (Góis-Marques & al., 2019).

Description. – Mericarp fossils dorsally compressed, ca. 9–13 × 6–7 mm, surface smooth and glabrous on both sides, elliptical to narrowly elliptical in shape, median and marginal ribs running horizontally from base to apex, crushed during fossilization, secondary wings well developed, width ca. 0.9–1.6 mm, margin irregularly dentate to undulate, wings without venation. Secondary wings strongly auriculate at the base, almost imbricate, converging at the apex (Fig. 2), stylopodium not preserved.

Comparison. – When compared with large fruits of Macaronesian neoendemic Apiaceae, the fossils studied fall within extant *Melanoselinum decipiens* mericarp morphological variability (Fig. 2D), especially in their size and in the morphology of the marginal wings, which are irregularly toothed to undulate, smooth surfaced, and auriculate. The extant mericarps of *M. decipiens* are pubescent (Fig. 2D), differing from the fossils (Table 1). Most probably, hairs were lost during diagenesis. *Monizia edulis* differs from the fossils due to the smaller teeth and the truncate to emarginate base of the fruit (see Table 1). *Melanoselinum decipiens* is a woody, perennial and monocarpic shrub growing up to 3 m (Cannon, 1994), a true giant among other *Daucus* species (Fig. 2B).

■ DISCUSSION

The new fossils from Madeira Island enable us to assign a minimum crown age of 1.3 Ma to the species *Melanoselinum decipiens* and to state clearly that a continental herbaceous ancestor of *Daucus* sp. (Banasiak & al., 2016) was part of the flora during the Calabrian stage of the Pleistocene or earlier. This inference is important, because there are no known fossils of *Daucus* older than 30 ka (Galloway, 1977), making the Madeiran *M. decipiens* the oldest recorded for the genus worldwide. The molecular dating of *M. decipiens* (Spalik & al., 2010) gives a Gelasian origin (ca. 2.5 Ma) of the species, although the associated 95% posterior probability intervals range more broadly from ca. 5.6 Ma (Miocene, Messinian) to ca. 290 ka (Middle Pleistocene). Our new fossils fall within this proposed age range (Spalik & al., 2010), but they contradict the younger end of the range, ruling out a Middle Pleistocene origin. The inclusion of recent insular fossils (i.e., Quaternary), when available, will certainly contribute to constraining and building better-calibrated phylogenetic trees.

The discovery of the *Melanoselinum decipiens* fossils most probably points to the presence of an already fully developed neoendemic Apiaceae on Madeira Island 1.3 Ma. To date, no *M. decipiens* stem or leaf fossils exist to directly affirm a fully developed plant with insular woodiness. However, several lines of other evidence from mericarp evolution and size, palaeoecology and taphonomy are indicative of the establishment of insular woodiness by this early date. According to Wojewódzka & al. (2019), *M. decipiens* mericarp wings can be interpreted as an evolutionary reversal from ancestral *Daucus* spp. with spiny fruits, an evolutionary adaptation to anemochory, because oceanic islands lack dispersal agents such as terrestrial mammals. The fossil mericarps are morphologically identical to those of the living species, pointing to a fully evolved *M. decipiens* at 1.3 Ma. Other indirect evidence can be found in the size of the mericarps of extant *Daucus* spp. when compared to the overall size of the plants. *Daucus* spp. have mericarps that are ≤5 mm, rarely 10 mm in size, borne on plants with maximum height varying from 25 to 220 cm (e.g., Pujadas Salvá, 2003). *Melanoselinum decipiens* has mericarps with 12–14 mm borne on plants reaching up to 300 cm in height (Cannon, 1994), meaning that an isometric growth relation can be inferred (except *M. edulis* with similar size, but distinct ecology and growth strategy; see Fernandes & Carvalho, 2014). Another indirect proof comes from synecology and taphonomy. Today, *M. decipiens* is found associated within the stink-laurel temperate forest series (Clethro arboreae–

Ocoteo foetentis sigmetum; Capelo & al., 2005), together with other neoendemic plants such as *Euphorbia mellifera* Aiton (Euphorbiaceae), *Isoplexis sceptrum* (L.f.) Loudon (Scrophulariaceae) or *Musschia wollastonii* Lowe (Campanulaceae), establishing communities that occupy natural openings within the forest, like land-slides and small streams (Capelo & al., 2003). Palaeobotanical evidence indicates that the stink-laurel temperate forest was present in Madeira Island from at least 1.8 Ma (Góis-Marques & al., 2018), meaning that the ecological conditions that could trigger insular woodiness were already in place. Neoendemics were most probably a part of this insular ecosystem at 1.3 Ma, occupying the same niche. This is further supported by taphonomic evidence. The sediments in which the mericarp fossils were found correspond to a naturally dammed valley, suggesting a streamside environment, similar to the habitat of *M. decipiens* extant plants. The Madeira Island fossils are the first palaeobotanical evidence of the insular woodiness syndrome.

The Apiaceae contain over 3700 living species and include several important crops, yet their fossil record is sparse and poorly understood (e.g., Friis & al., 2011; Banasiak & al., 2013). Apiaceae fossil pollen are known since as early as the Cretaceous (Banasiak & al., 2013 and references therein), but the identification below family rank was seldom attempted (e.g., Gruas-Cavagnetto & Cerceau-Larrival, 1984) due to morphological similarities among genera (Hofmann

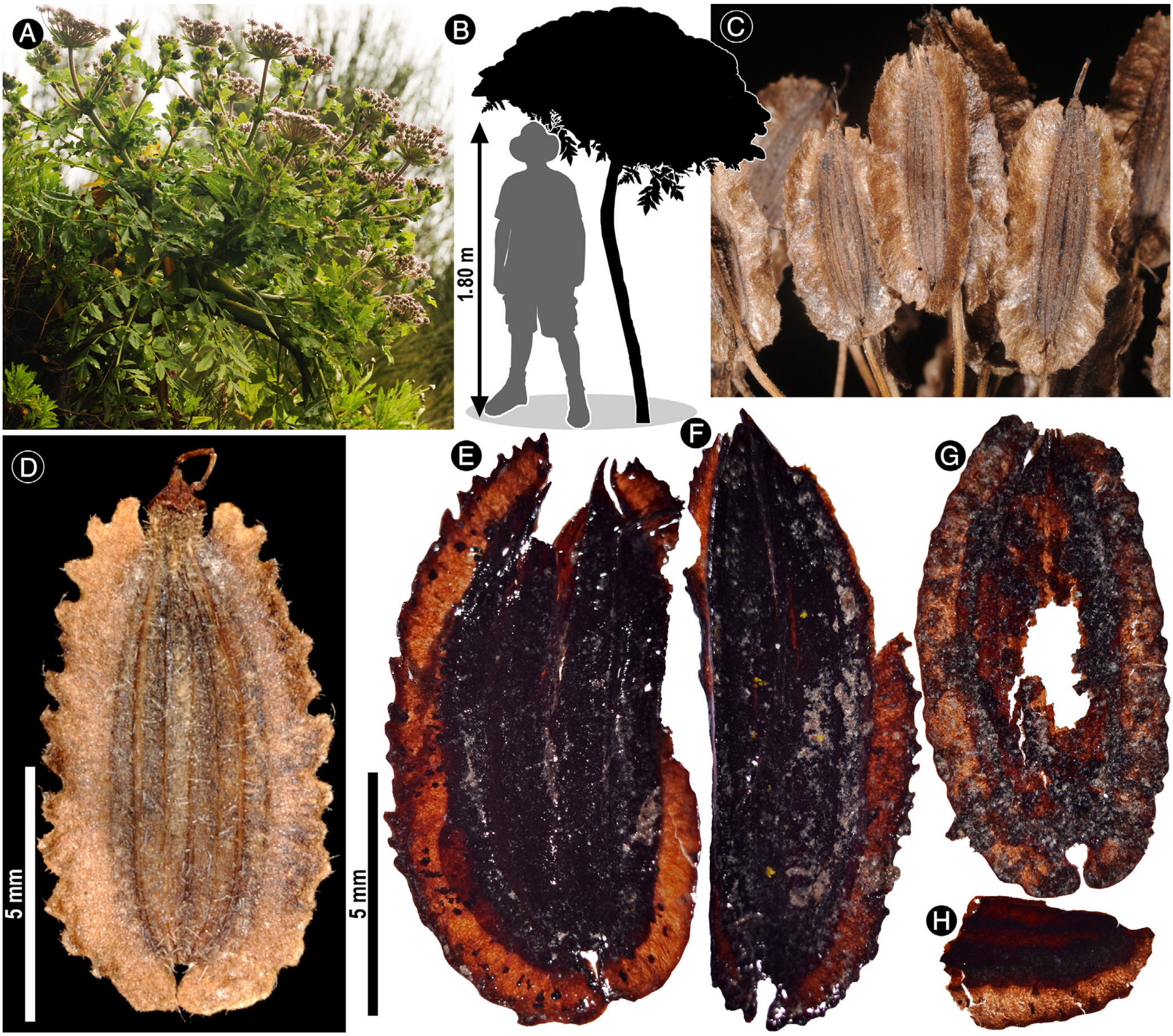

Fig. 2. *Melanoselinum* (≡ *Daucus*) *decipiens* and the fossil mericarps recovered from Porto da Cruz sediments. **A**, Flowering *M. decipiens* in the wild (Photo: M. Menezes de Sequeira); **B**, Drawing outline demonstrating the giant size attained by *M. decipiens*; **C**, Detail of an umbel with mature schizocarps, with winged mericarps; **D**, Detail of a mericarp (dorsal view); **E–H**, *M. decipiens* mericarp fossils studied: **E**, UMad-P501; **F**, UMad-P502; **G**, UMad-P503; **H**, UMad-P504 (fragment).

Table 1. Comparison of Macaronesian Apiaceae taxa mericarps from species with insular woodiness or with comparable mericarp sizes.

	Mericarp size	Shape	Surface texture	Lateral wings	Wing margin	Mericarp base	Hairs
Fossils in this study	ca. 9–13 × 6–7 mm	Oblong to narrowly oblong	Smooth	Present	Irregulary dentate to undulate	Strongly auriculate to almost imbricate	Glabrous
Melanoselinum decipiens	12–14 × 5–7 mm	Oblong to narrowly oblong	Smooth	Present	Irregulary dentate to undulate	Strongly auriculate to almost imbricate	Pubescent
Bupleurum salicifolium subsp. *salicifolium*	7 × 2.5–3 mm	Ovate	Smooth	Absent	–	–	Glabrous
Monizia edulis	9–13 × 3–6 mm	Elliptical to ovate	Smooth to tuberculate	Present	Entire to irregularly toothed	Truncate to emarginate	Pubescent
Angelica lignescens	3.5–7 × 5 mm	Oblong to suborbicular	Smooth	Present	Entire	Subcordate	Pubescent
Astydamia latifolia	12 × 5–6 mm	Ovate	Smooth	Absent	–	–	Glabrous

Information retrieved from references Cannon (1994), Press & Dias (1998) and Fernandes & Carvalho (2014).

& al., 2015). Putative Apiaceae macrofossil fruits (mericarps) like *Carpites ulmiformis* Dorf are also known from the Cretaceous, although their taxonomical affinities are not completely resolved (Manchester & O'Leary, 2010). Cenozoic mericarps include *Umbelliferospermum latahense* Berry (Berry, 1929), *Diachaenites heeri* A.Braun. and *D. ciclosperma* Heer (Heer, 1859), *Pimpinellites zizioides* Unger (Unger, 1838) and *Umbelliferites* Engelh. & Kink. (Engelhardt & Kinkelin, 1908), although these early identifications need a modern revision. Extant genera, including putative extinct species, are known from several Mio-Pleistocene records (see Mathias, 1965), mainly from mericarp fossils of *Oenanthe* L. (Bertoldi & Martinetto, 1995; Bińka & al., 2007), *Oxypolis* Raf. (Cockerell, 1908), *Peucedanites* Heer (Heer, 1883) and *Cicuta* L. (Matthews & Ovenden, 1990). Currently, the Apiaceae macrofossil record is scattered and understudied. A full review of these fossils, if still available in collections, is needed to elucidate and complement the evolutionary history of the family.

■ CONCLUSION

Palaeobotanical exploration of oceanic islands provides insights into the evolution of insular floras and also helps to expand our knowledge of related continental species. Our results clearly show the presence of the giant neoendemic Apiaceae *Melanoselinum decipiens* on Madeira Island at 1.3 Ma, which is the oldest macrofossil of a wild carrot and the first fossil of a plant displaying insular woodiness. The fossil provides a calibration point for future Apiaceae phylogenies. The truism of oceanic islands as natural biological laboratories to study the living biota is objectively strengthened by the addition of a palaeontological deep-time perspective.

■ AUTHOR CONTRIBUTIONS

CAG-M and MMdS performed field and laboratorial work; all authors contributed to the writing of the manuscript. — CAG-M, http://orcid.org/0000-0002-0255-7641; LdN, http://orcid.org/0000-0003-1085-2605; JMF-P, http://orcid.org/0000-0001-9741-6878; JM, http://orcid.org/0000-0003-4729-8994; MMdS, http://orcid.org/0000-0001-9728-465X

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