



# Phytoliths from modern plants in the Canary Islands as a reference for the reconstruction of long-term vegetation change and culture-environment interactions

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## Abstract

The Canary Islands were the first part of the Macaronesian archipelago to have been settled by humans. The various ways in which the indigenous inhabitants and later European colonisers interacted with the native and endemic flora is a central topic for archaeologists, geographers and ecologists. Floristic changes can be studied from phytoliths which are plant microfossils with a high potential for preservation in sediment deposits and they can help reconstruct past ways of life and vegetation changes through time. However, there is no comprehensive and systematic study and reference collection of phytoliths produced by the flora of the Canary Islands, so far. To make a start with a first phytolith reference collection of a selection of plants relevant for the study of past socio-ecological interactions there, we processed over a hundred modern plant specimens collected on the islands of Tenerife, Gran Canaria and La Palma to obtain the phytoliths from them, using the dry-ashing method. We then described the phytolith morphologies, and counted the numbers of morphotypes for each species. We have categorised taxa according to their phytolith concentration and production of morphotypes with diagnostic potential. Our results suggest that among the selected taxa, species within the Arecaceae, Boraginaceae, Cyperaceae, Poaceae and Urticaceae families are the main native producers of phytoliths in the archipelago. We also identified phytoliths with diagnostic potential in particular species within the Asteraceae, Brassicaceae, Cistaceae, Euphorbiaceae, Lamiaceae, Lauraceae, Ranunculaceae and Rubiaceae. We discuss how phytolith assemblages can be interpreted in archaeological sites and sediment records. Our growing reference collection is a significant step towards the application of phytolith analysis to disentangle the long-term climatic and human-driven transformation of this biodiversity hotspot, as well as the cultural use of plant resources.

**Keywords** Archaeobotany · Islands · Macaronesia · Palaeoecology · Phytoliths · Reference collection

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## Introduction

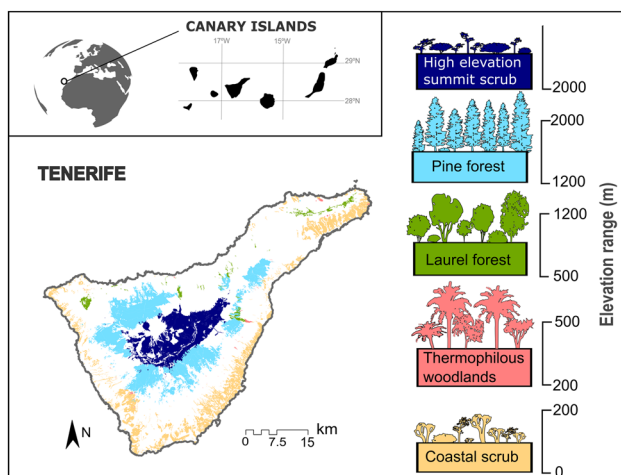
Islands in the Atlantic have been colonised during the late Holocene by African and European populations, resulting in various histories of adaptation to, and transformation and degradation of ecosystems there (Norder et al. 2020; Castilla-Beltrán et al. 2021; Raposeiro et al. 2021). The Canary Islands saw the arrival of humans ca. 2,000 years ago and were settled by people who developed their ways of life there based on crops and domesticated animals brought from the mainland of Africa, as well as using the resources of the islands, including endemic and native plants and animals (Morales et al. 2009; de Nascimento et al. 2020). There are many unanswered questions regarding how the indigenous inhabitants and then the European colonisers shaped the landscapes of these islands. Archaeology and palaeoecology can reveal particular relationships between cultural practices and adaptation to environmental change, as well as the human role in landscape degradation and extinctions of taxa.

The Canary Islands are situated off the northwest coast of Africa, Fuerteventura being just 96 km away from there (Fig. 1). This island group comprises seven islands, four islets and many rocks that vary in climate and height, from the dryer and lower eastern islands of Lanzarote and Fuerteventura to the higher and more ecologically diverse central and western islands of Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro. These islands display an outstanding habitat diversity, with an array of ecosystems that include coastal desert scrub, Mediterranean thermophilous woodlands, subtropical cloud forests, high altitude coniferous forests and scrub above the tree line (Fernández-Palacios et al. 2021). The varied environments

of the Canary Islands together with their isolation for more than 20 million years has created a considerable diversity of flora and fauna, with very many taxa found nowhere else, including over 650 endemic vascular plant species (Arechavaleta et al. 2010).

Upon the first colonization of the Canary Islands, humans introduced a series of domestic plants and animals, elements of a transported landscape directly brought from northwest Africa. Ethnohistorical and archaeological sources have confirmed the introduction of *Capra aegagrus hircus* (feral goats), *Ovis orientalis aries* (sheep), *Sus scrofa domestica* (pigs) and *Canis familiaris* (dogs), as well as cereals such as *Hordeum vulgare* (barley) and *Triticum durum* (hard wheat), legumes such as *Lens culinaris* (lentil), *Vicia faba* (faba bean) and *Pisum sativum* (pea), together with fruit trees such as *Ficus carica* (fig) (Machado Yanes 2007; Morales et al. 2009). While the herding of livestock has been proven to be a major subsistence activity among the indigenous populations, evidence of agriculture has also been found on all the islands (Morales and Gil 2014b; Hagenblad and Morales 2020; Morales et al. 2023). Abundant resources for various purposes were also provided by native taxa. Current knowledge on the use of plant resources by indigenous people is mainly limited to seed and charcoal analyses (Morales et al. 2021; Vidal-Matutano et al. 2021b). In comparison, there has been little study of the micro-botanical remains such as pollen, phytoliths and starch grains from archaeological contexts.

Palaeoecological research on the Canary Islands has followed two main lines of investigation, 1, the effect of climate changes on the vegetation, causing ecosystems to move to a different altitude or changing the composition of taxa over time; and 2, the effects of the arrival of humans on the vegetation. This has been studied from proxy evidence such as fossil pollen and macro- and microcharcoal particles stored in natural basins such as former lakes or small volcanic calderas (de Nascimento et al. 2009, 2016; Nogué et al. 2013; Ravazzi et al. 2021). These proxies, however, come with various biases. First, many plants are insect pollinated, and their pollen production and dispersal are low (de Nascimento et al. 2015; Nogué et al. 2022). Second, the persistent north-easterly trade winds blowing in these latitudes may carry pollen to the islands from ecosystems on the mainland of the Maghreb, Sahara or the Iberian Peninsula, so that the pollen detected on the Canary Islands may include some extra-regional components (Hooghiemstra et al. 2006). Phytoliths are not as easily transported by wind as pollen grains, and are thus less likely to travel long distances (Piperno 2006, p 21). Finally, pollen preservation conditions on the Canary Islands can be poor due to a lack of permanent water, oxidation and the coarseness of the sediments. In contrast, the volcanic soils show great potential for phytolith preservation (Delmelle et al. 2015), as they are generally acidic, varying



**Fig. 1** Inset, location of the Canary Islands. Main figure, Tenerife, current vegetation map including the windward zonal vegetation and its schematic altitudinal distribution (del Arco 2006)

from pH 5 to 7, only vertisols being slightly alkaline at around pH 8 (Fernández-Caldas et al. 1978).

Due to the large number of endemics in the native vascular flora of the Canary Islands, up to 50% (Fernández-Palacios et al. 2021), a specific modern phytolith reference collection is needed. Also, some taxa on the islands are affected by a ‘secondary island woodiness’ process, by which herbaceous taxa which arrive from the mainland in time become woody on islands (Lens et al. 2013; Zizka et al. 2022), potentially producing phytoliths that differ from their mainland relatives. Few studies have so far attempted to provide an understanding of phytoliths in plants and soils in Macaronesia. The first ones were archaeological (Afonso Vargas 2004, 2009, 2012) and another had an ecological and palaeoecological perspective, with selected morphotypes uploaded to the PhytCore online database, such as *Brachypodium distachyon*, *Bromus rubens*, *Cenchrus ciliaris* and *Sonchus oleraceus* (PhytCore 2022; Andréu Diez 2017). However, the preparation of a detailed quantitative and qualitative reference collection of phytoliths is fundamental for understanding their production by the plants of the islands and is still lacking. Here we build upon previous work to expand knowledge of phytolith production in a selection of plants relevant for the study of past socio-ecological interactions in the Canary Islands. We aim to provide a systematic quantification of morphotypes in 109 taxa of all major terrestrial ecosystems of this archipelago, including coastal scrub, thermophilous woodlands, laurel forest, pine forests on moister windward slopes or thinner pine woodlands on drier leeward slopes and mountain summit scrub at over 2,000 m (Fig. 1). This study can hopefully serve as a guide for future studies in Macaronesian archaeology and palaeoecology, because the Canary Islands share an important number of species and genera with other Macaronesian archipelagos, especially with Madeira. Our main research questions are 1, which species/genera/families are the main phytolith producers and 2, is there preliminary evidence for potentially diagnostic phytoliths and/or assemblages that can help identify particular plant species/genera/families in future archaeological and palaeoecological studies?

## Material and methods

### Collection and processing of plant material

Plant specimens of 109 taxa were collected on various field trips to the islands of Tenerife, Gran Canaria and La Palma between 2015 and 2021 (ESM 1 Table S1). As a first step in the creation of an extensive reference collection, we studied leaves and stems/branches of a single specimen per taxon, processing them together, and aiming to achieve a broad overview of the range of phytoliths produced by endemic

and native plants. Some fruits were also processed, including those of *Arbutus canariensis*, *Ficus carica* and *Juniperus turbinata* ssp. *canariensis* (ESM 1 Table S2).

Processing of the samples was carried out at the ecology laboratory of the Instituto Universitario de Enfermedades Tropicales y Salud Pública de Canarias (IUETSPC, University of La Laguna). Plant samples were processed using the dry-ashing procedure (Parr et al. 2001; Piperno 2006). Samples were first cleaned with laboratory detergent and placed in an ultrasonic bath for 30 min, then dried overnight at 90 °C. The dry plant content was weighed on a high precision scale, and then ashed in a muffle furnace at 550 °C for 3 h, after which the ashes were weighed again. They were then treated with HCl (10%) and HNO<sub>3</sub> (10%), and washed with distilled water. After drying the samples, we added 1 ml of water to each and extracted 50 µl of phytolith material after stirring. When the water evaporated, we mounted the material on to microscope slides using Canada balsam.

### Analysis of samples and recording phytoliths

We counted a maximum of 200 phytoliths at 400× and 500× in a maximum of 10 transects per slide. Photographs of the most characteristic morphotypes were taken. We named the phytolith morphotypes according to the principles of the International Code of Phytolith Nomenclature 2.0 (International Committee for Phytolith Taxonomy - ICPT 2019).

We calculated the phytolith concentration per g of dry plant material from the numbers of phytoliths recorded in the slide transects. We calculated percentages and concentrations of phytoliths in RStudio. We classified the plant species into three categories based on their phytolith content, 1) high producers, taxa with over 10,000 phytoliths per g of dry plant material, 2) medium producers with values less than 10,000 but above 500 phytoliths per g and 3) low producers, with values less than 500 phytoliths per g.

Contamination in the form of volcanic glass and phytoliths of other taxa, such as Poaceae short cells, was found in some samples. Some examples of contaminants are *Draacaena draco*, *Frankenia ericifolia*, *Juniperus turbinata* ssp. *canariensis* and *Pinus canariensis*. This can be explained by a process of strong adherence of phytolith silica structures to porous bark and stems (Tsartsidou et al. 2007). Phytoliths thought to be contamination were left out of the final sum. According to Albert et al. (2003) such contamination can represent up to 30% of the total amount of phytoliths recovered from these taxa.

### Statistical analyses

To assess the various species groups based on their phytolith assemblages we carried out cluster and ordination analyses

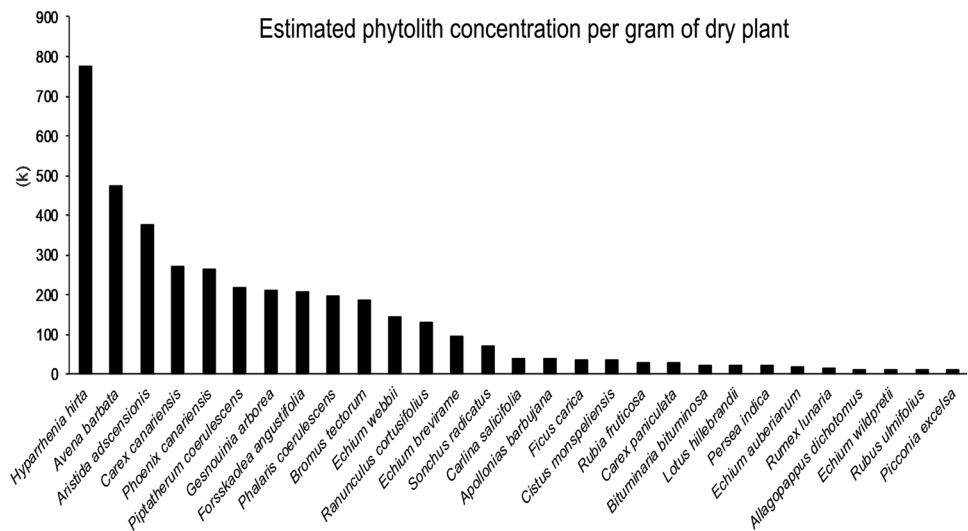
using the package RVEgan in Rstudio v. 1.1.456 (Oksanen et al. 2007). Cluster analysis using Ward's method, Euclidean distance, is useful to break species groups into clusters based on the similarity of their phytolith assemblages (Mercader et al. 2009). We analysed only the species that yielded over 10 phytoliths in the total sum of our counts, and those with fewer were excluded.

## Results and discussion

The resulting dataset (ESM 2) includes 123 phytolith morphotypes from 107 different plants, including trees, shrubs, herbs and ferns, and their quantification in estimated

concentrations of phytoliths per g plant material and percentages (Fig. 2, ESM 1 Table S2). These phytoliths consist of 16 broad morphotypes (Table 1, Figs. 3–6, ESM 1 Table S2). The current state of research suggests that surface 3D or 2D shape, texture and ornamentation are the most important features for identification (Table 1, 2). These are currently distributed across coastal scrub, thermophilous woodland, laurel forests, pine forests or woodlands and summit scrub ecosystems, and some are also typical of plants of abandoned and cultivated fields. In the following subsections, we will first focus on the diagnostic potential of selected phytoliths (Table 2), their likely anatomical origin and their significance for archaeological and palaeoenvironmental research in the Canary Islands. Then we discuss production

**Fig. 2** Phytolith concentration estimates (phytoliths per g of dry plant material) of the main phytolith producers in the reference collection



**Table 1** The main morphotypes with diagnostic potential in the phytolith reference collection of Canary Islands plants

Morphotype	Code	Number of observed types	Main identification features
ACICULAR	ACI	10	Segments, surface texture and ornamentation
ACUTE	ACU	2	Base margin
BILOBATE	BIL	2	Outline
BRACHIATE	BRA	1	3D morphology
BULBOUS	BUL	1	3D morphology
ELLIPSOIDAL	ELI	2	3D morphology
ELONGATE	ELO	6	General outline and surface
FUSIFORM	FUS	2	General shape, texture and surface ornamentation
HAIR-BASE	HAI	6	General and units outline, surface
HEXAGONAL	HEX	2	Surface
OVATE	OVA	1	3D morphology
POLYGONAL	POY	8	3D morphology, surface texture and ornamentation, infillings
RENIFORM	REN	1	3D morphology
SPHEROID	SPH	3	Surface texture and ornamentation
TABULAR	TAB	7	3D morphology, surface texture, ornamentation and infillings
TRACHEARY	TRA	4	General shape and ornamentation

and preservation biases and assess taxonomic groupings based on statistical analyses.

## Recorded phytoliths and their diagnostic potential

### Coastal scrub

The coastal scrub (*cardonal*, *tabaibal*) of the Canary Islands is a desert-like shrubby community that is thought to have occupied half of the area of the islands before human colonization (del Arco et al. 2010). This vegetation type is exposed to a strong water stress and is dominated by succulent species of the genus *Euphorbia*. The coastal scrub was an important ecosystem due to its resources and closeness to the coast, which were vital for island societies. This was probably the first ecosystem encountered and used by human settlers; for instance, some of the earliest radiocarbon dates in Tenerife come from the site of Las Estacas rock shelter (Galván Santos et al. 2000). As they are from leaves and stems, phytoliths of plants in this ecosystem could show plant use in archaeological sites, and complement pollen analysis for reconstructing changes in coastal scrub in response to human impact and climate.

We found diagnostic phytoliths in *Rubia fruticosa*, which has HAIR BASE STRIATE (HAI\_BAS\_STR\_3) (1.8%), ACICULAR STRIATE (ACI\_STR) (54%) and POLYGONAL STRIATE morphotypes (2%) (Figs. 3i, 4t, u). This species is distributed across all the coastal areas in the Canary Islands, as well as Madeira and the Selvagens islands off the coast of Morocco. Its use since pre-European times as a valuable fodder resource has been suggested (Pais Pais 1996). Another taxon, *Neochamaelea pulverulenta* had a high concentration of TRACHEARY PITTED (TRA\_PIT\_1) (80%) (Fig. 6o), similar to those produced by *Plocama pendula* (66%) (Fig. 6q), probably silicified vascular tissues for transporting water (Piperno 2006). *N. pulverulenta* is particularly relevant to archaeological studies due to its use for funerary practices by indigenous societies (Atoche Peña and Ramírez Rodríguez 2008). The consumption of its ripe fruits has also been ethnographically noted in Gran Canaria (Morales and Gil 2014b). The genus *Echium* includes *Echium auberianum*, *E. brevirame*, *E. webbii*, *E. wildpretii*, among many others, which are part of a group of ca. 25 endemic shrubs distributed in all vegetation communities. In the coastal scrub of La Palma the endemic species *Echium brevirame* is very abundant and is often used as fodder for livestock and as firewood (del Arco 1993; Pais Pais 1996). This species, as also the other studied *Echium* species, also has many phytoliths including ACICULAR PSILATE (61%) and ACICULAR NODULATE (ACI\_NOD\_1) (28%), HAIR BASE (HAI\_BAS\_1) (3%) and TABULAR BULBOUS (TAB\_BUL) (6.4%) (Figs. 3b, 4n, 6j).

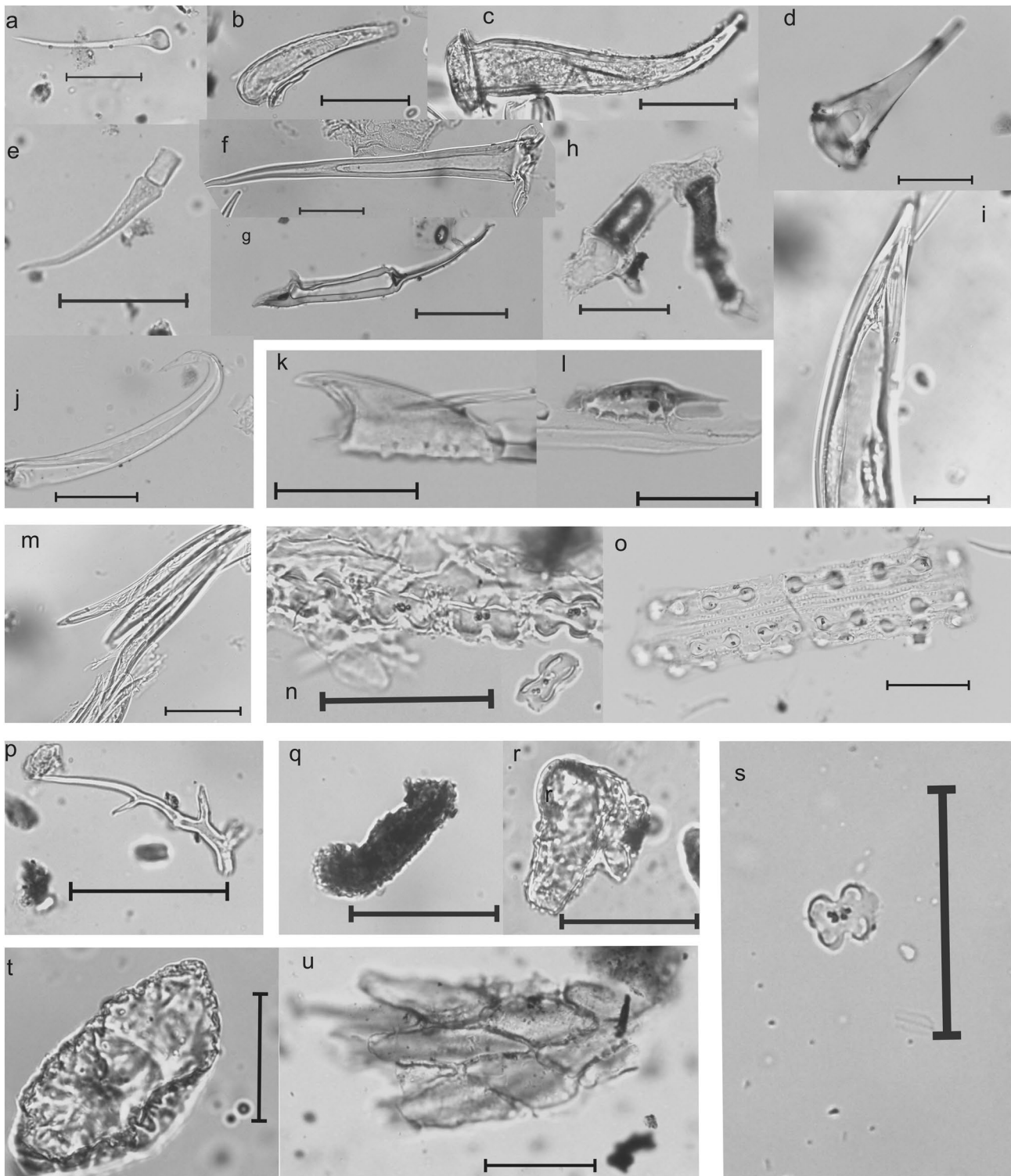
ACICULAR morphotypes found in *Echium* and *Rubia* are good examples of hairs that attach to hair bases, and their origin is the outer epidermal tissue of the plant (Piperno 2006).

*Rumex lunaria* (Polygonaceae) is extremely abundant in the coastal scrub, dominating recent lava flows, as well as disturbed areas on the coast and centre of the islands. It has been documented as having been used both for feeding livestock (Nogales et al. 1992) and for funerary purposes, mostly serving as a bed of litter for the deceased (Diego Cuscoy 1953; del Arco 1993). A variety of ELONGATE (32%) and BLOCKY (23%) forms, apparently without diagnostic potential, were found in this species. Their abundance in combination with other proxy evidence such as pollen could help identify their local presence. Finally, species of the Poaceae family, such as *Aristida adscensionis* and *Hyparrhenia hirta*, are commonly found in the coastal vegetation and are key resources for livestock grazing (del Arco 1993), and are likely to be some of the main phytolith producers. They produce BILOBATES with convex edges (BIL\_1) (20%) and CROSS (CRO) (6%) (Fig. 3n, s) in *H. hirta* as well as ACUTE BULBOSUS (7%). *Aristida adscensionis* also had ACUTE PSILATE (37%) types, together with diagnostic long-shaft BILOBATE (BIL\_2) (24%) (Fig. 3o).

### Thermophilous woodlands

Thermophilous woodlands (*bosques termófilos*) have some remarkable species yet they are some of the most heavily transformed ecosystems of the archipelago (Castilla-Beltrán et al. 2021). These woodlands are dominated by various trees, such as *Juniperus turbinata* ssp. *canariensis* (juniper), *Olea cerasiformis* (wild olive), *Pistacia atlantica* (African mastic), *Phoenix canariensis* (Canary palm) and *Dracaena draco* (Macaronesian dragon tree) (del Arco et al. 2006).

From these characteristic species, only *Phoenix canariensis* stands out as a high producer of diagnostic phytoliths. As with other palm species, its phytolith production is very great and dominated by SPHEROID ECHINATE (SPH\_ECH) (85%) (Levin 2019; An and Xie 2022) (Fig. 5q, r). These phytoliths are typical of leaf, stem and lignified tissues of palm trees (Piperno 2006). Articulated POLYGONAL and CIRCULAR bodies (POY&CIR) (1%) are also found (Fig. 5h, i). We did not find conical phytoliths in *Phoenix*, which are found in some other species within the Arecaceae (An and Xie 2022; Witteveen et al. 2022). This palm has proved to be a useful resource for humans. Ethnographic reports show how every single part was used for construction, roofing, making ropes, basket weaving, etc. (Morales and Rodríguez-Rodríguez 2007). Archaeobotanical analyses also show that *P. canariensis* seeds were burned in ritual contexts in La Gomera, together with other wild plant remains and cereals (Morales et al. 2011), and palm dates were also stored



by indigenous populations of Gran Canaria (Morales et al. 2018; Henríquez-Valido et al. 2020).

Among the abundant plants of the Asteraceae family distributed in the thermophilous woodland, we found potentially diagnostic phytoliths in the form of HAIR BASE STRIATE (HAI\_BAS\_STR\_1) (3%) (Fig. 4o) and articulated

POLYGONAL STRIATE (POY\_STR) (13%) in *Allagopapus dichotomus* (Fig. 5o), TABULAR SINUATE (TAB\_SIN\_1) (39%) (Fig. 6a) and articulated POLYGONAL (21%) in *Carlina salicifolia*, and articulated POLYGONAL LAMINAR (POY\_LAM) (19%) in *Sonchus radicans* (Fig. 5l). *Carlina falcata*, a species related to *C. salicifolia*, Canary and Macaronesian

**Fig. 3** **a**, ACICULAR BULBOUS (ACI\_BUL, *Sideritis soluta*); **b**, ACICULAR NODULATE (ACI\_NOD\_1, *Echium webbiai*); **c**, ACICULAR NODULATE (ACI\_NOD\_1, *Ficus carica*); **d**, ACICULAR PSILATE (ACI\_PSI\_1, *Forsskaolea angustifolia*); **e**, ACICULAR SEGMENTED (ACI\_SEG\_1, *Micromeria lachnophylla*); **f**, ACICULAR PSILATE (ACI\_PSI\_2; *Ficus carica*); **g**, ACICULAR SEGMENTED (ACI\_SEG\_2, *Nepeta teydea*); **h**, ACICULAR SEGMENTED (ACI\_SEG\_3, *Sideritis soluta*); **i**, ACICULAR STRIATE (ACI\_STR, *Rubia fruticoso*); **j**, ACICULAR UNCINATE (ACI\_UNC, *Forsskaolea angustifolia*); **k**, **l**, ACUTE BULBOSUS (ACU\_BUL, *Piptatherum coeruleascens*); **m**, ACUTE HELICAL (ACU\_HEL, *Bromus tectorum*); **n**, BILOBATE (BIL, *Hyparrhenia hirta*); **o**, BILOBATE (BIL, *Aristida adscensionis*); **p**, BRACHIATE (BRA, *Descurainia borgeauana*); **q**, BULBOUS GRANULATE (BUL\_GRA, *Pteridium aquilinum*); **r**, BULBOUS NODULATE (BUL\_NOD, *Heberdenia excelsa*); **s**, CROSS (CRO, *Hyparrhenia hirta*); **t**, ELLIPSOIDAL RUGOSE (ELI\_RUG, *Bituminaria bituminosa*); **u**, ARTICULATED ELLIPSOIDAL (ELI, *Juniperus cedrus*); scale bars = 50 µm

endemic species respectively, is nowadays used as fodder for livestock (Pais Pais 1996). On the other hand, *Sonchus* spp. leaves are tender and ethnographically known to be edible (Morales and Gil 2014b). Finally, among the endemic *Euphorbia* species that are distributed in the *medianías* (mid-elevation landscapes) at 500–1000 m, whose latex is reported to have a medical use (del Arco 1993), as well as the plant being gathered as fodder (Morales and Gil 2014b). An endemism of Tenerife, *E. atropurpurea*, contained articulated POLYGONAL and CIRCULAR types and articulated POLYGONAL NODULATE (POY\_NOD) (72%) (Fig. 5m, n). This contrasts with *E. lamarkii*, which only produced undiagnostic TRACHEARY HELICAL (4%) and PITTED (TRA\_PIT\_1) (47%) (Fig. 6p). POLYGONAL and TABULAR SINUATE phytolith types are good examples of cell walls from the leaves of various plants (Bozarth 1992; Piperno 2006). Finally, *Sideroxylon canariensis* (Sapotaceae), a rare tree that usually grows in the thermophilous woodlands and dry laurel forest, had TRACHEARY HELICAL (TRA\_HEL\_2) (55%) (Fig. 6l, m).

## Laurel forest

The laurel forest (*laurisilva*) is considered to be the survivor of the original palaeotropical geoflora that was distributed in central and southern Europe during the Paleogene and Neogene periods (Fernández-Palacios et al. 2017), and it is of remarkable historical and conservation value. The scarce production and dispersal of pollen by the endemic Lauraceae (*Apollonias*, *Laurus*, *Ocotea*, *Persea*) and other tree taxa of this forest (*Heberdenia*, *Ilex*, *Picconia*, *Prunus*, *Rhamnus*, etc.), which are mostly insect pollinated, make it a silent ecosystem in the palaeoecological record (de Nascimento et al. 2009, 2015; Nogué et al. 2013). Among the Lauraceae analysed in this study, we found potentially diagnostic phytoliths in *Apollonias barbujana*, *Laurus novocanariensis* and *Persea indica*. We found OVATE FACETATE (OVA\_FAC) in *Apollonias barbujana* and *Persea indica*, 6% and 2% respectively (Fig. 5c, d). TRACHEARY HELICAL (TRA\_HEL\_1) (44%)

(Fig. 6k), articulated POLYGONAL and articulated TABULAR SINUATE (TAB\_SIN\_2) occurred in *Laurus novocanariensis* (4%) (Fig. 6c).

The wood of the Lauraceae trees was used as weapons and poles by the indigenous people (del Arco 1993). Also, *L. novocanariensis* leaves and branches were found in indigenous granary contexts on Gran Canaria probably to repel insect pests (Morales et al. 2018; Vidal-Matutano et al. 2020, 2021b). TRACHEARY types which are abundant in laurel forest taxa are examples of silicified vascular tissues of the xylem and phloem (Piperno 2006). The confirmation that Lauraceae produce these phytoliths is a promising new way of recognising this particular ecosystem, which until now has been elusive in palaeoecological reconstructions.

The native tree heather *Erica arborea*, which dominates the *Erica-Morella* woody heath vegetation formation, is also present in the laurel forest and humid pine woods. *E. arborea* produced a variety of BULBOUS (23%) and SPHEROID PSILATE and ORNATE (51%) types, as well as OVATE FACETATE (OVA\_FAC) (19%) (Fig. 5e). Studies of ancient charcoal from archaeological sites on the high parts of Tenerife have identified *Erica* sp. which was used as fuel or for making tools, well above its natural distribution height (Vidal-Matutano et al. 2019; Morales et al. 2021). Another endemic Ericaceae tree, *Arbutus canariensis*, is commonly found on the edges of the laurel forest. It produced ELONGATE BULBOUS types with a granulate surface (ELO\_BUL\_1) (33%) (Fig. 4f, g), although in low concentrations. *A. canariensis* fruits were probably gathered for human consumption since pre-Hispanic times according to ethnohistorical and ethnographical sources (Viera y Clavijo 1776–1783; del Arco 1993). *Visnea mocanera* is the single species of the Pentaphragmaceae family found in the laurel forest. This tree was of great importance for the indigenous inhabitants, who used its fruits to prepare a sort of liquor known as “chacerquem” (Espinosa 1594/1980; del Arco Aguilar and Navarro Mederos 1987). While its phytoliths are scarce, some articulated POLYGONAL (POY) (37%) have been found, which have some diagnostic potential (Table 2; Fig. 5f).

*Picconia excelsa* (Oleaceae) is another endemic tree of the laurel forest and in the transition from this to the thermophilous woodlands, renowned for its hard wood. Indigenous people used it for making weapons (Diego Cuscoy 1961) and for firewood (Machado Yanes 1999). It contained abundant articulated POLYGONAL GRANULATE (POY\_GRA\_2) (29%) (Fig. 5k) and rare articulated TABULAR SINUATE GRANULATE (TAB\_SIN\_3) (1%) types (Fig. 6d). *Ranunculus cortusifolius* is an endemic buttercup of the Macaronesian laurel forests growing in moist environments. It has been used for its qualities for pain relief (Pérez de Paz and Medina 1988). It produces articulate ELONGATE (ELO\_STR\_2) and TABULAR SINUATE (TAB\_SIN\_4) phytoliths, with internal striate and circular patterns (6% and 7% respectively) (Figs. 4j and 6e).

**Table 2** Descriptors and codes for the morphotypes with diagnostic potential in the Canary Islands phytolith reference collection

Morphotype	Type	Code	Species	Fig.	Distinctive features
ACICULAR	BULBOUS	ACI_BUL	<i>Sideritis soluta</i>	3a	Needle or nail shape
	NODULATE	ACI_NOD_1	<i>Echium</i> sp.	3b	Nodules covering the entire surface
	NODULATE	ACI_NOD_1	<i>Ficus carica</i>	3c	Nodules around the base, can show segments
	PSILATE	ACI_PSI_1	<i>Gesnouinia arborea</i> , <i>Forsskaolea angustifolia</i>	3d	Thick walls
	PSILATE	ACI_PSI_2	<i>Ficus carica</i>	3f	Laminar fill
	SEGMENTED	ACI_SEG_1	<i>Micromeria lachnophylla</i> , <i>Bystropogon origanifolius</i>	3e	Hairs divided into segments
	SEGMENTED	ACI_SEG_2	<i>Nepeta teydea</i>	3g	Hairs divided into segments
	SEGMENTED	ACI_SEG_3	<i>Sideritis soluta</i>	3h	Hairs divided into segments, geniculate
	STRIATE	ACI_STR	<i>Rubia fruticosa</i>	3i	Thick walls
	UNCINATE	ACI_UNC	<i>Gesnouinia arborea</i> , <i>Forsskaolea angustifolia</i>	3j	Hook-shaped
ACUTE	BULBOSUS	ACU_BUL	<i>Piptatherum coeruleascens</i>	3k, l	Fine protrusions branching around the base
	HELICAL	ACU_HEL	<i>Bromus tectorum</i>	3m	Helical pattern in surface or infilling
BILOBATE	BILOBATE	BIL	<i>Hyparrhenia hirta</i>	3n	Convex ends
	BILOBATE	BIL	<i>Aristida adscensionis</i>	3o	Long shaft
BRACHIATE	BRACHIATE	BRA	<i>Descourainia bourgeauana</i>	3p	Branched
BULBOUS	GRANULATE	BUL_GRA	<i>Pteridium aquilinum</i>	3q	Granulate surface
	NODULATE	BUL_NOD	<i>Heberdenia excelsa</i>	3r	Nodules covering surface
CROSS	CROSS	CRO	<i>Hyparrhenia hirta</i>	3s	-
ELLIPSOIDAL	(ARTICULATED)	ELI	<i>Juniperus cedrus</i>	3u	Cluster, psilate (smooth) to granulate surface
	RUGOSE	ELI_RUG	<i>Bituminaria bituminosa</i>	3t	Irregular surface pattern
ELONGATE	AREOLATE	ELO_ARE	<i>Pteridium aquilinum</i>	4a	Areolate surface
	DENDRITIC/DENTATE	ELO_DEN	<i>Avena barbata</i>	4b	Serrate with ramifications
	BULBOUS	ELO_BUL_1	<i>Arbutus canariensis</i>	4f, g	Granulate surface
	BULBOUS	ELO_BUL_2	<i>Pinus canariensis</i> , <i>Echium webbii</i>	4c, d, e	Thin and flat, varying in size
FUSIFORM	CLAVATE	ELO_CLA	<i>Carex</i> spp.	4h, i	Club-shaped on edges
	STRIATE (ARTICUL.)	ELO_STR_2	<i>Ranunculus cortusifolius</i>	4j	Striate surface
	NODULATE	FUS_NOD	<i>Erysimum scoparium</i>	4k	Irregular nodules on the surface
	STRIATE	FUS_STR	<i>Erysimum scoparium</i>	4l, m	Striate surface
HAIR BASE	HAIR BASE	HAI_BAS_1	<i>Echium</i> sp.	4n	Psilate surface, big inner circle
	HAIR BASE	HAI_BAS_2	<i>Cistus monspeliensis</i> , <i>Helianthemum juliae</i> , <i>Tuberaria guttata</i>	4q	Psilate surface, small inner circle/polygon
HAIR BASE	HAIR BASE	HAI_BAS_GRA	<i>Cistus monspeliensis</i> , <i>Helianthemum juliae</i>	4p	Granulate surface
	HAIR BASE	HAI_BAS_STR_1	<i>Cistus monspeliensis</i> , <i>Allagopappus dichotomus</i>	4o	Striate surface
	HAIR BASE	HAI_BAS_STR_2	<i>Bituminaria bituminosa</i>	4r, s	Single or double
	HAIR BASE	HAI_BAS_STR_3	<i>Rubia fruticosa</i>	4t, u	Striate surface, big inner circle
HEXAGONAL	PSILATE	HEX_PSI	<i>Carex</i> sp.	5a	Psilate surface
	GRANULATE	HEX_GRA	<i>Carex</i> sp.	5b	Granulate surface only around the edge
OVATE	FACETATE	OVA_FAC	<i>Apollonias barbujana</i> , <i>Persea indica</i> , <i>Erica arborea</i>	5c, d, e	Many psilate faces
POLYGONAL	(ARTICULATED)	POY	<i>Visnea mocanera</i>	5f	Units arranged like a fan
	ACICULAR (ARTICUL.)	POY_ACI	<i>Mentha longifolia</i> , <i>Micromeria lachnophylla</i>	5g	Acicular projections on the surface
POLYGONAL	& CIRCULAR (ARTICUL.)	POY&CIR	<i>Phoenix canariensis</i>	5h, i	Units arranged in bulliform cluster
	GRANULATE	POY_GRA_1	<i>Rubus ulmifolius</i>	5j	Granulate surface only around the edge
	GRANULATE (ARTICUL.)	POY_GRA_2	<i>Picconia excelsa</i>	5k	Granulate surface
	LAMINAR (ARTICUL.)	POY_LAM	<i>Sonchus radicans</i>	5l	Laminations in circular pattern
	NODULATE (ARTICUL.)	POY_NOD	<i>Euphorbia atropurpurea</i>	5m, n	Nodule in the centre of polygonal cells
	STRIATE (ARTICUL.)	POY_STR	<i>Allagopappus dichotomus</i>	5o	Striate surface
	NODULATE	REN_NOD	<i>Heberdenia excelsa</i>	5p	Nodulate surface
SPHEROID	ECHINATE	SPH_ECH	<i>Phoenix canariensis</i>	5q, r	Regular echinate surface
	ORNATE	SPH_ORN_1	<i>Gesnouinia arborea</i> , <i>Forsskaolea angustifolia</i>	5s, t	Cystolith, nodulate ornamentation
TABULAR	ORNATE	SPH_ORN_2	<i>Ficus carica</i>	5u	Cystolith, rugose ornamentation, circular base
	BULBOUS	TAB_BUL	<i>Echium</i> sp.	6i, j	Rounded edges
	SINUATE (ARTICUL.)	TAB_SIN_1	<i>Carlina salicifolia</i>	6a	Psilate surface, cylindrical protrusions
	SINUATE (ARTICUL.)	TAB_SIN_2	<i>Ilex canariensis</i> , <i>Laurus novocanariensis</i>	6b	Club-like projections on edges
	SINUATE (ARTICUL.)	TAB_SIN_3	<i>Picconia excelsa</i>	6d	Granulate surface
	SINUATE (ARTICUL.)	TAB_SIN_4	<i>Ranunculus cortusifolius</i>	6e	Thick wall
	SINUATE (ARTICUL.)	TAB_SIN_5	<i>Forsskaolea angustifolia</i>	6f, g	With cystoliths, shows perforations
	SINUATE WITH ACICULAR (ARTICUL.)	TAB_SIN_6	<i>Micromeria lachnophylla</i>	6h	Acicular projections
TRACHEARY	HELICAL	TRA_HEL_1	<i>Laurus novocanariensis</i>	6k	Cylindrical-to-prismatic
	HELICAL	TRA_HEL_2	<i>Sideroxylon canariensis</i> , <i>Schizogyne sericea</i>	6l, m, n	Cylindrical
	PITTED	TRA_PIT_1	<i>Neochamaelea pulverulenta</i> , <i>Euphorbia</i> spp.	6o, p	Elongate to ovoid shapes, in clusters
	PITTED	TRA_PIT_2	<i>Plocama pendula</i>	6q	Ovoid to fusiform shapes, often in clusters



The cell wall phytoliths found in *Picconia* and *Ranunculus* probably originate from leaf epidermis, and while their preservation in soils is unlikely, they could be preserved in archaeological contexts (Piperno 2006). *Gesnouinia arborea* is a tall shrub in the Urticaceae, and present on the tracks in the humid laurel forest. Urticaceae are known to produce abundant phytoliths (Piperno 1988; Bozarth 1992). *G. arborea* produced ACICULAR PSILATE (ACI\_PSI\_1) (9%) (Fig. 3d) and ACICULAR NODULATE (17%) phytoliths, an assemblage that is similar to other hair-producing taxa such as *Echium*, but with abundant ACICULAR UNCINATE (ACI\_UNC) phytoliths (27%) (Fig. 3j) and also characteristic SPHEROID ORNATE (SPH\_ORN\_1) types (30%) with nodulate ornamentation, that fit the category of cystoliths or outgrowths of the cell wall (Piperno 2006) (Fig. 5s, t), and also articulated TABULAR SINUATE and articulated POLYGONAL phytoliths. Finally, *Ilex canariensis* (Canary holly) contained only articulated TABULAR SINUATE phytoliths (TAB\_SIN\_2) (36%) (Fig. 6b). The endemic tree *Heberdenia excelsa* had BULBOUS NODULATE (BUL\_NOD) (6%) and RENIFORM NODULATE (REN\_NOD) phytoliths (Figs. 3r and 5p).

Among the ferns found in this closed forest vegetation, we processed *Davallia canariensis*. Little is known about phytolith occurrence in the Davalliaceae (Mazumdar 2011). We found few phytoliths of unclear diagnostic value, varying between articulated TABULAR SINUATE and ELONGATE STRIATE, despite it being a low producer, together accounting for 100% of the assemblage. As for its potential uses, *D. canariensis* rhizomes have pharmacological and nutritive properties that might have served people with limited resources, such as on El Hierro (del Arco 1993; del Arco et al. 2001). In contrast, *Pteridium aquilinum* (bracken), typically found along tracks in the laurel forest, contained ELONGATE AREOLATE (ELO\_ARE) (29%) (Fig. 4a) and BULBOUS GRANULATE (BUL\_GRA) (26%) types (Fig. 3q). However, phytoliths of *Pteridium* have been reported elsewhere as ELONGATE GENICULATE with perforations (Afonso Vargas 2012).

## Pine forest and woodland

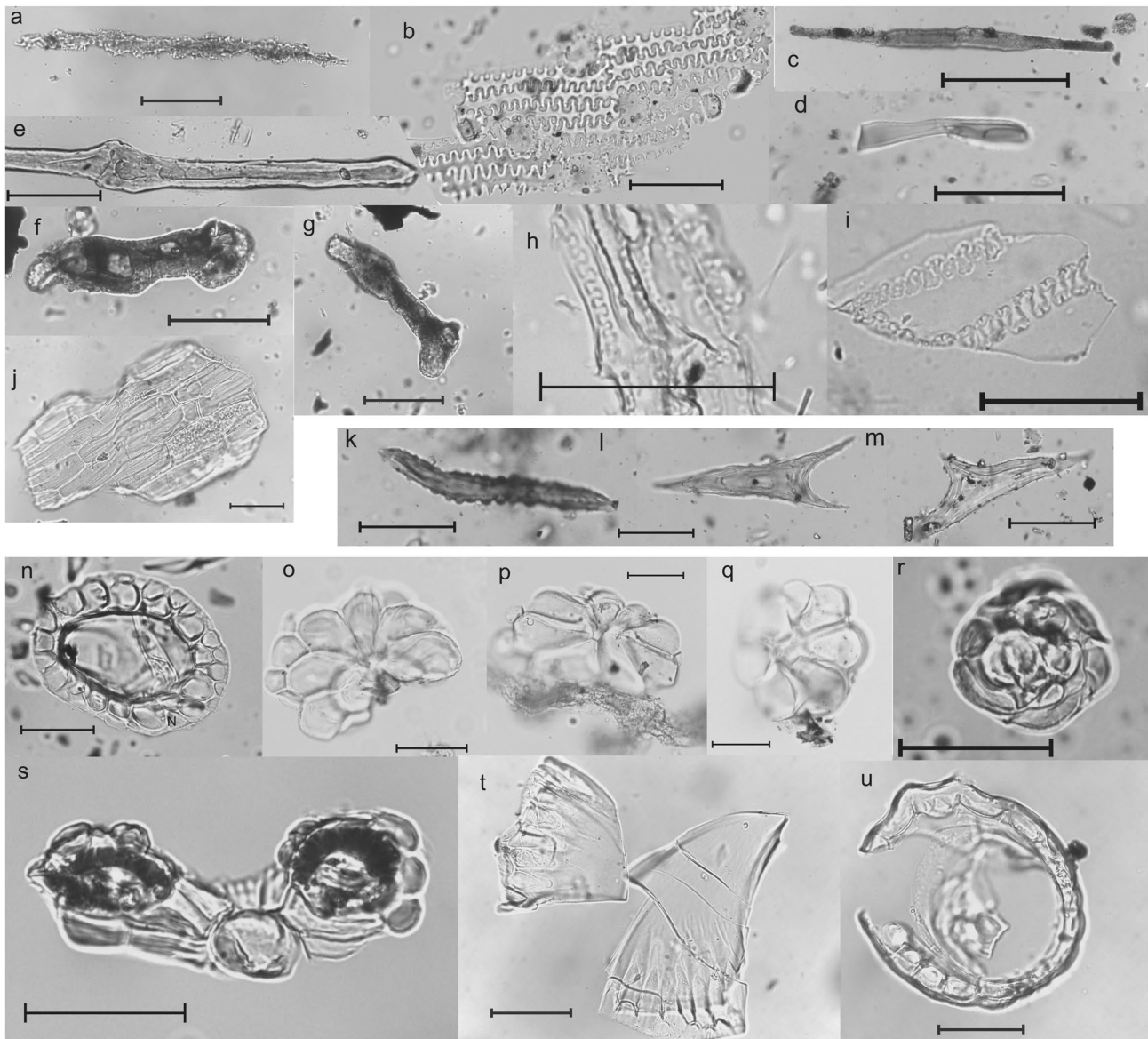
The pine forests and woods of the Canaries (*pinar*) are dominated by the endemic *Pinus canariensis* and grow in the central and western islands of Gran Canaria, Tenerife, La Gomera, La Palma and El Hierro, although only very fragmentarily in La Gomera. *P. canariensis* is probably the largest pollen producer in the archipelago (perhaps with *Erica* spp. and *Morella*), so *Pinus* pollen is frequently found outside areas of pine woods (de Nascimento et al. 2015). This endemic pine was a key fuel resource for the indigenous people (Vidal-Matutano et al. 2021a, Fig. 1 and references; Fernández-Palacios et al. 2023). We found medium phytolith production in *P. canariensis*, mostly consisting of ELONGATE BULBOUS (ELO\_BUL\_2) (Fig. 4c, d), as has been reported in

other *Pinus* species (Piperno 2006). We also found diagnostic phytoliths in some of the taxa growing in the understory of the pine woods, such as *Bystropogon origanifolius*, *Cistus monspeliensis* and *Sideritis soluta*, or, again, *Echium* spp. This provides researchers with a way of distinguishing true pine woods from other ecosystems with *Pinus* pollen, but from distant sources.

For instance, *Bystropogon origanifolius* has ACICULAR SEGMENTED (ACI\_SEG\_1) (33%) and HAIR BASE (6%) types, which are commonly found in other members of the Lamiaceae family studied here. Its leaves have traditionally been used for their medicinal value (Pérez de Paz and Medina 1988). ACICULAR BULBOUS (ACI\_BUL) (55%) and ACICULAR SEGMENTED (ACI\_SEG\_3) phytoliths were also found in *Sideritis soluta* (Fig. 3a, h). Cistaceae, on the other hand, seem to produce abundant epidermal phytoliths like HAIR BASE and POLYGONAL morphotypes, such as *Cistus monspeliensis*, which produced a large amount of HAIR BASE phytoliths with varying surface textures (psilate, granulate and striate, 12%, 17% and 9% respectively) (HAI\_BAS\_2, HAI\_BAS\_GRA, HAI\_BAS\_STR\_1) (Fig. 4o, p). Leaves of *C. monspeliensis* have been identified in an indigenous cemetery in Arteara, Gran Canaria, together with remains of *Pinus*, Rutaceae and Lamiaceae (Jorge-Blanco 1989). Finally, another endemic member of the Boraginaceae in La Palma is *Echium webbii*, which is usually found in the understory of open pine woods. As with other *Echium* species, this one has ACICULAR PSILATE (64%), ACICULAR NODULATE (ACI\_NOD\_1) (15%), HAIR BASE (HAI\_BAS\_1) and TABULAR BULBOUS (TAB\_BUL) (6%) phytolith morphotypes (Figs. 3b, 4n, 6i). Like *E. brevirame*, *E. webbii* was probably used as fuel and fodder (del Arco 1993). Finally, in *Scrophularia glabrata*, commonly found in the understory of the pine woods and the scrub above the tree line, we found long ACICULAR type (31%) (Fig. 6n).

## Summit scrub

At the top of the elevation gradient and above the tree line at over 2,000 m, the summit scrub (*matorral de cumbre*) is only represented in Tenerife and La Palma, the two highest islands of the archipelago. It is a scrubby community dominated by endemic Fabaceae species such as *Spartocytisus supranubius*, *Adenocarpus viscosus* or *Genista benehoavensis*, and it is thought that in the past, before the arrival of humans there, *Juniperus cedrus* ssp. *cedrus*, the endemic Canary Islands juniper, formed a vegetation belt above the pine forest and woods and below the summit scrub (Nogales et al. 2014). Fabaceae species do not typically produce diagnostic phytoliths in abundance (Piperno 2006), as confirmed by the present study, as only *Bituminaria bituminosa* which was present in most open habitats provided potentially diagnostic HAIR BASE STRIATE (HAI\_BAS\_STR\_2) (6.3%) and ELLIPSOIDAL



**Fig. 4** **a**, ELONGATE AREOLATE (ELO\_ARE, *Pteridium aquilinum*); **b**, ELONGATE DENTATE/DENDRITIC (ELO\_DEN, *Avena barbata*); **c**, **d**, ELONGATE BULBOUS (ELO\_BUL\_2, *Pinus canariensis*); **e**, ELONGATE BULBOUS *Echium webbii*; **f**, **g**, ELONGATE BULBOUS (ELO\_BUL\_1, *Arbutus canariensis*); **h**, **i**, ELONGATE CLAVATE (ELO\_CLA), *Carex* spp.; **j**, ELONGATE STRIATE (ELO\_STR\_2, *Ranunculus cortusifolius*); **k**, FUSIFORM NODULATE (FUS\_NOD, *Erysimum scoparium*); **l**, **m**, FUSI-

FORM STRIATE (FUS\_STR, *Erysimum scoparium*); **n**, HAIR BASE (HAI\_BAS\_1, *Echium webbii*); **o**, HAIR BASE STRIATE (HAI\_BAS\_STR\_1, *Cistus monspeliensis*); **p**, HAIR BASE GRANULATE (HAI\_BAS\_GRA, *Cistus monspeliensis*); **q**, HAIR BASE (HAI\_BAS\_2, *Tuberaria guttata*); **r**, **s**, HAIR BASE STRIATE (HAI\_BAS\_STR\_2, *Bituminaria bituminosa*); **t**, **u**, HAIR BASE STRIATE (HAI\_BAS\_STR\_3, *Rubia fruticosa*); scale bars = 50  $\mu$ m

RUGOSE (ELI\_RUG) (10%) types (Figs. 3t and 4r, s). We found a morphotype with diagnostic potential in *Juniperus cedrus* ssp. *cedrus*, a cluster of articulated ELLIPSOIDAL structures (ELI) (12%) (Fig. 3u). Juniper wood was used by the first colonizers of the archipelago, both for domestic and funerary purposes (del Arco 1993). There is archaeological evidence of *J. cedrus* ssp. *cedrus* and *J. turbinata* ssp. *canariensis* from the indigenous occupation of Las Cañadas, on the high

parts of Tenerife (Machado Yanes and Galván Santos 1998; Tomé et al. 2022).

*Helianthemum juliae*, is a very rare endemic species of Tenerife summit scrub, nowadays critically endangered due to climate change as well as being grazed by introduced rabbits and mouflons. Articulated POLYGONAL (POY) phytoliths (30%) and HAIR BASE GRANULATE (HAI\_BAS\_GRA) types (5%) have been found in it. For future studies, phytoliths recovered from the palaeoecological record will indicate whether it was always rare

or if its present status is the result of being grazed by the goats which were introduced by indigenous people. Brassicaceae is a family represented in the summit scrub by two abundant endemic species, *Descurainia bourgeauana* and *Erysimum scoparium*, both being very palatable for the introduced herbivores and both producing relevant phytolith morphotypes. We recorded characteristic BRACHIATE (BRA) (41%) (Fig. 3p), as well as articulated CIRCULAR (21%) types from *D. bourgeauana*. *Erysimum scoparium* had FUSIFORM NODULATE (FUS\_NOD) and FUSIFORM STRIATE (FUS\_STR) morphotypes (20% in total) (Fig. 4k-m), probably hairs from the epidermal tissues.

Other endemic species of *Echium* are found on the highest parts of Tenerife. These are *E. wildpretii* and *E. auberianum*, which produce abundant ACUTE PSILATE, ACICULAR NODULATE (ACI\_NOD\_1), ACICULAR STRIATE (ACI\_STR), and HAIR BASE (HAI\_BAS\_1) phytoliths, in accordance with other *Echium* species studied here. Their low production of pollen, as they are insect pollinated, shows the usefulness of a potentially diagnostic phytolith key to identify Boraginaceae in palaeoecological and archaeological records. Various species within the Lamiaceae family grow in the summit scrub including *Micromeria lachnophylla*, *Mentha longifolia*, and *Nepeta teydea*. They contain abundant phytoliths, including articulated POLYGONAL with ACICULAR (POY\_ACI) (*Mentha longifolia*, 43%) and articulated TABULAR SINUATE & ACICULAR (TAB\_SIN\_6) types (Fig. 6h) (*Micromeria lachnophylla*, 92%), as well as ACICULAR SEGMENTED (*M. lachnophylla* 1%, *N. teydea*, 13%) (ACI\_SEG\_1, ACI\_SEG\_2) (Figs. 3e, g, 5g, 6h). Other species of *Mentha*, such as *M. x piperita*, are used as herbal tea in Tenerife. *Nepeta teydea* is also known for its medicinal value (Pérez de Paz and Medina 1988).

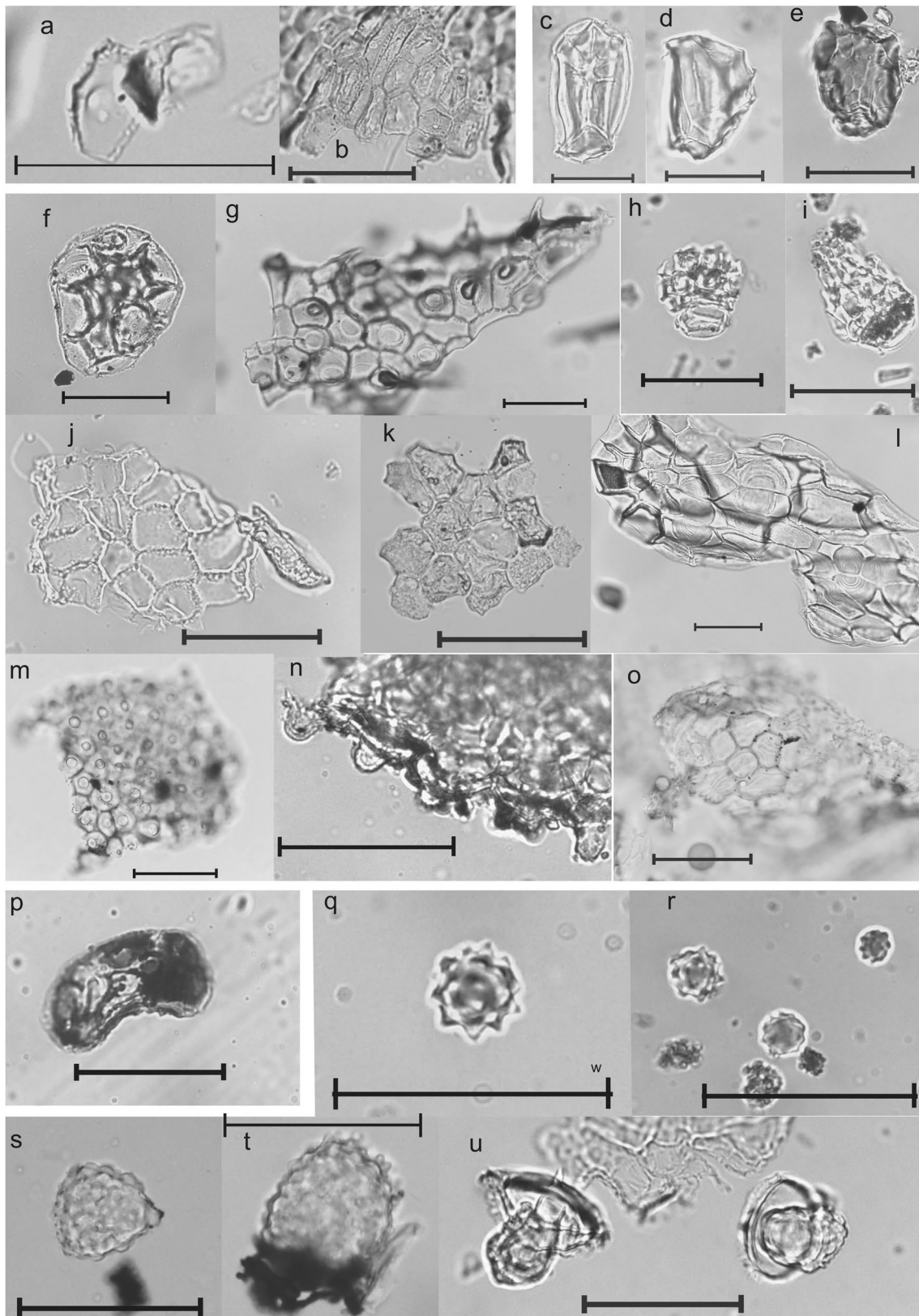
The wetland sedges have been commonly used for weaving and for making other plant fibre products throughout the history of the Canary Islands. This study only considers species within the genus *Carex* (Cyperaceae), the endemic *Carex canariensis* and native *C. paniculata*. These produced many phytoliths, including HEXAGONAL PSILATE/GRANULATE (HEX\_PSI and HEX\_GRA, 4 and 8% respectively) (Fig. 5a, b) (synonym of cone-shaped; Ollendorf 1992), probably originating from achene bracts (Piperno 2006), CONICAL (9 and 7% resp.), ELONGATE CLAVATE (4 and 26%), ACUTE BULBOSUS (11% *Carex p.*) and ELONGATE DENTATE (13 and 7%). Archaeobotanical evidence of *Carex* sp. has been recovered from indigenous sites in La Palma (Morales and Gil 2014b). However, its use remains unknown. The study of some plant materials that have survived since indigenous times has shown the use of other Cyperaceae like *Scirpus holoschoenus* (Galván Santos 1980). Other sedges like *Juncus effusus* (Juncaceae) and *Cyperus alternifolius* (Cyperaceae) have also been ethnographically documented as raw material for weaving (Cubas Hernández and Perdomo Molina 2001). Further analysis of these species is necessary to compare them with the morphotypes obtained from *Carex*.

## Ruderal plants, weeds of abandoned and cultivated fields

Ruderal plants grow as annual weeds in highly disturbed habitats resulting from human activities, such as settlements, farmed land and waste places etc., which here include taxa such as *Forsskaolea angustifolia*, *Pteridium aquilinum* and *Rubus ulmifolius*. Segetal plants, such as *Avena barbata*, *Bromus tectorum*, etc., are weeds that grow on cultivated land among crops. Although there are some ruderal taxa in the Canary flora (*Asphodelus*, *Artemisia*, *Forsskaolea*, *Patelifolia*, *Rumex*), the great majority of them (*Amaranthus*, *Chenopodium*, *Fumaria*, *Solanum*, etc.) were probably introduced, either by the indigenous people or Europeans (del Arco 2006; Morales et al. 2007). Among them, many produce diagnostic phytoliths.

There are very few endemic Poaceae in the Canary Islands and most of the others, including cultivated cereals, arrived by human action. Most Poaceae grow in open habitats, thus from a palaeoecological point of view, their presence indicates open land that may once have been wooded. *Piptatherum coeruleascens* in particular has ACUTE BULBOSUS phytoliths with dendritic projections (ACU\_BUL) (10%), which have diagnostic potential (Fig. 3k, l). In addition, *Bromus tectorum* contains ACUTE HELICAL (ACU\_HEL) (42%) types, also with diagnostic potential (Fig. 3m) and *Avena barbata* has PAPILLATE (3%) and ELONGATE DENDRITIC/DENTATE (ELO\_DEN) (17%) (Fig. 4b).

Among the tree species that we studied, *Ficus carica* (fig) needs to be mentioned due to its abundant and potentially diagnostic production of ACICULAR PSILATE (ACI\_PSI\_2) (Fig. 3f) (58%) and ACICULAR NODULATE (ACI\_NOD\_1) (7%) (Fig. 3b) morphotypes, as well as HAIR BASE types, also displaying numerous SPHEROID ORNATE (SPH\_ORN\_2) (10%) (Fig. 5u) attached to bases that fit the anatomical description of cystoliths (Bozarth 1992; Kealhofer and Piperno 1998) (Figs. 3c, f, 5u). *F. carica* was not part of the original flora of the Canary Islands, but was introduced by indigenous people into Gran Canaria and Tenerife (Morales 2003; Morales et al. 2009). Figs played an important role in the diet of the first inhabitants of Gran Canaria, suggesting their role as a staple food, a resource eaten on a regular basis and perceived as an essential part of the food of a group (Morales and Gil 2014a). Today, figs are very widespread due to their cultivation by local people. Another high producer of hair phytoliths is *Forsskaolea angustifolia* (Urticaceae), an endemic in the Canary Islands with a clear ruderal behaviour. Ethnographic studies of this plant suggest that it had medicinal properties (Pérez de Paz and Medina 1988), as well as fodder value. *F. angustifolia* produces abundant ACICULAR UNCINATE (ACI\_UNC) (23%) (Fig. 3j) and PSILATE (8%) phytoliths, in accordance with reports from other geographical areas (Piperno 1988; Bozarth 1992), as well as SPHEROID ORNATE



**Fig. 5** a, HEXAGONAL PSILATE (HEX\_PSI, *Carex canariensis*); b, HEXAGONAL GRANULATE (HEX\_GRA, *Carex paniculata*); c, OVATE FACETATE (OVA\_FAC, *Persea indica*); d, OVATE FACETATE (OVA\_FAC, *Apollonias barbujana*); e, OVATE FACETATE (OVA\_FAC, *Erica arborea*); f, POLYGONAL (ARTICULATED) (POY, *Visnea mocanera*); g, POLYGONAL ACICULAR (ARTICULATED) (POY\_ACI, *Mentha longifolia*); h, i, POLYGONAL AND CIRCULAR (POY&CIR, *Phoenix canariensis*); j, POLYGONAL GRANULATE (POY\_GRA\_1, *Rubus ulmifolius*); k, POLYGONAL GRANULATE (ARTICULATED) (POY\_GRA\_2, *Picconia excelsa*); l, POLYGONAL LAMINAR (ARTICULATED) (POY\_LAM, *Sonchus radicans*); m, n, POLYGONAL NODULATE (ARTICULATED) (POY\_NOD, *Euphorbia atropurpurea*); o, POLYGONAL STRIATE (ARTICULATED) (POY\_STR, *Allagopappus dichotomus*); p, RENIFORM NODULATE (REN\_NOD, *Heberdenia excelsa*); q, r, SPHEROID ECHINATE (SPH\_ECH, *Phoenix canariensis*); s, SPHEROID ORNATE (SPH\_ORN\_1, *Gesnouinia arborea*); t, SPHEROID ORNATE (SPH\_ORN\_1, *Forsskaolea angustifolia*); u, SPHEROID ORNATE (SPH\_ORN\_2, cystolith, *Ficus carica*); scale bars = 50 µm

(SPH\_ORN\_1) (46%) (that fit the category of cystoliths), articulated TABULAR SINUATE (TAB\_SIN\_5) (7%) and articulated POLYGONAL (0.5%) types (Figs. 6f, g and 5f).

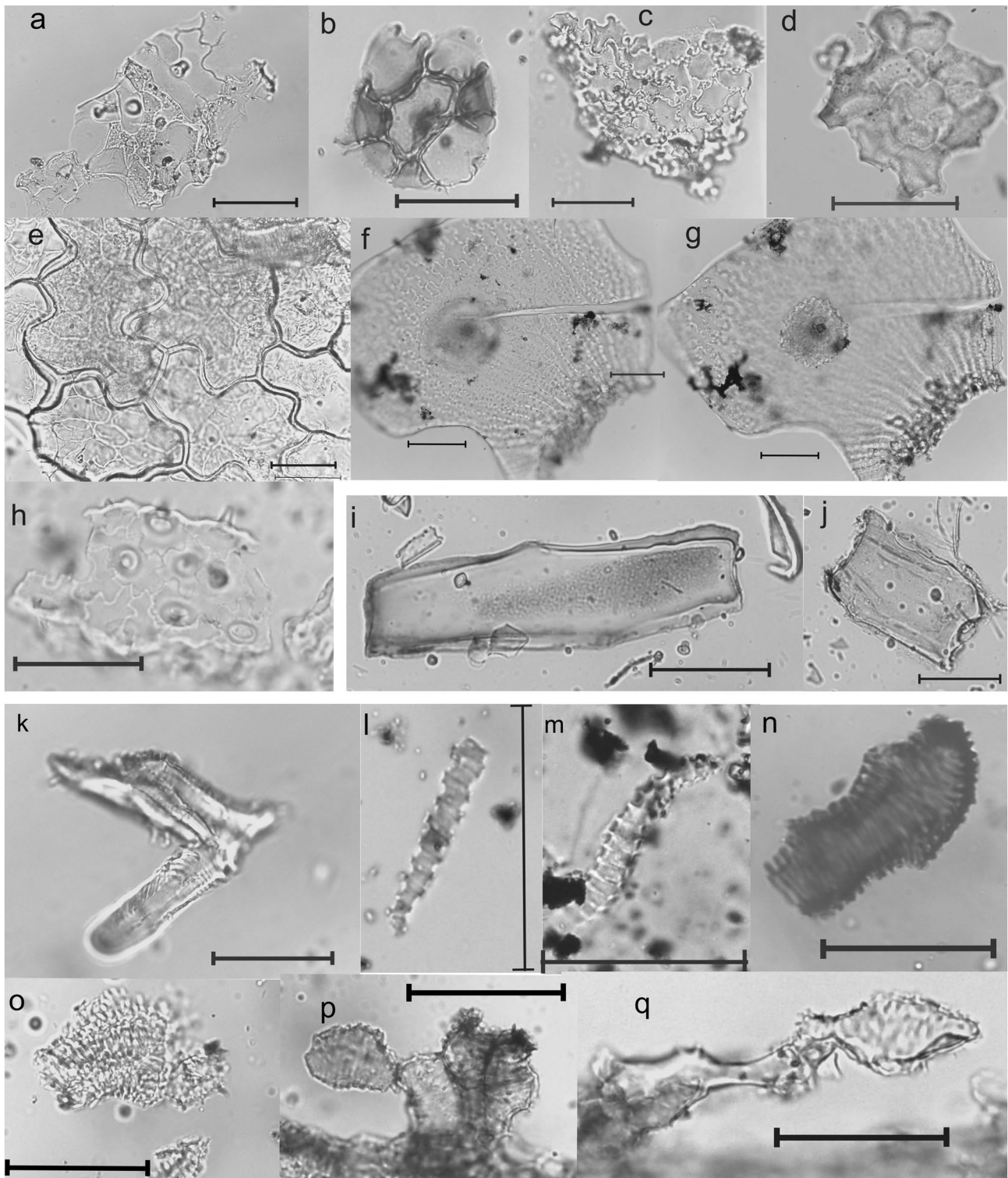
*Rubus ulmifolius* is an abundant non-endemic native blackberry of the Rosaceae family that, like the rare Canary *Rubus* endemics *R. bollei* and *R. palmensis*, grows in open, disturbed parts of the laurel forest or other moist habitats, such as ravine beds. We found articulated POLYGONAL GRANULATE (POY\_GRA\_1) (34%) in *R. ulmifolius* (Fig. 5j), which seems to be consistent with previous studies such as that on *R. praecipuus* (Piperno 1988), meaning that their presence in the sedimentary record could denote disturbance. In addition, *Rubus* sp. fruits have been consumed by humans in the Canary Islands since pre-Hispanic times (Viana 1968). For example, *R. idaeus* (raspberries) were traditionally used to make a raspberry wine or liquor (Morales and Gil 2014b). Finally, *Tuberaria guttata* (Cistaceae) is a native herbaceous species that has a wide global distribution. In the Canaries, it is found in grasslands, pasture, path edges and disturbed places in the thermophilous, laurel and pine woods, meaning that the detection of its HAIR BASE morphotypes (HAI\_BAS\_2) (20%) (Fig. 4q) could indicate disturbance at a site.

### Phytolith production and preservation

The resulting phytolith production values show that the main phytolith producers in the Canary Islands are species within the Arecaceae, Boraginaceae, Cyperaceae, Poaceae and Urticaceae (Fig. 2, ESM 1 Table S2). The Arecaceae, Cyperaceae and Poaceae are widely known to be prominent producers (Piperno 2006). High production of phytoliths in Boraginaceae and Urticaceae also goes in accordance with previous studies; for instance, Hodson et al. (2005) indicated a relatively high shoot silica concentration in both Boraginaceae and Urticaceae. Piperno (2006) also mentioned the production of phytoliths in Boraginaceae and Tsartsidou et al. (2007) noted high production of hair phytoliths in Urticaceae.

We did not recover phytoliths from four species, *Aeonium canariense*, *Euphorbia aphylla*, *Limonium pectinatum* and *Lycium intricatum*. This does not imply that they are categorised as non-producers, but rather that they need further study (ESM 1, Categorization of taxa by family). The low producers in our list include *Arbutus canariensis* (Ericaceae), *Artemisia thuscula* (Asteraceae), *Asphodelus aestivus* (Xanthorrhoeaceae), *Bencomia exstipulata* (Rosaceae), *Chamaecytisus proliferus* (Fabaceae), *Convolvulus floridus* (Convolvulaceae), *Davallia canariensis* (Davalliaceae), *Ferula linkii* (Apiaceae), *Olea cerasiformis* (Oleaceae), *Pericallis lanata* (Asteraceae), *Rhamnus glandulosa* (Rhamnaceae), *Spartocytisus supranubius* (Fabaceae) and *Tamarix canariensis* (Tamaricaceae) (ESM 1 Table S2). Three species belonging to the Asparagales (*Asphodelus aestivus*, *Dracaena draco* and *Drimys maritima*) are also relatively low producers, as well as *Lavatera acerifolia* and taxa within the Hypericaceae and Convolvulaceae. In sum, phytolith production in most families with published studies was as abundant as expected (Cyperaceae, Poaceae), but in others such as the Lauraceae it is promising, as their pollen grains are rarely present in sediment records. Species within the Asteraceae, Boraginaceae, Brassicaceae, Cistaceae, Euphorbiaceae, Lamiaceae, Ranunculaceae, Rubiaceae and Urticaceae have morphotypes of potential diagnostic value, which provides an incentive to expand the collection to more species of the Canary Islands and Macaronesia. While we found that common non-diagnostic morphotypes dominate the phytolith assemblages, there is diagnostic potential in some less common types. This means that upon finding an abundance of non-diagnostic phytoliths, it is by their association with less frequent yet diagnostic types that past plant presence can be inferred. Therefore, analysts should consider doing additional scans of their slides to find them in the sediment record.

Another aspect to consider is the differential preservation of morphotypes produced by the selected plants in both archaeological and palaeoecological contexts. It has been demonstrated that certain morphotypes are relatively less stable than others, such as grass silica short cell phytoliths preserving better than elongate ones, mostly depending on their surface area to volume ratio (Cabanes and Shahack-Gross 2015). For instance, we could expect worse preservation of flat morphotypes such as ACICULAR, ELONGATE, HAIR BASE and POLYGONAL cell walls compared with better preservation of spheroidal types such as ELLIPSOIDAL, OVATE and SPHEROID, leading to the under-representation of the former and over-representation of the latter. This, however, would depend on the context and type of deposit analysed in each study.



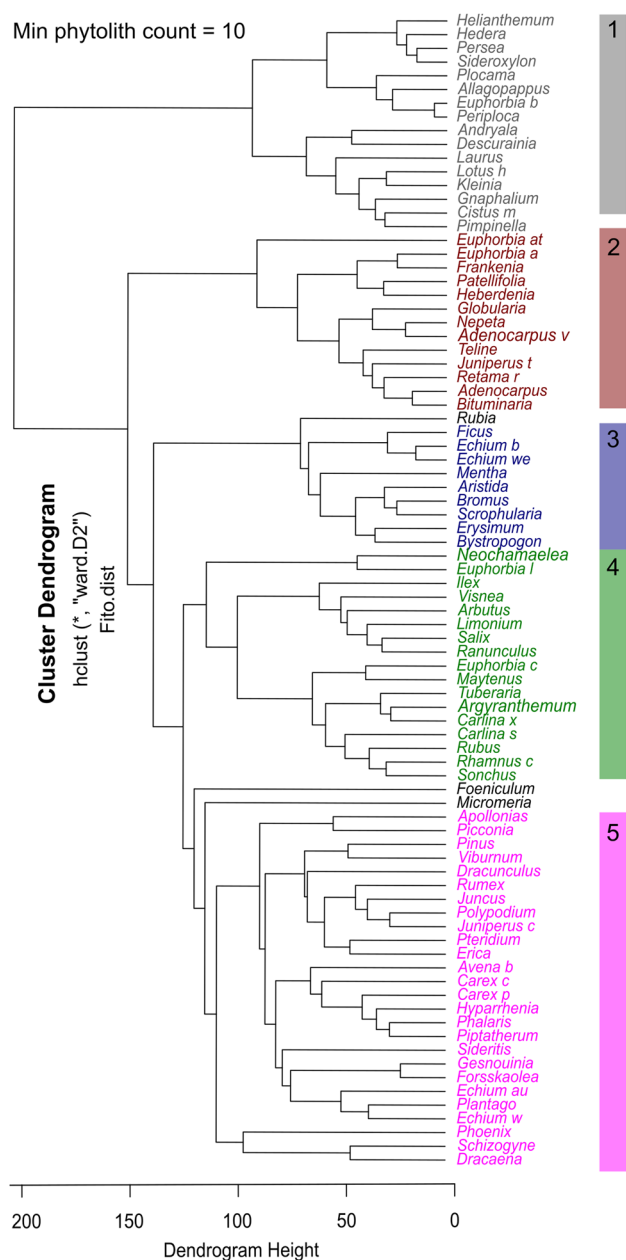
**Fig. 6** **a**, TABULAR SINUATE (ARTICULATED) (TAB\_SIN\_1, *Carlina salicifolia*); **b**, TABULAR SINUATE (ARTICULATED) (TAB\_SIN\_2, *Ilex canariensis*); **c**, TABULAR SINUATE (ARTICULATED) (JIG\_PSI\_2, *Laurus novocanariensis*); **d**, TABULAR SINUATE (ARTICULATED) (TAB\_SIN\_3, *Picconia excelsa*); **e**, TABULAR SINUATE (ARTICULATED) (TAB\_SIN\_4, *Ranunculus cortusifolius*); **f, g**, TABULAR SINUATE (ARTICULATED) (TAB\_SIN\_5, *Forsskaolea angustifolia*); **h**, TABULAR SINUATE with ACICULAR (ARTICULATED) (TAB\_SIN\_6, *Micromeria lachnophylla*);

**i**, TABULAR BULBOUS (TAB\_BUL, *Echium webbii*); **j**, TABULAR BULBOUS (TAB\_BUL, *Echium brevirame*); **k**, TRACHEARY HELICAL (TRA\_HEL\_1, *Laurus novocanariensis*); **l, m**, TRACHEARY HELICAL (TRA\_HEL\_2, *Sideroxylon canariensis*); **n**, TRACHEARY HELICAL (TRA\_HEL\_2, *Schizogyne sericea*); **o**, TRACHEARY PITTED (TRA\_PIT\_1, *Neochamaelea pulverulenta*); **p**, TRACHEARY PITTED (TRA\_PIT\_1, *Euphorbia balsamifera*); **q**, TRACHEARY PITTED (TRA\_PIT\_2, *Plocama pendula*); scale bars = 50  $\mu$ m

## Cluster and ordination analyses

The species have been grouped into five main clusters according to their most abundant morphotypes using RStudio v. 1.1.456 and these results are shown in a dendrogram (Fig. 7). Cluster 1 (in grey in Fig. 7) is composed of species that show combinations of abundant TRACHEARY, articulated POLYGONAL and hair bases, including Lauraceae trees (*Laurus novocanariensis* and *Persea indica*) and abundant producers of TRACHEARY such as *Euphorbia balsamifera*. Cluster 2 (brown) groups species such as *Juniperus turbinata* ssp. *canariensis*, *Bituminaria bituminosa* and *Adenocarpus foliolosus*, which produce varied assemblages that include SPHEROIDS and AMOEBOID (ESM 1 Fig. S1). Cluster 3 (blue) is composed of the four studied *Echium* species and *Ficus carica*, dominated by ACICULAR types (ESM 1 Fig. S1). Cluster 4 (green) includes producers of POLYGONAL types such as species within the Asteraceae. Cluster 5 (magenta) includes a wide variety of species including members of the Cyperaceae and Poaceae, as well as other species such as *Phoenix canariensis*.

The plot of the principal component analysis (PCA) shows the two most important gradients of phytolith morphotypes and species associations, with axis 1 accounting for 17% of the explained variance (eigenvalue 495) and axis 2 accounting for 10% (eigenvalue 272) (Fig. 8). The analysis reveals spread in three vectors (directions). There are three groupings of elements (species and morphotypes) in the diagram, those that plot in the lower left quadrant, those in the lower right, and those that cluster in the upper centre of the diagram (Fig. 8). The ordination analysis is useful to visualize how some morphotypes can help differentiate between species groups, including ACICULAR PSILATE, HAIR BASE, TRACHEARY, articulated POLYGONAL, SPHEROIDS, AMOEBOID and ELONGATE SINUATE. Their explanatory power in the ordination is a product of their great abundance. While an analyst can get a first overview of which species are likely to be represented in a sample as high percentages of these common types, they are not diagnostic of any particular species. It is by the combination of these common types, together with rare diagnostic ones, that particular plants can be identified. We suggest that when trying to record rare yet diagnostic phytoliths, analysts should make quick scans of slides before and after reaching the standardized minimum count of 250 phytoliths, as is recommended for archaeological samples (Zurro et al. 2016). Overall, quantitative analyses (cluster and ordination) show that there is no clear-cut pattern in terms of how taxonomic or ecological relationships are reflected in phytolith assemblages. For instance, *Apollonia barbuja* and *Picconia excelsa* grow in a similar habitat, laurel forest, but are in different taxonomic groups (Lauraceae vs. Oleaceae). They are clustered together, but far away from the other laurel forest

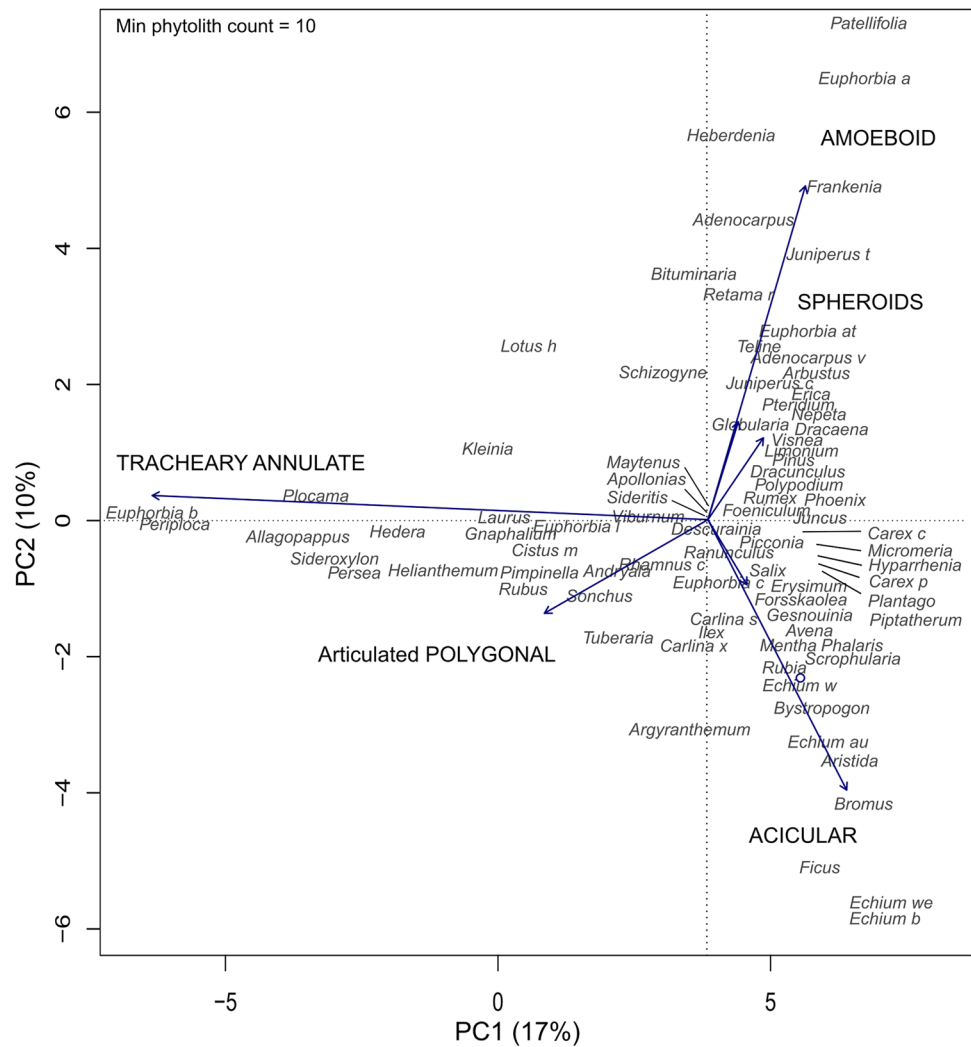


**Fig. 7** Cluster dendrogram (Ward's method, Euclidean distance, by Rstudio) of the main phytolith producers (with >10 phytoliths in the final count sum) grouped according to morphotype percentages. Coloured text and boxes on the right show the five main clusters

tree species (*Laurus novocanariensis* and *Persea indica*), which belong to the same Lauraceae family.

While some species within the same genus often produce similar phytoliths, as do *Juniperus cedrus* ssp. *cedrus* and *J. turbinata* ssp. *canariensis*, which cluster together, as well as both *Carlina salicifolia* and *C. xeranthemoides*, others such as the various species of *Euphorbia* produce very different

**Fig. 8** Principal component analysis plot showing the main associations of phytolith morphotypes (blue arrows, black lettering) and species (grey lettering, full species names in ESM 1 Table S1) in two axes (PC1, PC2). It includes species in the reference collection with a phytolith sum >10 in the total count



phytolith assemblages. The smallest distance analysed is between *Euphorbia balsamifera* and *Neochamaelea pulverulenta*, which belong to very distant families, but share the same habitat, indicating that their similar assemblages with articulated POLYGONAL and ANTICLINAL are probably a functional response to the same environmental factors (Tsartsidou et al. 2007). Another clear example is that of OVATE FACETATE phytoliths in laurel forest trees, which have been found in *Apollonias barbujana*, *Persea indica* and *Visnea mocanera*, and are similar to OVATE FACETATE found in *Erica arborea*. Such a pattern confirms that while taxonomy is central, adaptations to the environment can also play a role in phytolith production. This has interesting implications, as phytolith assemblages could be successfully linked to vegetation zones, if they are systematically studied in soils from different ecosystems and climatic zones in the islands.

## Conclusions and future directions

By assembling and studying the first reference collection of phytoliths for the Canary Islands, we have managed to categorise the various plant species depending on the types of phytoliths they produce and amounts, and also by noting types with diagnostic potential based on their general shape (either 3D or 2D), surface texture, ornamentation and wall thickness, among other features such as size and the distribution of surface ornamentation. From this we have presented here a first overview of the main phytoliths produced by taxa of the different vegetation zones in the Canary Islands. We have shown the complexity of interpreting phytoliths from there, as production and preservation biases need to be taken into account to interpret phytolith assemblages depending on their context.



Future directions in using this line of proxy evidence for archaeological and palaeoecological studies include the checking of phytoliths in various parts of plants with known cultural value, depending on archaeological research questions. A biogeographical perspective should also be taken into consideration. Many species in the Canary Islands show insular secondary woodiness, such as *Echium* and *Sonchus*; their phytoliths may be very different to those of their mainland relatives, a topic that should be explored in future studies.

The study of phytolith representation in modern and ancient soils of the islands would also help understand patterns of vegetation distribution of particular plant groups to reveal past ecological and climatic changes. Finally, particular case studies would help to understand issues of differential preservation and taphonomic processes. Combining phytolith studies with those of other macro- and microfossils, and using molecular analytical techniques, would reveal the full potential of phytolith studies in achieving a more complete understanding of past vegetation change and culture-environmental interactions in the Canary Islands and other islands in the Macaronesian region that share similar taxa.

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