GUEST EDITORIAL

Life, death and fossilization on Gran Canaria – implications for Macaronesian biogeography and molecular dating

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ABSTRACT

The Canaries have recently served as a test-bed island system for evaluating newly developed parametric biogeographical methods that can incorporate information from molecular phylogenetic dating and ages of geological events. To use such information successfully, knowledge of geological history and the fossil record is essential. Studies presenting phylogenetic datings of plant groups on oceanic islands often through necessity, but perhaps inappropriately, use the geological age of the oldest island in an archipelago as a maximum-age constraint for earliest possible introductions. Recently published papers suggest that there is little chance of informative fossil floras being found on volcanic islands, and that nothing could survive violent periods of volcanic activity. One such example is the Roque Nublo period in Gran Canaria, which is assumed to have caused the extinction of the flora of the island (*c.* 5.3–3.7 Ma). However, recent investigations of Gran Canaria have identified numerous volcanic and sedimentological settings where plant remains are common. We argue, based on evidence from the Miocene–Pliocene rock and fossil records, that complete sterilization of the island is implausible. Moreover, based on fossil evidence, we conclude that the typical ecosystems of the Canary Islands, such as the *laurisilva*, the *Pinus* forest and the thermophilous scrubland, were already present on Gran Canaria during the Miocene–Pliocene. The fossil record we present provides new information, which may be used as age constraints in phylogenetic datings, in addition to or instead of the less reliable ages of island emergences or catastrophic events. We also suggest island environments that are likely to yield further fossil localities. Finally, we briefly review further examples of fossil floras of Macaronesia.

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The increasing efforts to integrate methods and results in historical biogeography with molecular phylogenetic dating are extremely important, because ignoring temporal information will obscure biogeographical patterns and give erroneous results (Donoghue & Moore, 2003; Ree & Sanmartín, 2009). Today's dating methods yield sufficiently realistic divergence times between organism lineages to be incorporated into biogeographical studies. These new methods (reviewed by e.g. Anderson, 2007) are not dependent on a strict molecular clock and they allow for calibration with multiple age constraints from the fossil record or geological evidence.

Unless combined with temporal information, biogeographical inference is highly sensitive to the problems of pseudo-congruence (i.e. two groups showing similar patterns but with a different temporal origin are unlikely to have been affected by the same biogeographical events) and pseudo-incongruence (i.e. distributional noise obscuring a common pattern) (see e.g. Vanderpoorten *et al.*, 2007). Divergence times can be used to discriminate between alternative biogeographical scenarios – such as in the old debate between dispersal and vicariance – by comparing the divergence times of the disjunct taxa with the timing of the geographical barrier.

Through an integration of methods and results in dating and biogeography we can gain information on how speciation and biodiversity change over time owing, for example, to climatological and other geological events, (mass-)extinctions and new dispersal routes. During the last few years, new analytical methods have been developed (e.g. Nylander *et al.*,

2008; Ree & Smith, 2008; Sanmartín *et al.*, 2008), which are exciting and promising for historical biogeography research. The model-based methods, importantly, as opposed to previous parsimony methods, provide the possibility of incorporating external data, such as palaeogeographical and palaeontological information (e.g. distance between areas or the fossil occurrence of a lineage in an area at a certain time).

The new methods provide more possibilities – but they also introduce a larger demand for accurate additional data. It is well known that the most important factor in molecular dating, regardless of the method used, is the quantity and quality of age constraints (e.g. Bremer *et al.*, 2004; Britton, 2005). It is a sensible assumption that biogeographical inferences are just as dependent on geological reconstructions and age constraints for obtaining reasonably reliable results. Ignoring fossil data hence leads to less well-constrained analyses and therefore to less reliable results.

Unfortunately, we feel that at present the geological processes (and their time-scale) that can lead to, for example, vicariance events are often being misjudged or over-simplified. For example, the actual split of continents is a long process involving several events, and the subsequent drifting will lead to vicariance on a continuous time-scale, varying for different organism groups. Furthermore, fossil records that can constrain and/or corroborate hypotheses are frequently overlooked. We believe that the great rigour and effort put into creating biological datasets needs to be extended to the use of the geological data that biogeographical inferences are dependent on.

Volcanic oceanic island chains, such as the Hawaiian and Macaronesian islands, are very commonly used as examples when exploring new biogeographical methods and models (e.g. Ree & Smith, 2008; Sanmartín *et al.*, 2008; Whittaker *et al.*, 2008). There are several good reasons for using Macaronesia as a test-bed system. There is a high degree of endemism on the islands, both within Macaronesia and between the islands, and the lineages can frequently be traced back to mainland Africa or the Mediterranean region. Furthermore, the litho- and chronostratigraphy of volcanic islands are often relatively well known, even though their history is quite complex (see e.g. Carracedo, 1999; Whittaker *et al.*, 2008, and references therein). In the absence of a fossil record, molecular dating of phylogenies relies on other, less reliable, temporal information. Some authors apply a strict molecular clock on 'average rates' from their own data, and others use ages or 'average rates' from other studies of organism groups (e.g. Kim *et al.*, 1996; Emerson, 2003; Caujapé-Castells, 2004; Oberprieler, 2005; Díaz-Pérez *et al.*, 2008). Some studies avoid absolute dating, or discuss relative dating results in the light of geological and climatological data (e.g. Navascués *et al.*, 2006). When geological information is used, it is based either on the date of the emergence of an island (e.g. Böhle *et al.*, 1996; Percy *et al.*, 2004; Kim *et al.*, 2008) or on a catastrophic event as a maximum age for a clade or the whole flora of an island (Emerson, 2003).

Maximum ages are always a problem in dating, as they in effect put a hard bound on a crown group's age (most dating methods do not allow for overriding constraints, that is, finding a solution outside the boundaries of the age constraints). As opposed to minimum ages they are not open to the possibility of a 'ghost range' (the time interval between the first fossil occurrence and the actual divergence) of as yet undiscovered fossils or a mistakenly calculated island age. When applied in biogeography, putting a maximum constraint on the crown-group node implicitly means there was one single colonization event, and diversification started immediately upon arrival. From these considerations it follows that an erroneous maximum age could cause underestimates of all divergence times in the phylogeny. In the case of the Canary Islands, where numerous (now submerged) seamounts allow for the existence of earlier islands, (e.g. Geldmacher *et al.*, 2001; Ancochea & Huertas, 2003), and when using the aerial age of Fuerteventura, the oldest island of today (21 Myr old), we are possibly severely underestimating the age of dispersal events of plant lineages from the mainland (e.g. the five plant groups dated by Kim *et al.*, 2008).

In this paper we explore two assumptions about oceanic volcanic islands in general, and about Gran Canaria in particular, of direct relevance to the biogeographical interpretation of island floras. First, we address the assumption that catastrophic volcanic events can potentially sterilize whole islands. We take as an example the development of the Roque Nublo stratocone volcano, which is suspected to have sterilized Gran Canaria *c.* 5.3–3.5 Ma. Second, we consider whether there is little or no chance of discovering informative (plant) fossils on volcanic islands (e.g. Whittaker *et al.*, 2008; Rodríguez-Sánchez *et al.*, 2009). In this paper we present direct evidence from the fossil record of Gran Canaria and other Macaronesian islands that disproves the second assumption and, in combination with an evaluation of the strata of the Roque Nublo group, sheds doubt on the first. This will provide valuable data for future research, both for empirical studies and for refining island biogeography models and assessing their validity.

ROQUE NUBLO AND THE STERILIZATION HYPOTHESIS

Early geology and windows of opportunity

The geology of Gran Canaria has been intensively studied for more than two centuries (Carracedo *et al.*, 2002). This has resulted in detailed accounts of the island's stratigraphy, a densely sampled isotope geochronology (e.g. Pérez-Torrado *et al.*, 1995, 1997; van den Bogaard & Schmincke, 1998; Guillou *et al.*, 2004) and the publication of detailed geological maps (e.g. Mapa Geologica de España, Instituto Geológico y Minero de España).

The early subaerial volcanism of Gran Canaria, following emergence at *c.* 14.5 Ma, commenced with a short (*c.* 0.5 Myr) basaltic shield-building phase (e.g. Schneider *et al.*, 2004) (Fig. 1a). Towards the end of this period the main shield volcano collapsed, forming the Caldera de Tejeda (e.g. van den
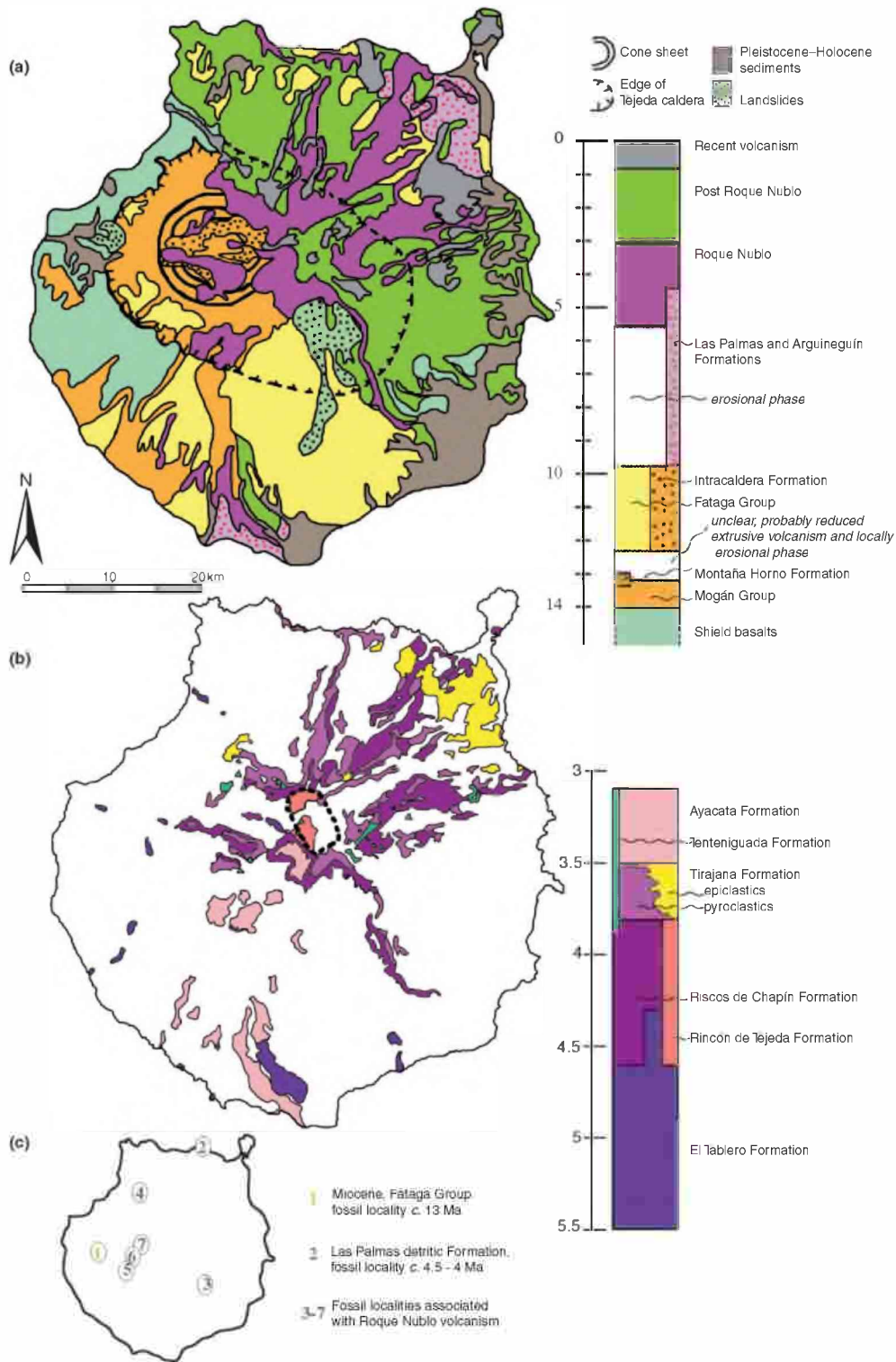
Figure 1 (a) Simplified map of the geology of Gran Canaria, showing the distribution of pre-Roque Nublo (Miocene), Roque Nublo (Pliocene) and post-Roque Nublo (Pliocene–Holocene) strata on Gran Canaria. The map is based on Carracedo *et al.* (2002); colours are mainly adopted from Mapa Geológico de España (Instituto Geológico y Minero de España) and (chrono)stratigraphy from van den Bogaard & Schmincke (1998). (b) Distribution of the main formations of the Roque Nublo Cycle. The map and stratigraphy are based on Pérez-Torrado *et al.* (1995); colours are mainly adopted from Mapa Geológico de España (Instituto Geológico y Minero de España), with chronostratigraphic synthesis from Pérez-Torrado *et al.* (1995), Guillou (2003) and Guillou *et al.* (2004). For a description of the various phases, see text. (c) The main areas with fossil localities described in this paper. 1, Barranco de Mogán–Azulejos; 2, Las Cuevas del Guincho; 3, Barranco de Tirajana; 4, Berrazales–El Hornillo; 5, Soria; 6, Embalse de Cueva de las Niñas, Pajonales; 7, Casa Forestal de Pajonales.

Bogaard & Schmincke, 1998). Post-caldera volcanism was characterized by intense and violent eruptions, resulting in large volumes of ignimbrites and silicic lavas. Two main magmatic phases, the Mogán Group (*c.* 14–13.3 Ma) and the Fataga Group (*c.* 12.4–9.9 Ma), were separated by the compositionally transitional Montaña Horno Formation (van den Bogaard & Schmincke, 1998). Hiatuses of *c.* 30–140 kyr between ignimbrite eruptions of the Mogán Group (evidenced by isotopic dating, erosional unconformities and soil formation; van den Bogaard & Schmincke, 1998) provided windows of opportunity for plant introductions from mainland Africa and the Mediterranean as well as from the older Canarian islands (Carine, 2005).

These earliest volcanic phases were followed by a long period of erosion (*c.* 3 Myr), with only minor eruptions on the northern slopes of the island. The erosion caused a radial pattern of deep barrancos, which controlled the distribution of the products of later volcanic activity (e.g Pérez-Torrado *et al.*, 1995). Large volumes of sediments formed by erosion were deposited predominantly in the south (Arguineguín Formation) and in the north-east (Las Palmas Detritic Formation) as well as off the coast (Schneider *et al.*, 1998). The long period of quiescence was followed by three further phases of volcanism: Roque Nublo, post-Roque Nublo and recent volcanism (Fig. 1a,b).

Extinction?

The hypothesis that Roque Nublo volcanism was a catastrophe that killed all life on Gran Canaria probably stems from the work of Hausen in 1962 (Rothe, 2008), and has since been used as the earliest possible age of (re-)introduction and evolution of the *laurisilva* and pine-forest communities, for example by Marrero & Francisco-Ortega (2001), Emerson (2003) and Whittaker *et al.* (2008). If this assumption is wrong (and we argue that it is) and is used as an age constraint for integrated phylogenetic dating and biogeography, the reconstructions will be erroneous. Indeed, the Roque Nublo volcanism was violent and protracted (lasting *c.* 2 Myr) and produced a volume of eruptive products estimated at *c.* 100–200 km^3 at an average eruption rate of 0.1 km^3 kyr^{-1}. However, as we demonstrate, the volcano did not erupt continuously throughout this interval. Distributions of the various formations of the Roque Nublo cycle provide evidence that at any one time during the evolution of the volcanic sequence, large areas of the island were relatively unaffected by volcanism. We envisage that early Roque Nublo volcanism was more likely to have been responsible for habitat fragmentation than for complete extinction. Below we present a synthesis of the evolution of the Roque Nublo cycle and how the various phases affected the flora of the island. The current distributions of the formations of the Roque Nublo sequence are illustrated in Fig. 1b (see also figure 2 in Pérez-Torrado *et al.*, 1995). The geographical extent and hypothetical geomorphology of the Roque Nublo stratocone prior to its gravitational collapse are provided in figure 4 of Pérez-Torrado *et al.* (1995).

The Roque Nublo event(s)

Broadly speaking, from *c.* 5.3 to 3.7 Ma volcanism was restricted to the development of scattered cinder cones (El Tablero Formation) and effusive (rather than explosive) basaltic lava flows (Riscos de Chapín Formation). Subsequently, from *c.* 3.7 to 3.1 Ma, more explosive volcanic activity (Tirajana Formation) built an asymmetrical stratovolcano cone with shallow northern and steep southern slopes, which at its maximum development was *c.* 2.5–3 km high (Pérez-Torrado *et al.*, 1995). The volcanic cone eventually became unstable, and in the period *c.* 3.5–3.1 Ma experienced large gravitational flank collapses that formed the Ayacata Formation (Funck & Schmincke, 1998; Guillou, 2003; Guillou *et al.*, 2004). The latest phase of activity, which was mainly intrusive, developed within the amphitheatre-shaped collapse scars between 3.11 and 2.87 Ma (Guillou *et al.*, 2004). The volcanic stratigraphy of the sequence is thus characterized by basaltic lava flows in its basal part, crudely bedded tuffaceous phonolitic rocks and breccia sheets interbedded with lava flows in its lower middle part, thick massive breccia sheets in its upper middle part, and a few small lava flows in its upper part (van den Bogaard & Schmincke, 1998).

Initial cinder-cone eruptions and basaltic lavas were of limited lateral extent, whereas later more voluminous basaltic lava flows were channelled down deep palaeo-*barrancos* (palaeo-valleys) (draining the north-east and eastern sectors of the island), which had formed in the volcanic hiatus prior to Roque Nublo volcanism (Pérez-Torrado *et al.*, 1997). Detailed observation of the evolution of the Roque Nublo sequence provides clear evidence for long periods of quiescence. The evolution of the chemical composition of Roque Nublo cycle volcanism, from basaltic to phonolitic, indicates magmatic differentiation of subvolcanic magma chambers. This process requires considerable periods of volcanic quiescence (e.g. Frisch & Schmincke, 1969). Isotopic dating of the volcanic sequence, although not complete at a flow-by-flow level, indicates that hiatuses in volcanic activity in any one location were of the order of tens of thousands of years (e.g. Pérez-Torrado *et al.*, 1995; van den Bogaard & Schmincke, 1998; Guillou *et al.*, 2004). Both geographical localisation of the deposition of volcanic products and hiatuses would appear to allow ecosystem recovery. Only two phases of the Roque Nublo sequence, the emplacement of the Tirajana Formation ignimbrites and the massive Ayacata Formation flank collapses, appear to be of such magnitude that they might plausibly have led to an island-wide extinction event. As detailed below, we consider that even these dramatic events would fail to cause mass extinctions.

Potentially catastrophic eruptions

The Roque Nublo ignimbrites (Tirajana Formation) originated from hydrovolcanic eruptions as rising magma came into contact with groundwater at high levels in the crust (Pérez-Torrado *et al.*, 1997). Eruptions originated from multiple

successive vents with estimated diameters of *c.* 300 m. Successive eruptions broke through closed vents created by magma solidification in the vent conduits of preceding eruptions (Pérez-Torrado *et al.*, 1997). The relatively wide vents together with the incorporation of rock components from the old vent conduits meant that the volcano could not sustain vertically buoyant eruption columns, and instead eruptions were characterized by tephra fountains (Pérez-Torrado *et al.*, 1997). Ignimbrite flows originating from these vents contained a lot of water and were relatively cool (*c.* 300 °C in proximal areas, but dropping below 100 °C distally). During initial eruptions, ignimbrites were confined to palaeo-*barrancos* (Pérez-Torrado *et al.*, 1995). Between valley systems, the ridges and plateaus were relatively unaffected by volcanic deposition, as during the preceding basaltic activity. Where *barrancos* broadened close to the palaeo-coast, ignimbrite flow deposits thinned to *c.* 2 m, and the separation of water and rock components produced lahar-like flows (Pérez-Torrado *et al.*, 1997). Unconformities and conglomerates interbedded within the ignimbrites in these areas provide evidence of quiescent periods between eruptive events (Pérez-Torrado *et al.*, 1997). As volcanism continued, *barrancos* were eventually filled and overtopped. Volcanic material then formed broad aprons that extended from the Roque Nublo crater area chiefly to the northern half of the island (Funck & Schmincke, 1998). The location and asymmetry of the cone formed during this period (Pérez-Torrado *et al.*, 1995) again allowed large sectors of the island to remain as viable habitat.

Potentially catastrophic collapses

The Roque Nublo stratovolcano was subject to at least three collapse events (Ayacata Formation), which are separated chronologically and stratigraphically by periods of scarp erosion and volcano regrowth (Carracedo & Day, 2002). These collapses were of only moderate size (estimated volumes of the order of 20–70 km^3) and dominantly affected the south and west of the island (Carracedo & Day, 2002). The largest collapse (affecting the south flank at *c.* 3.5 Ma; Funck & Schmincke, 1998) locally filled *barrancos* with up to 500 m of avalanche debris, as well as depositing thinner debris layers on intervening plateau surfaces. However, mountain crest/ridge environments remained debris-free (Mehl & Schmincke, 1999). Toreva blocks (kilometre-scale mega-blocks that retain their internal stratigraphy) were rafted laterally (1–2 km) during the collapse event but underwent only minor rotation (e.g. Belousov *et al.*, 2001). The geometry of sector-collapses allows large geographic areas of the island to remain unscathed following each event, and stratigraphical intervals between collapses provide time for vegetation recovery.

Survival

In summary, Roque Nublo volcanism was protracted and in part violent. However, the volcano did not continuously erupt (either violently or effusively) during this interval (e.g. Pérez-

Torrado *et al.*, 1997), and no single pyroclastic eruption is implicated as devastating the entire island. We see ample evidence both in the volcanic rock record and in the geometry of debris avalanche deposits for the survival of very broad and diverse habitats and ecosystems throughout the Roque Nublo cycle. Although the flora of the island did face many challenges, leading to random survival and mosaic habitats, a complete extinction of all species on the island seems impossible.

To date, geologists and biologists are unsure of the extent to which the island's biota was affected. It would be incorrect to suggest that all papers referring to the Roque Nublo eruptions as killing Gran Canaria's vegetation assume complete extinction. Navascués *et al.* (2006), in addressing the extinction of pine forests, suggested the possibility of a few ridge-top refugia from which recolonization could occur. Araña & Carracedo (1980) took the view that all the vegetation of the island went extinct, although there was a possibility that some coastal species managed to survive. Marrero & Francisco-Ortega (2001) estimated an approximate extinction rate of 50% if volcanism comparable to Roque Nublo were to occur today.

FOSSIL FLORAS OF GRAN CANARIA

The published fossil record of Gran Canaria, to date, comprises floras that, although pointing to diverse vegetation on the island throughout the Neogene, are confined to only rudimentary plant descriptions (Schmincke, 1967, 1968; García-Talavera *et al.*, 1995; Pérez-Torrado *et al.*, 1995; Schneider *et al.*, 2004). In order to address this we have reinvestigated previously published localities, and explored additional potential palaeobotanical targets, for example unconformities with evidence for subaerial weathering, soil/palaeosoil formation and epiclastic (re-worked volcanics) and clastic sediments (fluvial, alluvial and lacustrine). This has yielded *c.* 30 plant fossil horizons of Miocene–Pliocene age; that is, fossils from both before and during the Roque Nublo cycle. The localities are spread around the island, and represent several different vegetation types. Below we summarize the main findings and localities in a broadly chronological order.

Miocene thermophilous scrubland

García-Talavera *et al.* (1995) briefly described a Miocene flora from the Barranco de Mogán, south-western Gran Canaria. The flora pre-dates Roque Nublo, and occurs in the Montaña Horno Formation, which is bracketed between the Mogán and Fataga Groups and dates to *c.* 13.3–13.0 Ma.

The fossil twigs, leaves and fruits were not described in detail, but some tendencies were distinguished. The four leaf morphotypes described were all small and suggested to have been leathery, belonging to smaller shrubs. This was indicative of palaeo-vegetation adapted to semi-arid conditions and characteristic of the present scrub on drier slopes and *barrancos* of the Canary Islands. The authors listed extant taxa of these environments, for example *Bystropogon*, *Chamaecytisus*,

Echium, *Cistus*, *Carlina*, *Maytenus* and *Kleinia*, but did not make direct morphological/anatomical comparisons that would indicate possible taxonomic affinities of the fossil material.

We investigated further exposures within the same stratigraphic interval (but located further to the WNW, locality 1 in Fig. 1c). Here, ash and tuff fall-deposits subjected to later epithermal alteration contain at least 10 leaf morphotypes preserved as moulds and by carbonate permineralization (see Figs S1 & S2 in Supporting Information). Some of these appear to correspond morphologically to the four illustrated by García-Talavera *et al.* (1995).

Based on leaf morphology, the overall assemblage appears to be dominated by leaves of the large woody eudicots characteristic of the present-day thermophilous scrub vegetation. Venation and cuticular patterns are most often preserved, but cell structures are less common. Based on leaf morphology and initial microscopic examinations of venation and epidermal characters we note morphological similarities between the fossil leaves and some of the genera mentioned by García-Talavera *et al.* (1995), and possibly also *Euphorbia* and Crassulaceae. However, detailed anatomical investigations of material from both fossil localities are required for correct phylogenetic placement.

Laurisilva vegetation transported by lahar-like flows and deposited at Las Cuevas del Guincho

The Las Cuevas del Guincho coastal section (locality 2 in Fig. 1c) exposes the Middle Member of the Las Palmas Detritic Formation (Schneider *et al.*, 2004) formed between *c.* 4.5 and 4 Ma (Pérez-Torrado *et al.*, 2002). This dominantly sedimentary unit was formed by the accumulation of volcanic and debris-flow materials around the north-east margin of the Roque Nublo stratovolcano. The flora here includes disarticulated and fragmentary leaves, and twigs and fruits that have been transported by lahar-like flows. The leaves are preserved as moulds and compressions and by permineralization, often with detailed cuticular patterns and cell structures (see Fig. S3). As yet we have no secure taxonomic descriptions for our material, but at least 10 distinct leaf morphotypes of eudicots and Lauraceae can be distinguished. Several different monocot leaves are also present, and at least one fern. Coarse conglomeratic horizons in the area contain abundant evidence of entrained vegetation, including tree trunk moulds and permineralized wood fragments.

The Pliocene thermophilous scrub of Barranco de Tirajana

Deposits relating to the earliest explosive phase of the Roque Nublo stratovolcano preserve perhaps the most dramatic evidence of volcanism impacting upon vegetation. Pérez-Torrado *et al.* (1995) reported a fossiliferous pyroclastic agglomerate that lies directly above a lava flow dated at *c.* 3.9 Ma. It locally marks the base of the Tirajana Formation

and can be traced for 7 km along the Tirajana valley (southeast of the central stratovolcano) (locality 3 in Fig. 1c). The agglomerate has abundant vegetation impressions at various places along its base. Reinvestigations of this section have revealed the presence of a diverse flora comprising abundant fragmentary leaves and trunk and branch moulds, less common permineralized branch/trunk fragments, plus less frequent articulated eudicot foliar branches and palm fronds. Based on morphology, and initial optical- and scanning-electron-microscope investigations of anatomical features, the articulated specimens appear to represent *Euphorbia* (Fig. 2a,b) and Arecaceae (*Phoenix*) (Fig. 2c,d). External moulds of woody stems and branches from the locality are often collapsed; however, three-dimensional examples with faithful replication of stem features such as ribs, leaf/branch scars and protuberances are not uncommon. At least four stem morphotypes with morphological features comparable to the large woody perennial shrubs that are typical of Macaronesian thermophilous scrubland are present (see Fig. S4).

Tetraclinis forests and *laurisilva* of Berrazales–El Hornillo, Pajonales and Soria

The volcanologist Hans Ulrich Schmincke was the first to discover and describe a Miocene–Pliocene flora on Gran Canaria (Schmincke, 1967, 1968). He reported several localities with well-preserved twigs and leaves, and even 10-m-long tree trunks that were associated mainly with the Roque Nublo breccias (Tirajana/Ayacata Formations). Two specific localities were mentioned. At Berrazales, small dolomitized stems were found, often with root or shoot scars and cellular preservation. At Pajonales he described well-preserved leaves of laurel-like plants and impression fossils reminiscent of palm leaves, and stems from a 'bamboo-like' plant.

In the Berrazales area we investigated extensive fossiliferous deposits occurring in the valley to the north and east of El Hornillo (locality 4 in Fig. 1c). Here, a sedimentary sequence 60–100 m thick comprises coarse boulder conglomerates above a landscape unconformity cut into early Roque Nublo basaltic lavas and felsic to rhyolitic ashes, ignimbrites and lavas of the Miocene Fataga Group. The sedimentary sequence is mapped as the epiclastic member of the Tirajana Formation and is thus younger than *c.* 3.9 Ma (Pérez-Torrado *et al.*, 1995). Towards the top it is dominated by fluvial channel conglomerates, gravels, sands and silts. The fluvial sequence is capped by rubble-based basaltic lavas related to the post-Roque Nublo rift volcanism. The latter commenced *c.* 3.5 Ma, but in the Berrazales area appears to have been active in the period *c.* 2.7–1.7 Ma (Guillou *et al.*, 2004). Typically, plants occur as casts/moulds of *in situ* tree stumps with associated prostrate logs within coarse breccias. Sediments within moulds that fill the cavity created by the decay of trunks/branches often contain taxonomically identifiable permineralized wood and bark fragments. *In situ* and in-growth-position stumps are particularly common directly above the unconformity between early Roque Nublo basaltic lavas within the El Hornillo valley.
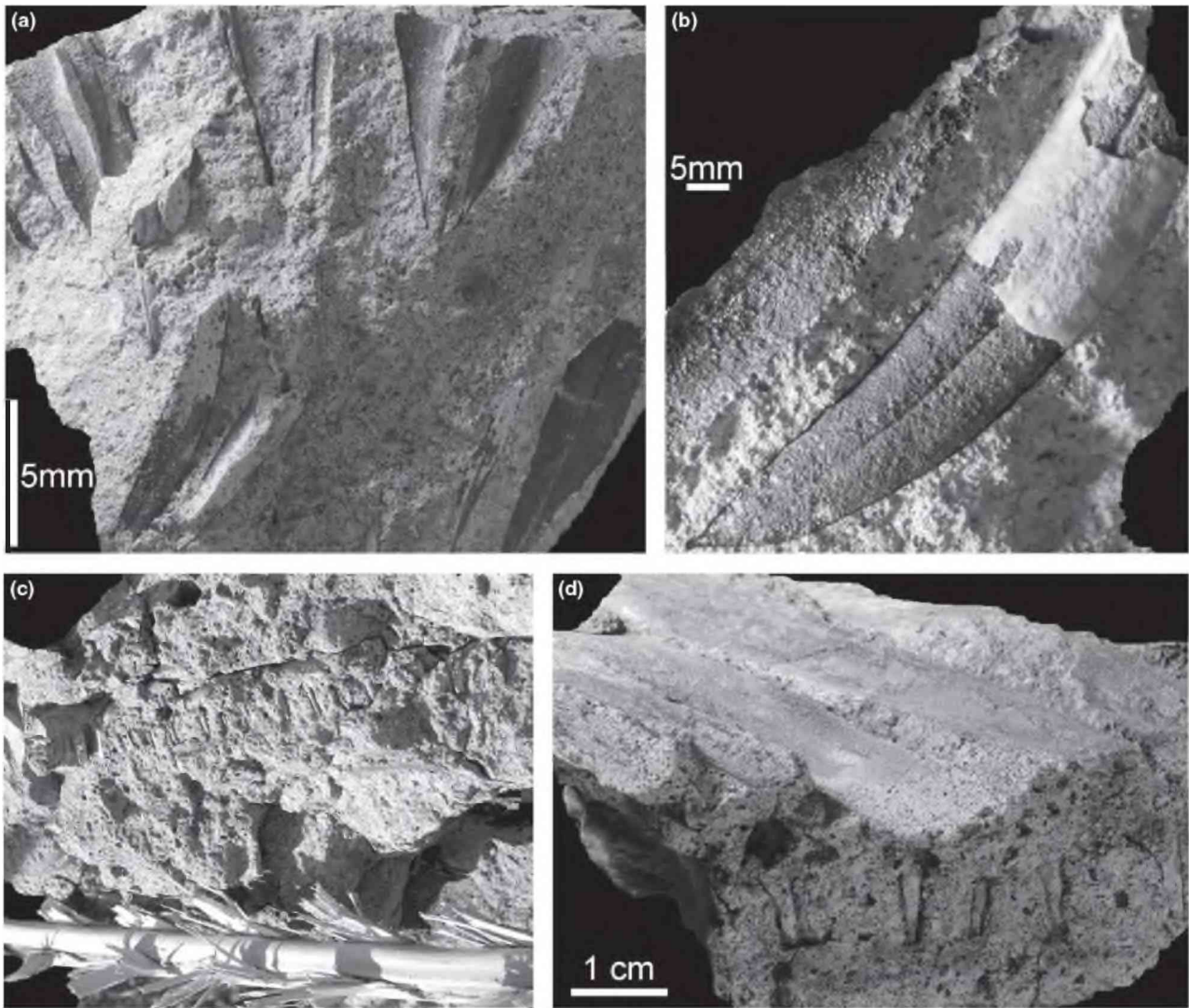
Figure 2 Fossils from Barranco de Tirajana (locality 3, Fig. 1c). (a) Articulated leaves of *Euphorbia* preserved as moulds with partial carbonate permineralization of tissues. The leaf arrangement in rosette-like groups is reminiscent of several *Euphorbia* species that have rosettes at the tip of branches and inhabit the thermophilous scrubland of today. (b) Detail of leaf with prominent mid-vein and partially permineralized epidermis. (c) Field photograph of fossil rachis of a palmate palm frond. The rachis is triangular in cross-section, with near-parallel pairs of leaflet/pinnae attachment point scars. These are orientated almost perpendicularly to the rachis long axis. The parallel configuration of scars indicates the former presence of tightly longitudinally folded pinnae. A dried rachis of the frond of *Phoenix canariensis* acts as a scale. (d) Block with rachis mould on front face and strap-like pinnae with parallel venation on top surface.

At this and many other localities, carbonate permineralized root systems are observed to encrust the weathered top and vertical fissure/joint surfaces of the basaltic lavas below the unconformity. Transported trunks (Fig. 3a), branches (Fig. 3b), twigs, leaves (Fig. 4a–f), fruits/capsules (of Lauraceae and/or eudicots) (Fig. S5), and monocot stems and leaves are common within the finer-grained fluvial sediments above the basal conglomerates. Cellular preservation of wood, bark and leaf tissues by carbonate permineralization is common throughout the El Hornillo sequence (Figs 3 & 4). Within silt lenses, leaves are preserved as external moulds (Fig. 4a), sometimes lined with clays, with partially permineralized veins. Laterally extensive horizons containing iron-stained tubes with

dominantly vertical orientations mark probable root horizons that occur at various levels throughout the section.

The leaf assemblage, often with well-preserved morphology, leaf venation and cuticular characters, appears to be dominated by members of the broad-leaved sclerophyllous genera of today's Macaronesian *laurisilva*. Preliminary interpretations, yet to be confirmed, include genera of Lauraceae, and the eudicot genera *Arbutus* (Ericaceae) (Fig. 4c,e), *Ilex* (Aquifoliaceae) (Fig. 4b,d) and *Hedera* (Araliaceae). Articulated permineralized fern fronds, possibly of the genus *Asplenium*, are less common elements of the flora (Fig. 3g,h).

Wood fragments (Fig. 3e,f) include the gymnosperm *Tetraclinis* (Cupressaceae). This conifer was an element of
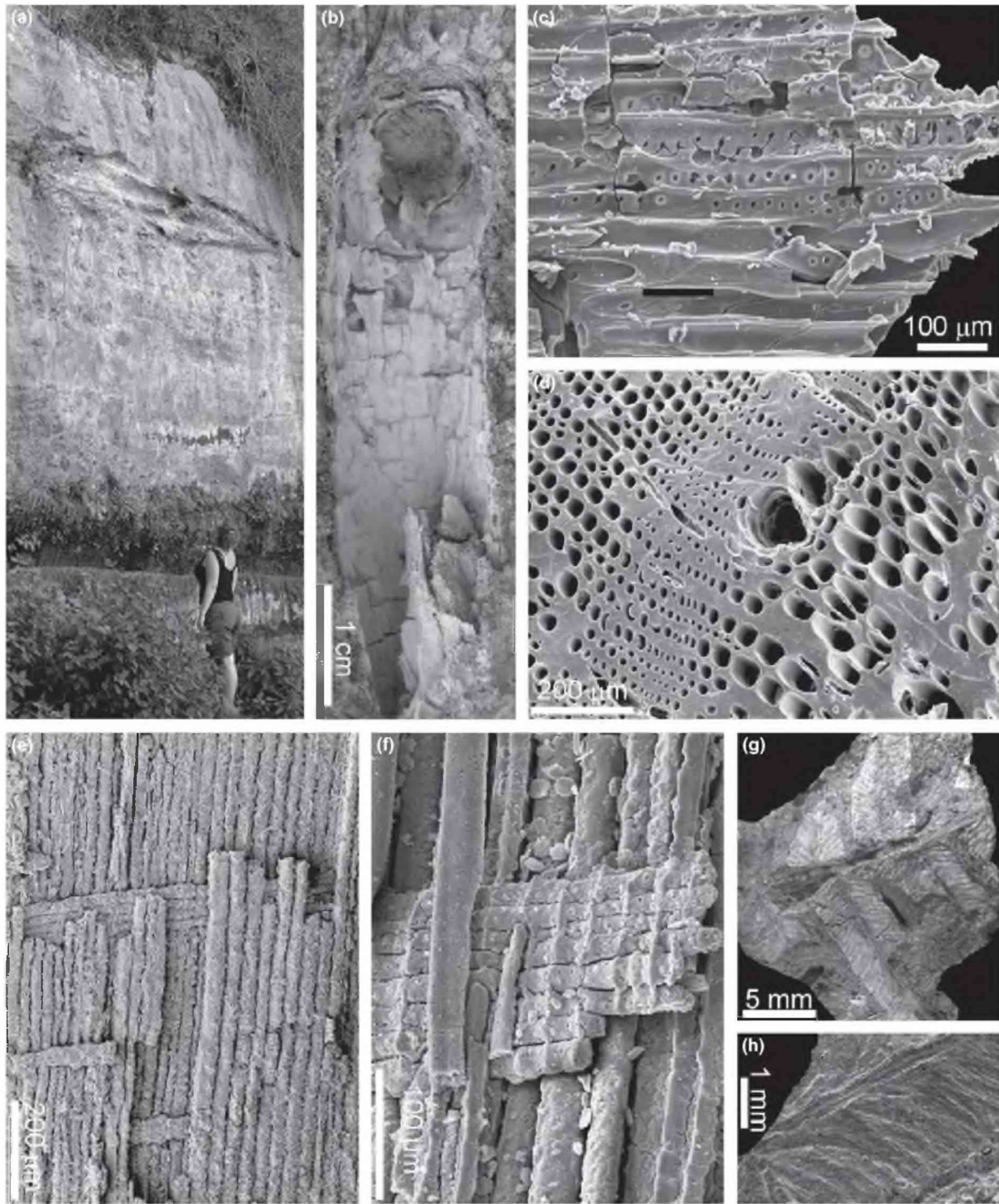
Figure 3 (a–f) Typical field and microscopic features of Pliocene wood of the Roque Nublo Cycle, Gran Canaria. (a) Coarse epiclastic sediments with large, transported, branching trunk preserved as external mould. El Hornillo (locality 4, Fig. 1c) (road section). (b) Partially permineralized branch fragment. Typical preservation includes permineralized wood plus bark. El Hornillo (Berrazales area). (c,d) Char-coalified *Pinus* wood. Forestal de Pajonales area (locality 7, Fig. 1c). (c) Longitudinal fracture-section illustrating tracheids with bi-, but dominantly uni-seriate bordered pits. (d) Transverse section showing transition from early to late wood and resin duct. (e,f) Radial sections of carbonate permineralized conifer wood cf. *Tetraclinis*. El Hornillo (road section). (e) Tracheids with files of uni-seriate bordered pits and rays (two cells high). (f) Ray (eight cells high) with cupressoid crossfield pitting. (g,h) Fragmentary pinnate fern, possibly of the genus *Asplenium*. El Hornillo (road section). (g) The pinnae alternate along the rachis. Pinnae are unstalked, longer than their width, slightly asymmetrical and 'eared' towards the base. Margins are smooth. Veins are mostly simple, sometimes forked. (h) Scanning electron microscope detail of pinnule surface, showing the main venation that bifurcates down to the ear and along the rest of the pinnule.
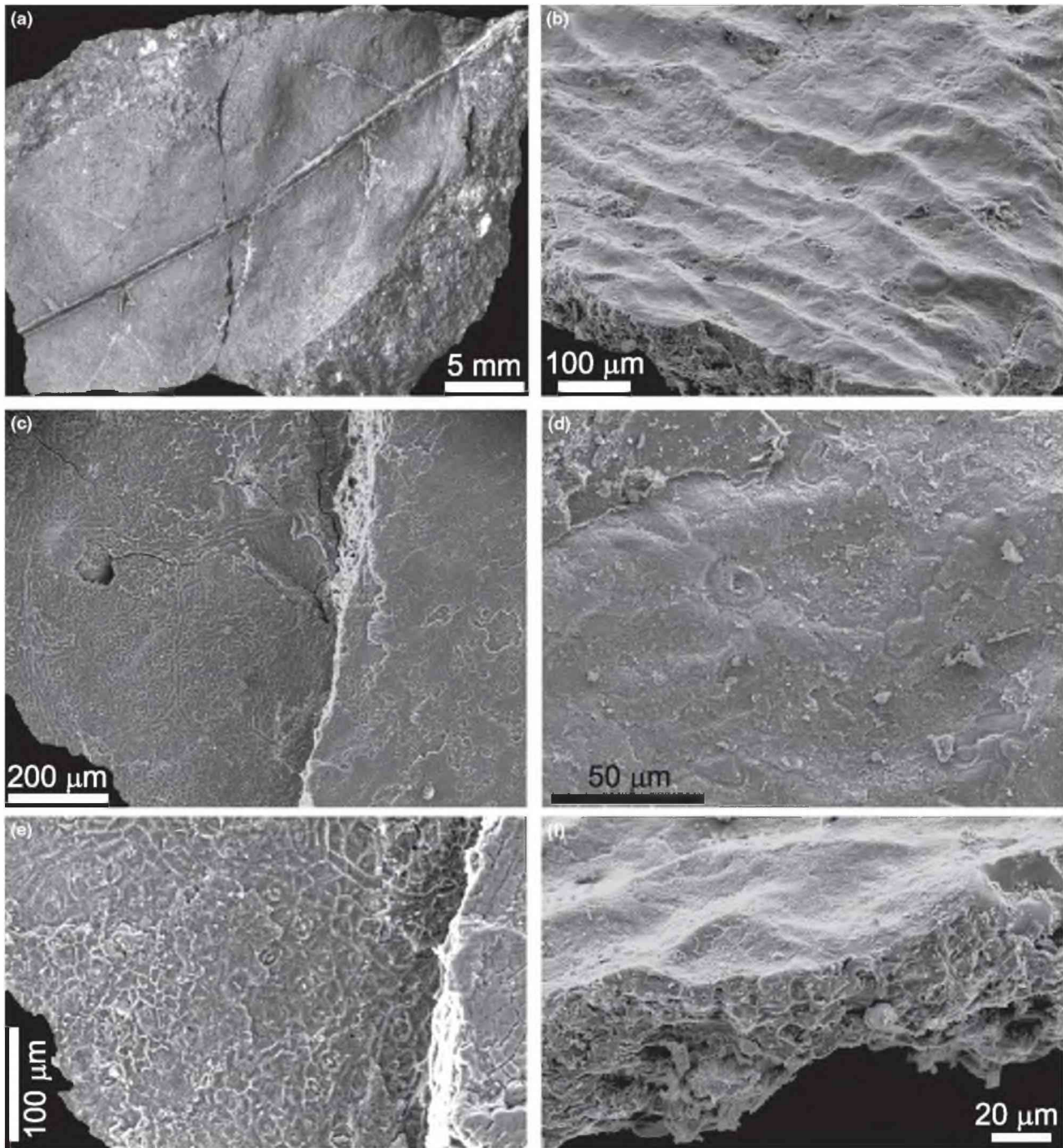
Figure 4 Typical preservation features of lauraceous and eudicot leaves from the El Hornillo–Berrazales area (locality 4 in Fig. 1). (a) Leaf specimen (cf. *Ocotea*) with preserved mid rib, petiole, parts of smooth margin and net venation. (c,e) Carbonate permineralized eudicot leaf (cf. *Arbutus*) with axial and abaxial surfaces exposed. (c) Abaxial surface (left side of image) with epidermal cells and stomata between polygonal vein network. Adaxial surface (right side of image) lacks stomata. (e) Detail of abaxial epidermis, polygonal epidermal cells and numerous stomata. (b,d) Carbonate permineralized leaf (cf. *Ilex*) with preservation of cuticular and epidermal features. (d) Epidermis with stomata and lobed epidermal cells. (f) Transverse section through leaf illustrating anatomical preservation.

the widespread European *laurisilva* during the Palaeogene, but became almost extinct during the Neogene climate change (e.g. Kvaček *et al.*, 2000; Kvaček, 2007, and references therein). The presence of Pliocene *Tetraclinis* fossils therefore suggests a more humid climate on Gran Canaria at this time. Today

relict populations occur in Malta, south-east Spain and north-west Africa. This is the first evidence that this genus had a distribution that included Macaronesia. It also appears to be the first direct palaeobotanical evidence of extinction on Gran Canaria.

Tetraclinis wood and evidence of *laurisilva* genera have also been observed at further localities to the south within deposits mapped as Roque Nublo collapse deposits (Ayacata Formation), for example around Soria (locality 5 in Fig. 1c) and Embalse de Cueva de las Niñas in the Pajonales area (locality 6 in Fig. 1c).

The pine forest of Pajonales

The Pajonales area has extensive exposures of Roque Nublo volcanic breccias (Tirajana Formation) and landslide deposits (Ayacata Formation) occurring within palaeo-*barrancos* cut into Middle Miocene ashes, tuffs and ignimbrites. Small outcrops of fluvial conglomerates and cross-bedded sands containing pods of silts are preserved within shallow (*c.* 20-m-deep) valleys between the two volcanic units.

In one fossil locality in Forestal de Pajonales (locality 7 in Fig. 1), at about 1400-m altitude, charcoalified *Pinus* wood (Fig. 3c,d) occurs within Roque Nublo volcaniclastics. We speculate that this locality belongs to another ecosystem, resembling the pine-dominated high-altitude forests of today. The *Pinus* wood has abundant epithelial cells surrounding resin ducts, which may suggest affinity with the only indigenous species of the genus present in the western islands of Macaronesia, the endemic *Pinus canariensis*. Other outcrops in Forestal de Pajonales have yielded, as yet unidentified, charcoalified plant fragments, probable monocot stems, partially dolomite permineralized wood and twigs plus root horizons.

FURTHER MACARONESIAN FOSSIL FLORAS AND POTENTIALLY FOSSILIFEROUS STRATA

It is fair to say that fossil floras of the Macaronesian oceanic volcanic islands are so far virtually unexplored. However, the absence of a fossil record is far from reality, and plant remains have been reported from several Macaronesian islands beside Gran Canaria. We briefly review records from other Canary Islands, Madeira and Azores in Appendix S1.

What we have learned from our initial explorations of Gran Canaria is that the volcanism of the Macaronesian islands has a much greater potential for fossilization than was previously thought. Good potential targets include islands that had protracted subaerial volcanic development phases punctuated by erosional episodes. We believe that many fossil localities are waiting to be discovered.

IMPLICATIONS

It could be argued that the fossils we have recorded are those of plants killed in events leading to the 'sterilization' of Gran Canaria (Emerson, 2003). However, we have observed evidence of plant growth in the form of *in situ* stumps of trees and root horizons at many localities. These, and the presence of numerous stacked plant fossil horizons containing transported but taxonomically similar plants, to us instead represent the persistence of vegetation through the period. Equally it could be argued that we are recording successive waves of recolonization from other islands, as would be anticipated if sterilization had occurred (Carine, 2005). However, we see little evidence of floral turnover, because in localities with stacked fossil horizons contained within sediments derived from the same source region, the same vegetation returns following each destructive event.

Palaeobotanical exploration of Gran Canaria is in its rather belated infancy (given that the first report of fossils is from the late 1960s). Already an emerging picture provides evidence that three ecosystems typical of the Canary Islands now were also present during the Mio-Pliocene. *Laurisilva* and *Pinus*-dominated forest ecosystems were present on Gran Canaria during major late Miocene/early Pliocene volcanic events, supporting the concept of these elements of the island's flora as Miocene relicts (Vargas, 2007). At lower elevations, sclerophyllous scrub vegetation was most probably present during the Miocene. As of today, however, these observations are insufficient to pinpoint the clearly intricate patterns of vegetation evolution and historical biogeography that biologists are trying to elucidate (Rodríguez-Sánchez *et al.*, 2009). Further research (particularly relating to plant taxonomy and taphonomy) is clearly needed to address these and the countless other questions that the presence of a fossil flora is bound to raise.

If our tentative interpretations of plant genera gain support from further investigations, this could push back the age of the introduction of several plant lineages in Gran Canaria, when compared to molecular clock studies using island ages (e.g. *Aeonium*, Kim *et al.*, 2008; *Echium*, Mansion *et al.*, 2009) or the Roque Nublo extinction hypothesis as age constraints. Future studies of pre-existing collections and new discoveries should provide important data for inferences of phylogeography and biogeography.

One major problem when reconstructing Canary Island biogeography is the large numbers of probable extinctions on Lanzarote and Fuerteventura. These islands have undergone extensive erosion, and have therefore lost many potential habitats. The endemic pine forests and *laurisilva* might have been there when the islands still had high mountains, which are necessary for the moist north-east winds to drop their rain. Some of the biogeographical patterns we recognize through molecular phylogenies are most probably obscured by these extinctions. Several phylogenies suggest that numerous plant groups have spread from the mainland to Tenerife or Gran Canaria and then westwards (e.g. *Adenocarpus*, Percy & Cronk, 2002; *Bystropogon*, Trusty *et al.*, 2005; *Descurania*, Goodson *et al.*, 2006; *Cistus*, Guzmán & Vargas, 2009), whereas in reality they might have spread from the mainland to the eastern islands much longer ago. It is notable that the plant groups exhibiting this pattern often have a preference for higher-altitude habitats. The highly eroded Selvagens archipelago is *c.* 30 Myr old, and the Dacia seamount, which is regarded as a former island, is in the age range *c.* 9–47 Ma. Numerous other seamounts allow for the possibility that several other Maca-

ronesian islands with overlapping ages have existed (e.g. Geldmacher *et al.*, 2001, 2005). One implication of this is that the *laurisilva* could actually be a 'true ancient' flora, contemporary with the large European distribution of this ecosystem before the Miocene–Pliocene climate changes, rather than a more recent element (see references in e.g. Vargas, 2007; and Rodríguez-Sánchez *et al.*, 2009). When using the aerial age of Fuerteventura, the oldest island of today (21 Myr old), we are possibly severely underestimating the dispersal of Macaronesian plant lineages from the mainland.

We hope that this report will generate further palaeontological and palynological interest in Macaronesia. So often within our separate disciplines we hold key data/knowledge for others, but frequently we do not manage to integrate them. With the new methods in historical biogeography we not only can, but should begin to, integrate the fossil and rock records with phylogenetics, molecular dating and biogeography.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 A brief review of further Macaronesian fossil floras and potentially fossiliferous strata.

Figures S1 and S2 Leaf morphotypes of the Miocene thermophilous flora WNW of Barranco de Mogán/Azulejos.

Figure S3 Las Cuevas del Guincho *laurisilva* vegetation transported by lahar-like flows. Examples of preservation of twigs, wood, and leaf cuticles.

Figure S4 Anatomical and taphonomical features of stem morphotypes from Pliocene thermophilous scrub of Barranco de Tirajana.

Figure S5 Unidentified infructescence and unidentified fruit/seed from El Hornillo.

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