

Article

Phytoliths and Pollen from a Desert Wetland Through the Last Glacial–Interglacial Cycle in Azraq, Jordan

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Abstract

Phytoliths, pollen, and spores in a stratigraphic sequence from the Shishan Wetland (Azraq Basin, Jordan) and supported by modern pollen and phytolith data provide information on vegetation, climatic trends, and the influence of fire through MIS 2 and MIS 1. Additionally, a pilot study introduces an innovative approach that uses shape and morphometric parameters of BULLIFORM phytoliths to assess hydro-climatic changes. The phytolith terrestrial–aquatic ratio, grass–pollen size, and the *Artemisia*–Amaranthaceae ratio (A:C) indicate that during the Last Glacial Maximum (LGM), the study area was a wetland surrounded by steppe, and that during the deglaciation period (c. 20–11 ka), the wetland vegetation remained almost unchanged but the surrounding area tended to aridity. The phytoliths’ terrestrial ratio, the presence of C₄ grass phytoliths, and the low A:C is characterized by a reduced wetland and the establishment of a hot desert, like the present. The record at Shishan Marsh shows effective moisture trends concurrent with other records in the western southern Levant, but climatic events (Heinrich Stadial 1 and Younger Dryas) are not recorded because of the low time-resolution of the studied sequence. This study shows that combining pollen and phytoliths strengthens vegetation reconstruction by discerning local from regional floristic components and that BULLIFORM phytoliths are a potential tool to reconstruct hydro-climatic conditions.

Keywords: pollen; phytoliths; last glacial maximum; deglaciation period; Holocene; desert wetlands; Levant; bulliform phytoliths; Azraq Oasis



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1. Introduction

The climatic changes that occurred from the Last Glacial Maximum (LGM) to the onset of the current interglacial (the Holocene) in the Levant are crucial for understanding the environmental context of human societal changes that led to sedentism and the eventual development of agriculture and sedentary societies [1–3]. The paleoclimatic background for that period derives from various terrestrial records, including speleothems in caves,

sediment and landforms in the Dead Sea, and other lakes [4–10], most of which are from the western part of the Levant, closer to the Mediterranean Sea. In contrast, the more arid, eastern part of the southern Levant lacks a solid and continuous paleoclimatic record, given its fragmented sedimentary record [11].

Nevertheless, the archaeological record in the dry parts of the Levant during the glacial–interglacial transition document significant cultural changes, concurrent in large part with those in the western part of the Levant, especially in relation to the transition to sedentism and the use of plants and their ecosystems [3,12]. The southeastern Levant, which encompasses practically all the territory of Jordan, has a variety of climates and ecological zones, including a gradient from Mediterranean woodlands to deserts (Figure 1a). Within this area, the Azraq Basin has been the focus of archaeological research, especially in areas along streams and around oases.

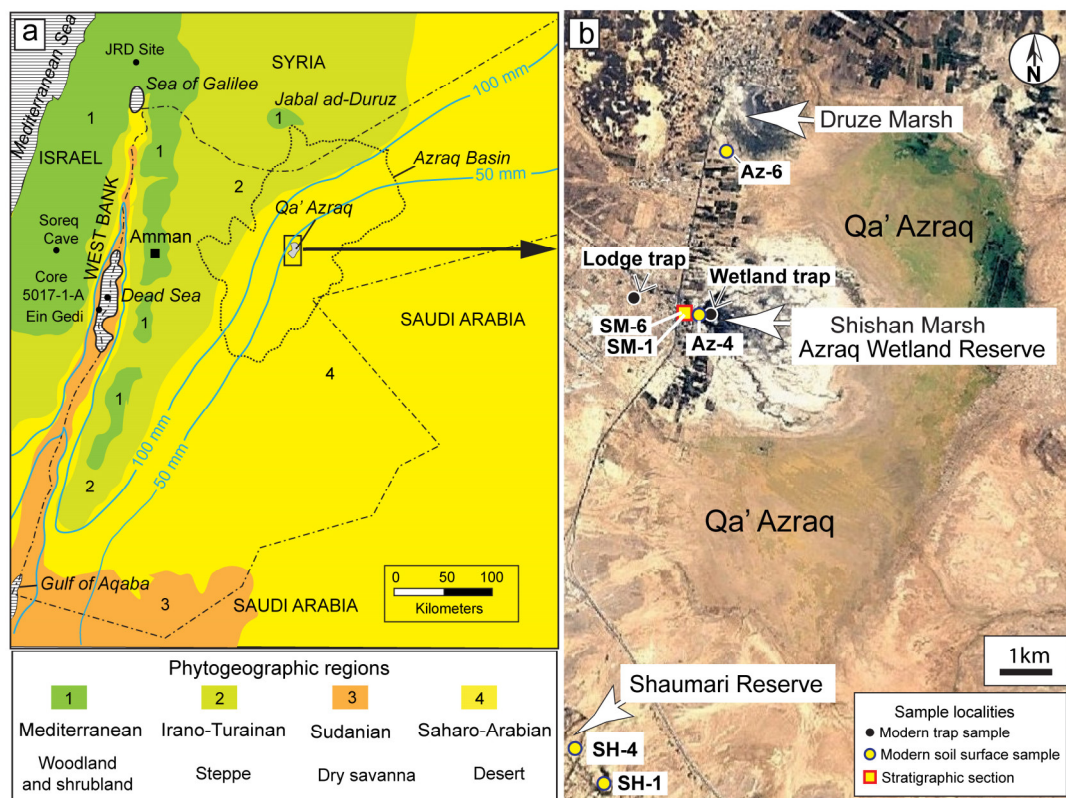


Figure 1. Regional and local context of this study: (a) Phytogeographic map of Jordan and adjacent countries [13,14] with localities mentioned in text, and (b) the Greater Azraq Oasis Area (GAOA) with sampling localities and stratigraphic sections.

The Greater Azraq Oasis Area (GAOA), located in the central part of the Azraq Basin (Figure 1), has produced various paleoclimatic records based on sedimentological parameters [15–17], pollen [18,19], and phytoliths [20,21]. Although these are short, fragmented, or have low resolution, they have been the basis for understanding local changes associated with certain periods of prehistoric and historic human occupation around the oases.

During several years of research in the GAOA, the Azraq Marshes Archaeological and Paleoecological Project (AMAPP) has focused on dating sediments and testing different paleoclimatic proxies. This resulted in the discovery of some potential sources of material for reconstructing paleoenvironments, such as sedimentological analyses, faunal remains, and pollen and phytoliths [17,22–24]. Although many of the stratigraphic sections tested show high potential for paleoenvironmental reconstruction, others have low time resolution because of low sedimentation rates and erosional gaps. However, section SM-6, located

in the Shishan Marsh area presents a record of wetland sedimentation spanning the last glacial maximum (LGM), the Deglacial Period, and the Holocene. Despite lacking the ideal resolution for deriving a detailed sequence of environmental change, section SM-6 permits reconstruction of patterns of vegetation change from full glacial to full interglacial conditions, thus providing information for interpreting previous glacial and interglacial conditions associated with the late Early and Middle Paleolithic in the Azraq Basin and the broader driest regions of the Levant.

One of the main questions regarding the climatic conditions of the LGM in the southern Levant refers to the effects of global cold conditions on regional moisture and their influence on flora, fauna, and human subsistence. Records from the Dead Sea levels (i.e., Lake Lisan) and stable isotopes from cave speleothems imply more effective moisture than today [6,8] despite evidence that the restricted distribution of arboreal pollen taxa indicates less moisture than today [8,10]. The apparent cause of the divergence of records has to do with the precipitation–evaporation balance and low temperatures caused by low summer insolation that would create a positive balance for bodies of water and water percolating into the sub-surface [8,25]. Stable carbon isotopic composition in speleothems shows a high abundance of C₃ over C₄ plants during the LGM, which suggests water availability in soils after rain and cold conditions [9]. This predominance of C₃ plants concurs with the low abundance of C₄ plants (e.g., *Amaranthaceae*) in pollen records [8,10,14].

Although there are no records for the LGM in the Azraq Basin, the climatic conditions recorded in the Dead Sea and Soreq cave would have been influenced by low temperatures caused by low summer insolation, except that being farther away from the source of rainfall (the Mediterranean) it would have been much drier. Nevertheless, the important presence of Early Epipaleolithic (c. 23–19 ka) occupations and the abundance of game in the faunal record suggest that the local environment during the LGM appears not as harsh as the current desert conditions [2,15,16,20]. Sedimentological records at the Druze and Shishan marshes and 'Ayn-Qasiyya in the GAOA (Figure 1b) indicate widespread organic deposits representing wetlands associated with Early Epipaleolithic occupation [15,17,22,26], suggesting that wetlands were an important contributor to the subsistence lifeways of Early Epipaleolithic people during the LGM [1,2,12].

This study uses phytoliths and pollen to reconstruct vegetation changes in the Shishan Marsh and surrounding areas during the past 26,000 years. Additionally, proxies such as burnt phytoliths and coprophilous fungi ascospores provide additional data to understand the ecological changes during this period. The aim of this study is to reconstruct the context of faunal species and human occupations in the GAOA during the LGM, Deglaciation, and Holocene. Furthermore, this study should contribute to understanding climatic conditions across previous glacial and interglacial periods to interpret Early and Middle Paleolithic occupations in the GAOA.

2. Study Area

2.1. Environmental and Archaeological Context

The SM-6 section is in the area known as 'Ayn Sawda in the Shishan Marsh, within the complex of wetlands and springs west of Qa' Azraq, located in the center and lowest part of the endorheic Azraq Basin, in the Eastern Jordanian Desert (Figure 1). All the drainages of the Azraq Basin are ephemeral, which under intense rains carry water into the salt flat (Qa' Azraq), where it evaporates [27].

The mean annual precipitation in the study area is between 50 and 100 mm, occurring intermittently between October and April [28]. Temperatures in the wintertime can drop to 0 °C but usually stay around 15 °C during the day, while daytime temperatures during the summer are often between 40° and 45 °C. Despite the intense evaporation, the flow of

water from springs connected to near-surface aquifers has fed several wetlands [28]. That process was dynamic until the springs dried up, since water from the aquifer has been tapped to supply the most populated regions of the country. The Shishan Marsh has been partially replenished by water pumped from a deeper aquifer, thus creating a wetland that is now the Azraq Nature Reserve. The Druze Marsh to the north remains dry to this day.

Marine limestones of Upper Cretaceous to Miocene age constitute most of the geologic units in the Azraq Basin, with the Umm Rijam Chert Limestone dominating in the central part of the basin [29,30]. Basalts of the Neogene and Pleistocene ages, originating from a complex of volcanic vents extending into the Jebel Druze mountain complex in Syria, dominate the geology of the northern part of the Basin [29,30]. Fractures in the limestone constitute an important factor supporting the springs of the Shishan Marsh, while porosity of the basalt conducts water from the north from Jebel Druze in Syria to the springs north of Qa' Azraq, being the main source of water that feeds the Druze Marsh (Figure 1b) [28,30].

The archaeological record of the GAOA has been explored and documented in the late part of the past century, especially around springs and along fluvial drainages [31–33]. Nevertheless, the wetlands remained largely unexplored until their drying forced local inhabitants to dig deeper to reach the falling water table, thus exposing sedimentary layers rich in archaeological materials and faunal remains [21,23,24,32–34]. This permitted the study of numerous occupation deposits comprising the late Lower, Middle, and Upper Pleistocene [17,22,23,26]. In addition to organic layers and spring deposits, the stratigraphy of the wetlands includes lacustrine, fluvial, and eolian sedimentary facies, sometimes marking gaps between occupations [15,17].

In the GAOA, outside the former wetlands, extensive areas of surface material encompass periods from the Lower Paleolithic to Middle Paleolithic, with smaller and more concentrated areas of Neolithic [35]. Most of the surface material is exposed by deflation or redeposited in the wadi drainages. In situ archaeological materials are limited to deposits in the former wetlands, especially the Druze Marsh, Shishan Marsh, and smaller oasis areas such as the C-Spring and Lion's Spring, located in the vicinity of Shishan Marsh [17,21,33,36]. These studies have revealed stratified materials encompassing the late Acheulean (c. 500–300 ka), the Middle Paleolithic (c. 250–47 ka), very limited Upper Paleolithic (c. 47–26 ka), Epipaleolithic (c. 23–11.5 ka), and other younger periods during the Holocene.

2.2. Vegetation and Phytolith-Producing Plants

Vegetation in the Azraq Basin includes the Saharo–Arabian and Irano–Turanian floristic provinces (Figure 1a). The Saharo–Arabian province consists of desert vegetation, predominantly shrubs of the Amaranthaceae family, such as *Noaea mucronata* and *Anabasis articulata*, and the Fabaceae family, such as *Retama raetam* [13,14]. The Irano–Turanian province, which occupies the western third of the Basin, consists of a steppe, including a variety of grasses and herbs, as well as shrubs such as *N. mucronata* in the lowest parts and *Artemisia herba-alba* in the highest parts. However, given the heavy impact of pastoral activities, most of this region consists of scrub, which sometimes makes it difficult to differentiate the Irano–Turanian from the Saharo–Arabian province [14].

Around the study area, desert vegetation belongs to the Saharo–Arabian province, though very important here is the salt plain and the wetlands. The salt plain (i.e., Qa' Azraq), which sustains mostly halophytic scrub and shrubs such as *Atriplex halimus* and *Nitraria retusa*, tall shrubs such as *Tamarix* spp., and clumps of *Aeluropus litoralis* grass [13].

The wetlands sustain mainly aquatic graminoids, notably the reed grass, *Phragmites australis*, and several species of the Typhaceae, Juncaceae, and Cyperaceae families. Around the wetlands and former springs, *Phoenix dactylifera* (date palm) is common, though they

are probably cultivated, as their characteristic pollen and phytoliths are absent in the prehistoric layers of the local deposits (see Sections 4 and 5).

The diagnostic phytoliths in this region are produced by grasses (Poaceae), sedges (Cyperaceae), and palms (i.e., *Phoenix dactylifera*) [3,20,21]. Of these, the Poaceae have the most diverse phytolith morphotypes that permit the determination of different grass taxa, usually at the level of subfamily and tribe (Table 1), each of which indicates environmental or climatic conditions, rendering phytoliths a good proxy for reconstructing paleoclimates and paleoenvironments.

Table 1. Modern native grasses in the Azraq region and surroundings *.

Subfamily	Tribe	Name	Photosynthetic Pathway	Habitat
Pooideae	Poeae	<i>Lolium rigidum</i> Gaudin	C ₃	Terrestrial
		<i>Phalaris minor</i> Retz.	C ₃	Terrestrial
		<i>Poa bulbosa</i> L. <i>Poa sinaica</i> Steudel	C ₃	Terrestrial
		<i>Polypogon monspeliensis</i> (L.) Desf.	C ₃	Terrestrial
		<i>Rostraria berythea</i> (Boiss. & Blanche) Holub	C ₃	Terrestrial
	Triticeae	<i>Hordeum glaucum</i> Steudel <i>Hordeum spontaneum</i> C. Koch <i>Taeniatherum crinitum</i> (Schreber) Nevski	C ₃	Terrestrial
		<i>Stipa arabica</i> Trin. & Rupr. <i>Stipa hohenackeriana</i> Trin. & Rupr. <i>Stipa capensis</i> Thunb.	C ₃	Terrestrial
Panicoideae	Andropogoneae	<i>Imperata cylindrica</i> (L.) Raeusch.	C ₄	Subaquatic
	Paniceae	<i>Setaria verticillata</i> (L.) P. Beauv	C ₄	Terrestrial, disturbance
Chloridoideae	Cynodonteae	<i>Aeluropus littoralis</i> (Gouan) Parl	C ₄	Halophytic
		<i>Cynodon dactylon</i> (L.) Pers.	C ₄	Terrestrial, disturbance
Aristidoideae	None	<i>Stipagrostis lanata</i> (Forsk.) De Winter <i>Stipagrostis</i> Nees.	C ₄	Terrestrial
		There are nine species in Jordan		Terrestrial
Arundinoideae	None	<i>Phragmites australis</i> (Cav.) Trin. ex. Steud.	C ₃	Aquatic
		<i>Arundo donax</i> L.	C ₃	Aquatic, invasive, usually in disturbed places
Danthonioideae	Danthonieae	<i>Schismus arabicus</i> Nees var. <i>minus</i> (Roemer & Schul) Boiss. <i>Schismus barbatus</i> (L.) Thell.	C ₃	Terrestrial

* Based on C.E.C. botanical survey and collection of specimens.

Grasses are divided by their photosynthetic pathway, with C₃ species adapted to lower temperatures and more moist conditions, and C₄ species adapted to higher temperatures and dryness [37]. However, given that the rainy season in this region is in the coldest part of the year, most of the terrestrial grasses observed today in the landscape are C₃, with C₄ found mainly in wet or disturbed areas, or on salt flats, with other species found in the desert [13,14,38] (Table 1). The majority of the C₃ grasses in the region belong to the subfam-

ily Pooideae [14], though other grasses such as *Schismus arabicus* and the aquatic *Phragmites australis* belong to the Danthonioideae and Arundinoideae subfamilies, respectively.

The only prominent C₄ grasses today in the area are *Aeluropus litoralis* (subfamily Chloridoideae) on salt flats, and *Stipagrostis* species (subfamily Aristidoideae) on sandy and stony soils in the desert. Other C₄ grasses of the Panicoideae and Chloridoideae subfamilies appear occasionally in irrigated areas and disturbed wet areas, where competition with *P. australis* is absent.

The most important aquatic grass is *Phragmites australis* (subfamily Arundinoideae), which is a tall reed that forms dense stands that provide shelter to several species of waterfowl and provides humans with construction material for huts and linings for daub roofs and walls [28]. Additionally, the wetland supports several species of Juncaceae and Cyperaceae, of which the latter is the only one that produces diagnostic phytoliths (see Section 3.3).

3. Materials and Methods

3.1. Sampling

Samples from section SM-6 were collected from each discrete sedimentary layer or bed. However, in layers thicker than 10 cm, more than one sample was taken. Samples were transported to the laboratory at Oklahoma State University, where they were first sieved through a 125 µm mesh, weighed, and separated for extraction of phytoliths (1–3 g) and pollen (15 g). Samples to test modern pollen and phytolith assemblages were collected directly from soil surfaces at the Shaumari Reserve and the Azraq Wetland Reserve, the Shishan Marsh, and the Qa' Azraq (Figure 1b). Two traps consisting of plastic jars with a mesh and a roof to collect airborne pollen and phytoliths were installed for two years on the roof of the Azraq Lodge and on the roof of the birdwatching watch hut inside the Azraq Wetland Reserve (see locations on Figure 1b). Finally, a reference collection of 45 specimens, mostly grasses, was collected and processed as a reference collection of phytolith morphotypes used in the classification described in Section 3.3.

3.2. Processing and Analysis

The methods used for processing phytoliths and pollen from modern soil surface and section SM-6 samples are described in Appendices A.1 and A.2. Modern airborne pollen and phytolith samples were processed by removing carbonates with 35% HCl and unwanted organics with 10% KOH before being mounted on microscope slides using Entellan as a medium. The same slides were used for counting phytoliths and pollen.

Pollen data are presented as a percentage of the total pollen sum, though only those taxa with more than 1% relative abundance appear in the diagrams; full counts are included in the Supplementary Material. Spores are presented as percent of the total sum of pollen and spores. Additionally, pollen data are summarized in groups of environmental and climatic importance: Amaranthaceae, *Artemisia*, grasses, aquatics, Mediterranean trees, and other smaller groups. Grass pollen is divided into two groups. Those with diameter > 22 µm are attributed to terrestrial grasses, while those with diameter < 22 µm to *Phragmites australis* [19,39]. Although the latter is an aquatic grass, it is excluded from the group of aquatic taxa, which encompasses the aquatic Typhaceae, *Potamogeton*, *Persicaria*, and Haloragaceae, among others. As for the Mediterranean trees group, the pollen taxa include *Olea europaea*, *Quercus* spp., and *Pistacia* spp.

To better characterize the bioclimatic information inferred from pollen spectra, this study uses the *Artemisia* Amaranthaceae ratio (A:C) ratio, calculated by dividing the *Artemisia* (A) by the total Amaranthaceae (C) pollen counts and multiplying it by 100, $([A/C] \times 100)$. The A:C ratio is generally regarded as a proxy for moisture in the arid lands

of Eurasia, especially in relation to cold and wet desert vegetation [40], though in the Middle East it is also used to differentiate the Irano–Turanian steppe from the Saharo–Arabian desert [41,42].

3.3. Phytolith Classification

The classification of phytoliths uses the International Phytolith Nomenclature 2.0 (Neumann et al., 2019) [43]. They include the GSSCP (grass silicified short-cell phytoliths) (Table 2; Figure 2) and other morphotypes belonging to grasses, Cyperaceae, woody plants, and palm trees (Table 3; Figure 3). Other morphotypes are not used here because of their poor diagnostic value and redundancy across different groups.

Table 2. Grass silica short-cell phytolith (GSSCP) morphotypes and their taxonomic associations.

Morphotype and Code	Subtype	Code	Figure	Taxonomic Association
RONDEL (RON)	RONDEL TRAPEZOID	RON_TRP	Figure 2a	Several subfamilies, mostly Pooideae
	RONDEL HORNED	RON_HOR	Figure 2b	Several subfamilies
CRENATE (CRE)		CRE	Figure 2c	Pooideae and <i>Schismus</i> (subfamily Danthonioideae)
TRAPEZOID	TRAPEZOID LONG	TRP_LON	Figure 2d	
SADDLE (SAD)	SADDLE COLLAPSED	SAD_COL	Figure 2e	Chloridoideae
	SADDLE ROUND	SAD_ROU	Figure 2f	<i>Stipagrostis</i> spp. (subfamily Aristidoideae)
	SADDLE PLATEAUED	SAD_PLA	Figure 2g	<i>Phragmites australis</i> (subfamily Arundinoideae)
BILOBATE (BIL)	BILOBATE LONG NARROW	BIL_LON_NAR	Figure 2h	<i>Aristida</i> spp. (subfamily Aristidoideae)
	BILOBATE COLLAPSED WIDE	BIL_COL_WID	Figure 2i	Panicoideae
	BILOBATE COLLAPSED LONG	BIL_COL_LON	Figure 2j	Panicoideae
	BILOBATE TRAPEZOID	BIL_TRP	Figure 2k	Stipeae tribe (subfamily Pooideae)
CROSS (CRO)		CRO	Figure 2l	Panicoideae
POLYLOBATE		POL	Figure 2m	Panicoideae, Aristidoideae, and some Stipeae

The GSSCP defines grass subfamilies and, in some cases, grass tribes (Table 1). The subfamily Pooideae, the typical grasses found across different ecoregions of Jordan, produce the common RONDEL (i.e., RONDEL TRAPEZOID), the CRENATE, and the TRAPEZOID LONG Figure 2a,b,d), while the Stipeae tribe, also in the subfamily Pooideae, produce the BILOBATE TRAPEZOID (Figure 2k). *Phragmites australis*, subfamily Arundinoideae, the dominant grass in the wetland today, produces the SADDLE PLATEAUED (Figure 2g).

Grasses in the subfamily Chloridoideae produce the typical SADDLE COLLAPSED (Figure 2e), which are rare in the modern landscape but are found in disturbed areas or where there is water during the summer, while *Aeluropus litoralis* is common on the salt flats of Qa' Azraq (Table 1).

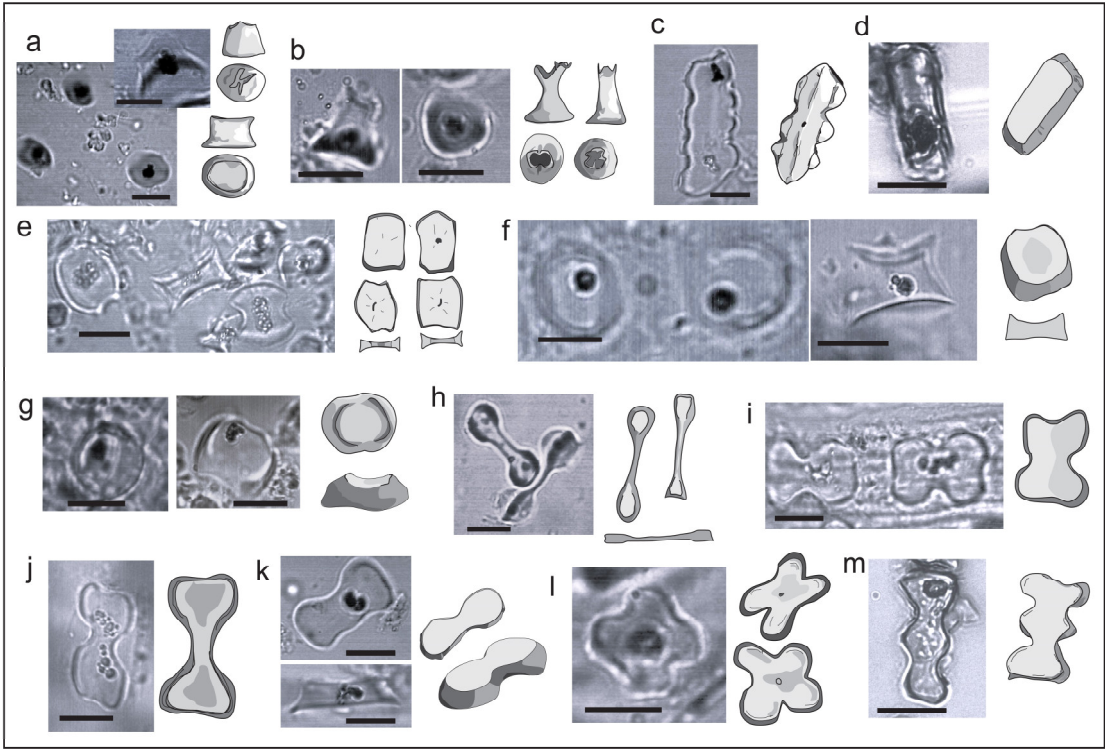


Figure 2. Grass silica short-cell phytoliths (GSSCP): (a) RONDEL TRAPEZOID (RON_TRP); (b) RONDEL HORNED (RON_HOR); (c) CRENATE (CRE); (d) TRAPEZOID LONG (TRP_LON); (e) SADDLE COLLAPSED (SAD_COL); (f) SADDLE ROUND (SAD_ROU); (g) SADDLE PLATEAUED (SAD_PLA); (h) BILOBATE LONG NARROW (BIL_LON_NAR); (i) BILOBATE COLLAPSED WIDE (BIL_COL_WID); (j) BILOBATE COLLAPSED LONG (BIL_COL_LON); (k) BILOBATE TRAPEZOID (BIL_TRP); (l) CROSS (CRO); (m) POLYLOBATE. Scale bar: 20 μm.

Table 3. Non-GSSCP phytoliths and associated taxa.

Morphotype and Code	Subtype	Code	Figure	Taxonomic Association
PAPILLATE		PAP	Figure 3a,b	Cyperaceae
SPHEROID	SPHEROID ORNATE	SPH_ORN	Figure 3c	Woody plants
	SPHEROID PSILATE	SPH_ORN	Figure 3d	Several dicots, including woody plants
	SPHEROID ECHINATE	SPH_ECH	Figure 3e	Palms (Arecaceae) <i>Phoenix dactylifera</i>
ACUTUS	ACUTUS BULBOSUS	ACU_BUL	Figure 3f	Poaceae and Cyperaceae
ELONGATE		ELO	Figure 3g,h	Poaceae and Cyperaceae
BLOCKY	BLOCKY TABULAR	BLO_TAB	Figure 3i,j	Poaceae and Cyperaceae
BULLIFORM	BULLIFORM FLABELLATE	BUL_FLA	Figure 3k–m	Poaceae
	BULLIFORM FLABELLATE LONG	BUL_FLA_LON	Figure 3n,o	Poaceae, particularly <i>Phragmites australis</i>

The only prominent genus in the subfamily Aristidoideae is *Stipagrostis*, which produces the SADDLE ROUND (Figure 2f), and is characteristic of the Saharo-Arabian desert. In the same subfamily, the genus *Aristida* produces the BILOBATE LONG NARROW (Figure 2h). Although associated with dryness or with overgrazing, it is rare in Jordan, as observed during sample collection and herbaria.

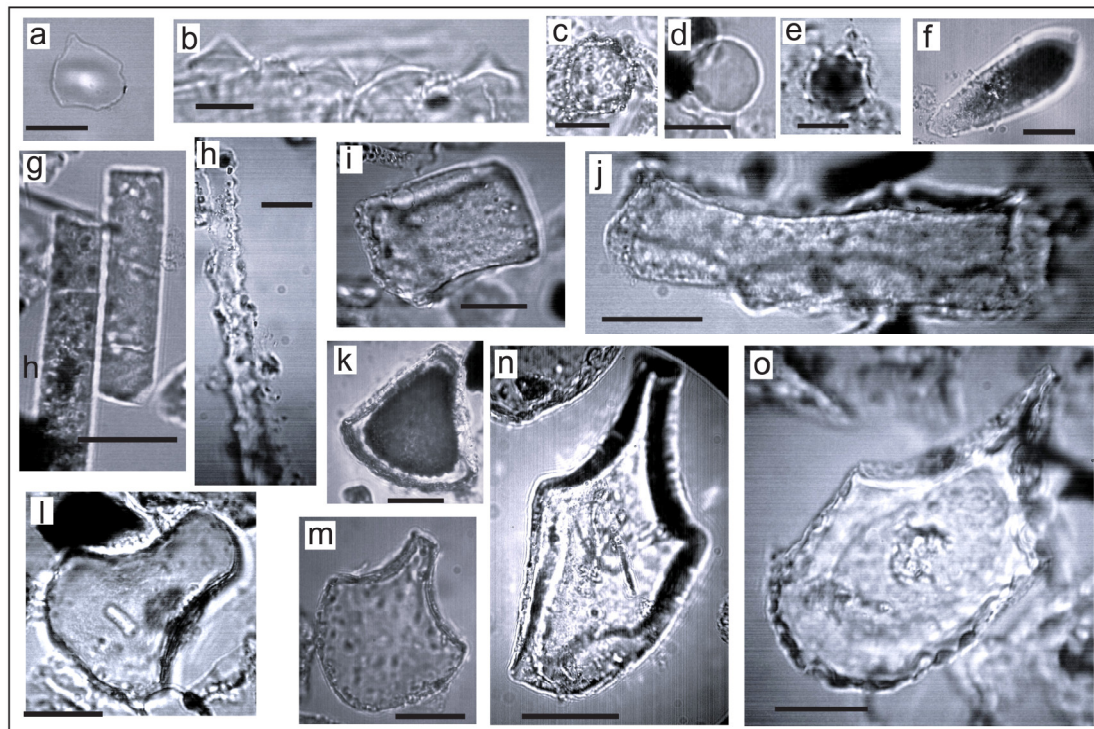


Figure 3. Other phytolith morphotypes used in this study: (a,b) PAPILLATE (PAP); (c) SPHEROID ORNATE (SPH_ORN); (d) SPHEROID PSILATE (SPH_PSI); (e) SPHEROID ECHINATE (SPH_ECH); (f) ACUTUS BULBOSUS (ACU_BUL); (g,h) ELONGATE (ELO); (i,j) BLOCKY TABULAR (BLO_TAB); (k–m) BULLIFORM FLABELLATE (BUL_FL); (n,o) BULLIFORM FLABELLATE LONG (BUL_FL_LON). Scale bar: 20 μ m.

Extremely rare in the region are grasses of the subfamily Panicoideae, which produce BILOBATE COLLAPSED NARROW, BILOBATE COLLAPSED WIDE, and CROSS morphotypes (Figure 2i,j,l). Their rarity has to do with the lack of summer rain, though it might be found in wet or disturbed areas. However, *Arundo donax* (subfamily Arundinoideae) produces BILOBATE morphotypes like those produced by Panicoideae (Table 2), though as mentioned earlier, this species is rare and associated with modern disturbed areas.

Two GSSCP morphotypes that appear in the assemblages, RONDEL HORNED (Figure 2b) and POLYLOBATE (Figure 2m), appeared in more than one family (Table 1). Although they are reported in the graphs, they are excluded from some of the climatic and paleoenvironmental indices.

Common phytoliths associated with Poaceae and Cyperaceae, among other groups, are ELONGATE and ACUTUS BULBOSUS morphotypes (Figure 3f–h). The PAPILLATE (Figure 3a,b) are commonly produced by Cyperaceae. The SPHEROID morphotypes (Figure 2f,g) include the SPHEROID ECHINATE produced by palms (Arecaceae), which, in this region is represented by *Phoenix dactylifera*. Other SPHEROID morphotypes, like the SPHEROID ORNATE are typically produced woody plants; the SPHEROID PSILATE, which is produced by woody plants, is also found in other plants [43].

Most grasses produce FLABELLATE BULLIFORM morphotypes (Figure 3k–o). However, the FLABELLATE BULLIFORM LONG (Figure 3n,o), a long and asymmetric variation of BULLIFORM types, is typically produced by *Phragmites australis* [44]. BLOCKY TABULAR morphotypes have different forms, from square to more rectangular or elongated (Figure 3i,j), and are usually produced by Poaceae and Cyperaceae, though they may be found in other plants. For that reason, they do not have a particular link to a taxonomic group.

3.4. Phytolith Indices and Measurements

The climatic associations of phytoliths are conveyed by indices (Table 4). The indices used here include the climatic index (Ic), which expresses the relationship between C₃ and C₄ [37,45], and the water stress index (Fs), which expresses a relationship with evapotranspiration [46]. Although the Fs was created in a tropical area, it is used here to test its usability in the subtropical dry environment of the study region. Additionally, the T:A ratio is used as a relation between terrestrial and aquatic grasses by using the SADDLE PLATEAUED as the aquatic part, given that it is the typical GSSCP produced by *Phragmites australis*. Other common phytolith indices are not used here, as in the case of the Aridity Index (Iph), because of the scarcity of C₄ grass subfamilies (Chloridoideae, Panicoideae, and Aristidoideae). The D:P ratio, which expresses the relation between woody plant and grass phytoliths, is not used here because of the scarcity of typically woody plant phytoliths (i.e., SPHEROID ORNATE and SPHEROID ORNATE).

Table 4. Phytolith indices and ratios.

Indices	Calculation	Source
Ic * Climatic index	$\frac{\text{All diagnostic GSSCP}}{\text{Sum of all GSSCP} - \text{SAD_PLA}} \times 100$	[37,45]
Fs Water stress index (%)	$\frac{\text{Percentage of all BULLIFORM FLABELLATE}}{\text{Sum of all grass phytoliths} - \text{All E}_{\text{LONGATE}}} \times 100$	[46]
T:A Terrestrial to aquatic grass ratio	$\frac{\text{All GSSCP} - (\text{RON_HOR} + \text{SAD_PLA})}{\text{SAD_PLA}}$	This study

*Adapted to the local conditions.

In addition to the phytoliths and indices, this study uses two other analytical variables tested on 25 random BULLIFORM morphotypes in each sample from section SM-6. The first variable is the classification of BULLIFORM FLABELLATE into three types and their frequency in each sample. These are Type 1, or the fan-shaped (e.g., Figure 3m), Type 2, or the typical BUL_FLA_LON (Figure 3n,o), and Type 3, which includes all other shapes. The second variable involves the length and width of all 25 BULL_FLA types, which is presented as averages per sample and the minimum and maximum length per sample. These parameters will permit an independent way to assess the Fs (water stress index), in which the calculation of BULLIFORM morphotypes plays an important role.

3.5. Radiocarbon Dating

The chronology of section SM-6 is supported by 18 radiocarbon dates derived from three different materials (Table 5) (Appendix A.3). Three samples of unidentified plant material were processed at the Center for Accelerator Mass Spectrometry (CAMS) of the Lawrence Livermore National Laboratory, USA. Sedimentary pyrogenic carbon (isolated through the hydrogen pyrolysis method) and pollen concentrates were processed and analyzed at the Chronos 14Carbon Cycle Facility of the University of New South Wales, Australia [47–49] (Appendix A.3).

Table 5. Average length and width in µm on modern samples of BULLIFORM morphotypes.

Sample	Avg L	Avg W	Type 1	Type 2	Type 3	Total N
SH4	55.28	38.24	1	8	16	25
Az-4	58.64	39.96	3	17	5	25
Az-6	58.92	39.68	2	19	4	25

The age model was constructed using rbacon [50], applying the Intcal20 calibration curve [51]. Of the age model outputs, the median for each depth was used (Supplementary Material). Additionally, one Optically Stimulated Luminescence (OSL) age from a correlative layer from a section nearby [34] was assessed into the model.

4. Results

4.1. Modern Phytolith Data

The phytolith morphotype assemblages in the modern samples vary considerably between desert, wetland, and salt flat (Figure 4). The dominant GSSCPs in the desert samples are those associated with the subfamily Pooideae, especially CRE and BIL_TRP, while those in the wetland and to a certain extent in the salt flat are associated with *Phragmites australis*, namely the SAD_PLA.

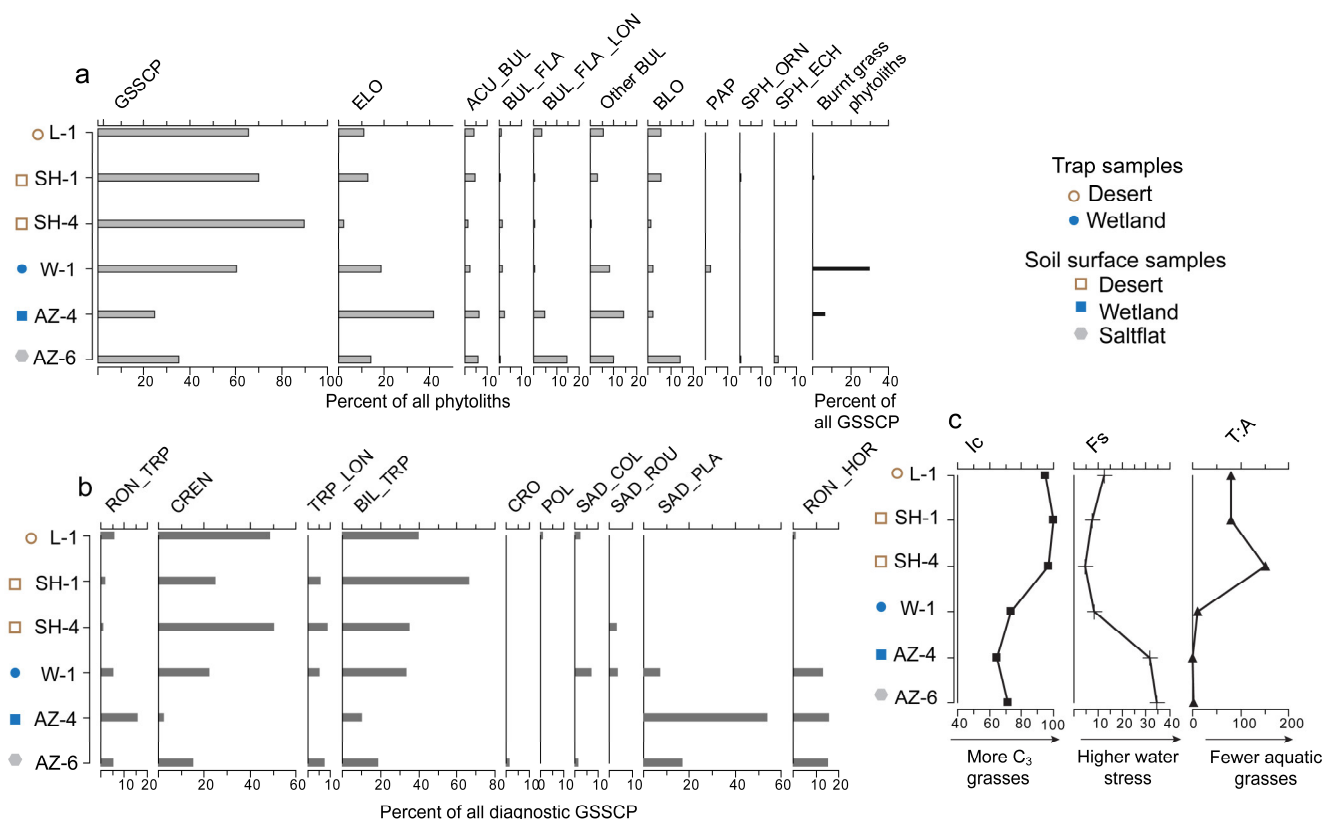


Figure 4. Modern phytolith assemblages from traps and surface. (a) Distribution of diagnostic morphotypes; (b) Distribution of diagnostic GSSCP; (c) Phytolith indices: climatic index (Ic), water stress index (Fs), and terrestrial to aquatic grass ratio (T:A).

GSSCP are proportionally more abundant in the desert samples, while ELO, BLO, and all BUL are more abundant in the wetland and salt flat. BUL_FL_LON, the typical BULLIFORM produced by *P. australis*, is totally absent in the desert samples. However, the trap sample in the wetland (W-1), located almost 3 m above the ground, has fewer BULLIFORM and BLOCKY than the soil sample in the wetland (AZ-4), which could be explained by their larger size making them more difficult to be transported by wind. PAPILLATE morphotypes are very rare despite the abundance of Cyperaceae in the wetland. Likewise, SPHEROID phytoliths are rare, with only one sample in the wetland producing SPH_ECH because of palm trees nearby. The percent burnt grass phytoliths are only important in the wetland, where recent fires have occurred.

The Ic reflects overall the dominance of C₃ grasses; however, the index is lower in the wetland, suggesting that some C₄ grasses may grow in wet and disturbed grounds. The Fs is higher in the wetland samples due to the higher production of BULLIORM in that area. The T:A ratio is high in the desert and salt-flat samples (L1, SH-1, SH-4) and low in the wetland and salt-flat samples (W1, Az-4 and Az6).

BULLIFORM measurements of length and width and classification into three types were possible only in samples SH-4, Az-4, and Az-6 (Table 5). The rest of the samples (L-1, SH-1, and W-1) did not contain the pre-established number of 25 counts for the measurement. The most salient aspect is that Type 1 (BUL_FLA_LON) is more abundant in the wetland (Az-4) and salt flat (Az-6) than in the desert sample (SH-4). Likewise, average and maximum length and width are larger in Az-4 and Az-6 than in SH-4.

4.2. Modern Pollen Data

The number of modern pollen samples is smaller than that of phytoliths, because in two of the samples (SH-4 and AZ-4) pollen was not preserved well enough for a reliable count. Still, the remaining samples show the regional pollen rain (Figure 5). The most notable differences are in the Poaceae (grasses) and aquatic taxa, which appear in higher proportions in the wetland samples. Higher proportions of Poaceae < 22 µm in the wetland samples are attributed to *P. australis*. Besides these differences, the only notable difference is the abundance of *Noaea*-type in SH-1 and *Nitraria* in W-1. The A:C ratio is generally low or 0 because of the high incidence of Amaranthaceae pollen in the general region, especially *Suaeda*-type pollen, which is produced by most species of this family.

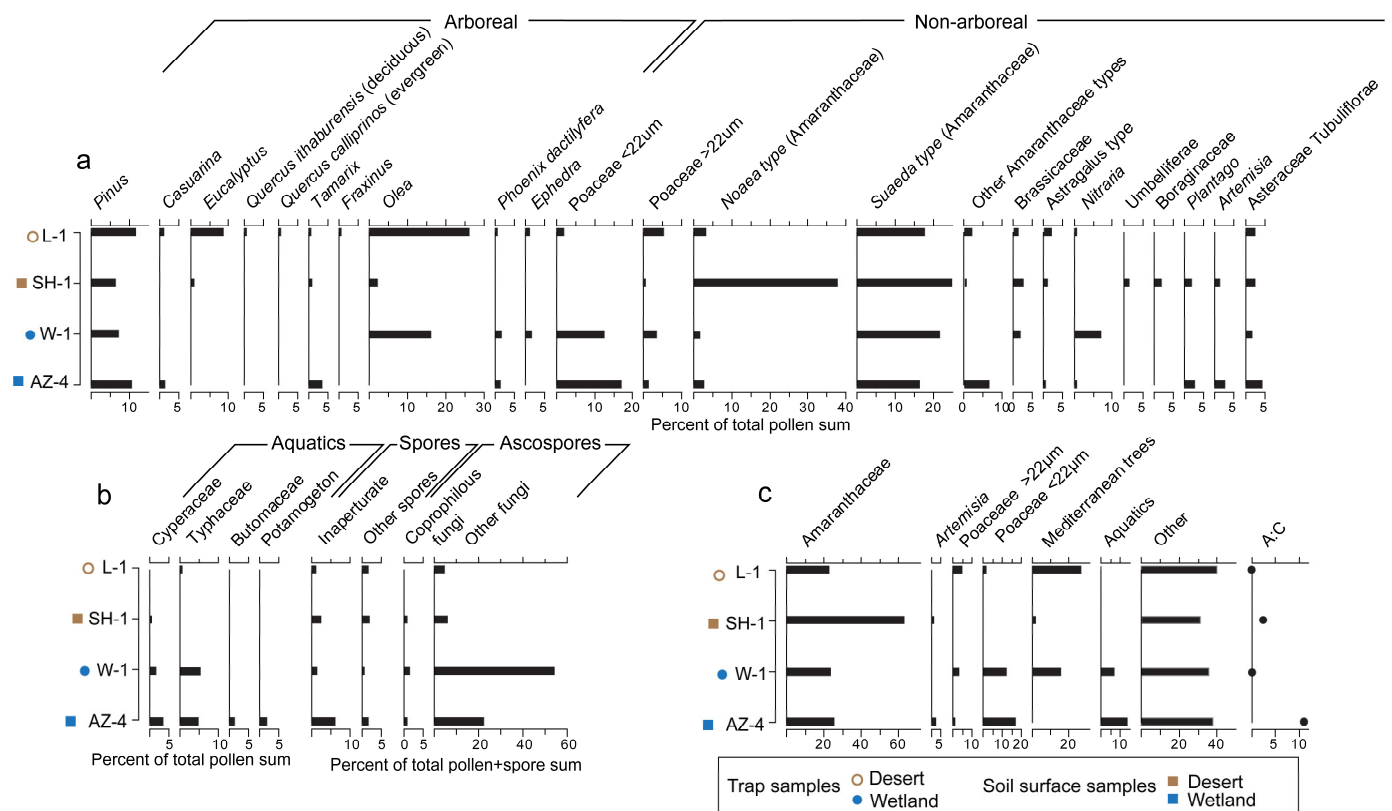


Figure 5. Modern pollen spectra from traps and surface. (a) Spectra of arboreal and non arboreal pollen; (b) Aquatics pollen, spores and ascospores; (c) Percentage by pollen group and A:C ratio.

Among the trees, *Pinus* is abundant, as it is usually carried from long distances, including natural forests and plantations. *Olea* pollen is high, given the extensive olive plantations all over Jordan, even in Azraq, where trees are sustained by irrigation. Pollen of introduced

trees such as *Eucalyptus* and *Casuarina*, common in Azraq, appear in considerable amounts in the modern samples. Non-local Mediterranean tree pollen, such as from *Quercus* and *Pistacia*, are practically absent or minimal in most samples, with the few grains counted being the result of long-distance wind transport from woodlands in the western highlands of the Jordanian plateau.

4.3. Stratigraphy and Chronology

Section SM-6 consists of various sedimentary facies, including gravel, sand, silt, and organic sediments associated with fluvial, organic wetland, spring, and eolian environments (Figure 6). The provenance of phytolith samples includes all layers, except 7b at the bottom, which has been correlated with a layer associated with Late Acheulean lithics and dated as older than 270 ka [17].

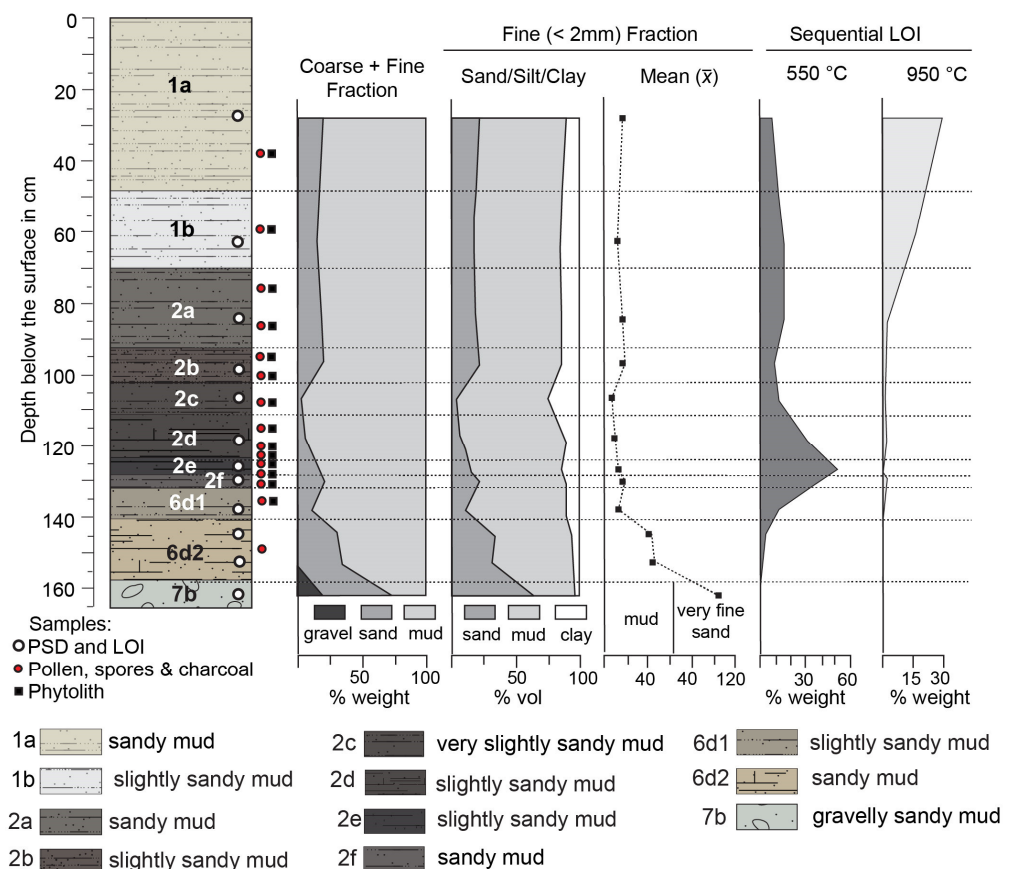


Figure 6. Stratigraphic section SM-6 with pollen and phytolith samples and texture data.

At the bottom of the sampled sequence is layer 6d2, a pale-yellow, sand-silt deposit overlain by 6d1, a darker sandy silt deposit with less sand and more organics. These two layers represent low-energy alluvial environments fining up towards the top (Figure 6). Layers 2f to 2a are a sequence of fine-grained organic deposits of very dark color, with some carbonized plant material. Above this sequence is layer 1b, a fine-grained, highly carbonated spring deposit with organic sediment lenses overlain by layer 1a, a more massive and sandier carbonated deposit that also has some organic lenses.

Radiocarbon dates were obtained from most layers (Figure 7; Table 6), except layers 7b and 1a. Identified outliers were excluded from development of the final age–depth model. Additionally, correlation with a dated deposit connected to a dam built at the beginning of the Umayyad period around the 7th century AD [52] provides an age of 1490 years for layer 1a [34]. Most of the outlying ages are too young, and samples are from

unidentified plant remains, suggesting this material derives from intrusive roots, likely of aquatic grasses growing across the site at different points in the past. Despite this, the age model provides a robust determination of the time of deposition, spanning from c. 26 ka in layer 6d2 to c. 6.5 ka in layer 1b (Figure 7).

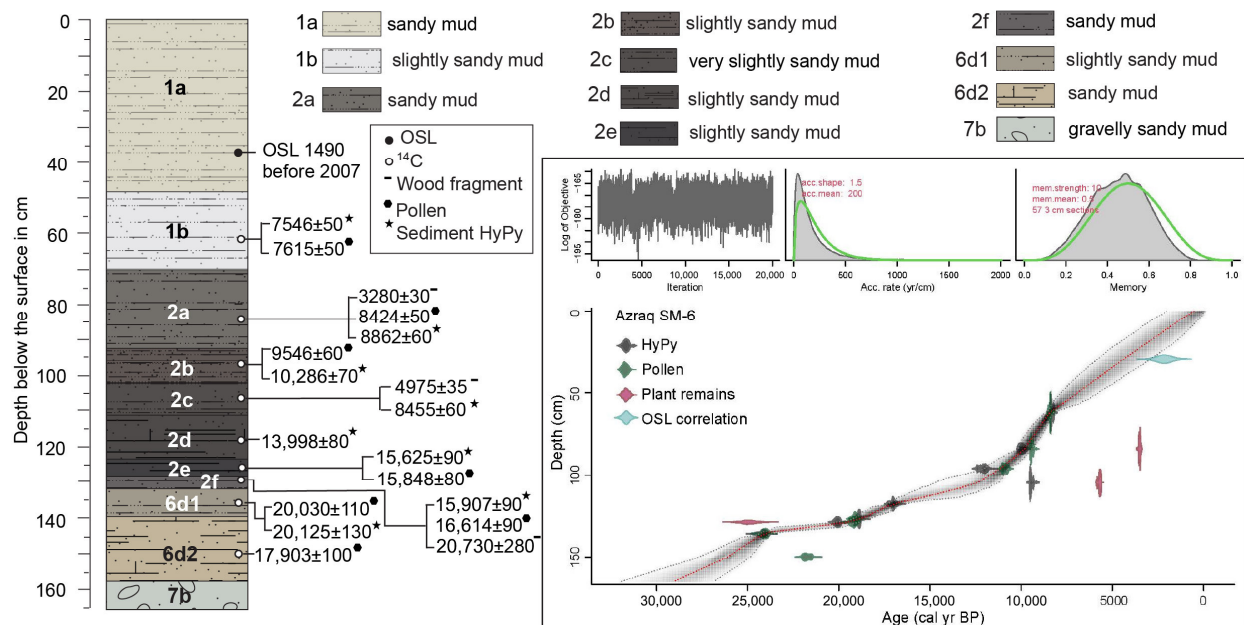


Figure 7. Stratigraphic section SM-6 with uncalibrated dates and age model.

Table 6. Radiocarbon dates.

Lab ID	Depth cm	Layer	Material Dated	C ¹⁴ Age	Error
UNSW-1229	62	1b	Sediment HyPy *	7546	50
UNSW-1237	62	1b	Pollen concentrate	7615	50
UNSW-1230	84	2a	Sediment HyPy	8862	60
UNSW-1238	84	2a	Pollen concentrate	8424	50
CAMS-169738	84	2a	Plant fragment	3280	30
UNSW-1231	96	2b	Sediment HyPy	10,286	70
UNSW-1239	96	2b	Pollen concentrate	9546	60
UNSW-1232	105	2c	Sediment HyPy	8455	60
CAMS-169739	105	2c	Plant fragment	4975	35
UNSW-1233	118	2d	Sediment HyPy	13,998	80
UNSW-1234	127	2e	Sediment HyPy	15,625	90
UNSW-1240	127	2e	Pollen concentrate	15,848	80
UNSW-1235	129	2f	Sediment HyPy	16,614	90
UNSW-1241	129	2f	Pollen concentrate	15,907	90
CAMS-169740	129	2f	Plant fragment	20,730	280
UNSW-1236	136	6d1	Sediment HyPy	20,125	130
UNSW-1242	136	6d1	Pollen concentrate	20,030	110
UNSW-1243	150	6d2	Pollen concentrate	17,903	100

* Hydrogen pyrolysis.

4.4. Phytoliths in Section SM-6

The distribution of diagnostic phytolith morphotypes along section SM-6 (Figure 8) is highly variable along the profile, with GSCCP increasing in frequency toward the Holocene, while some BULLIFORM types decline. ELONGATE phytoliths remain approximately the same frequency throughout, while BLOCKY phytoliths vary, increasing in the middle of the section, roughly between 15 and 10 ka. PAPILLATE morphotypes are rare through the

section, as is the case with modern samples (Section 4.1). Likewise, SPHEROID morphotypes are rare, suggesting poor representation of woody plants throughout the time span of this section. Burnt grass phytoliths are abundant between c. 24 and 17 ka, after which they decline, becoming less important during the middle Holocene.

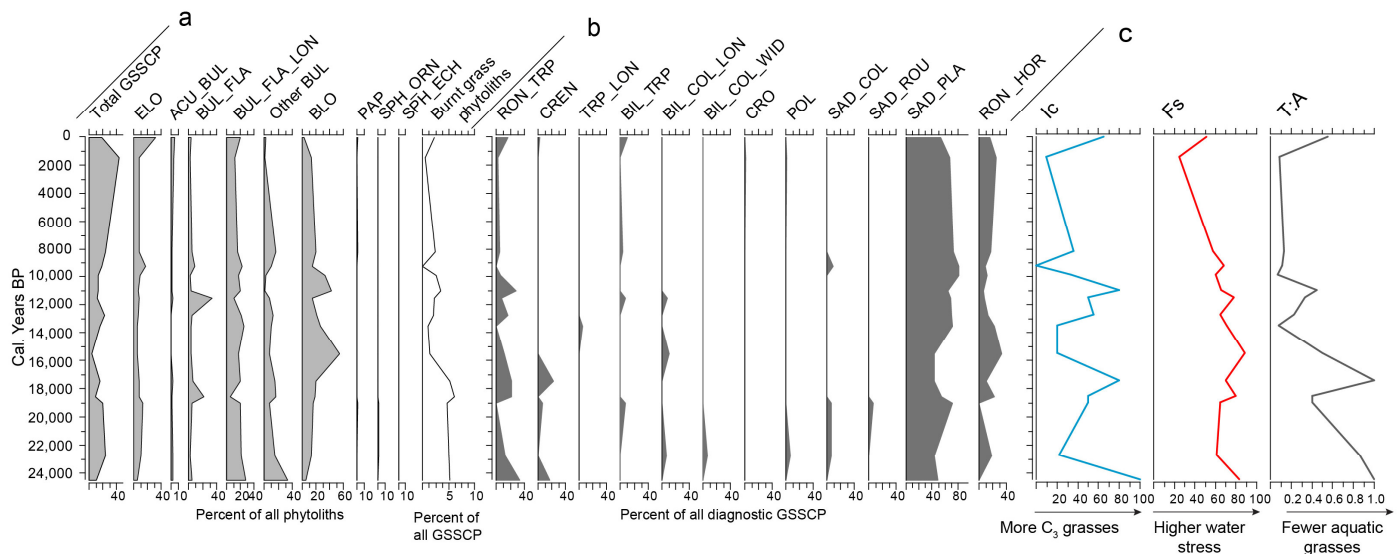


Figure 8. Section SM-6 Phytoliths; (a) Diagnostic morphotypes (light gray) and burnt phytoliths (line), (b) GSSCP (dark gray), and (c) phytolith indices (various line colors).

The Ic index varies dramatically through the profile, with high peaks around 24 ka, 17 ka, and 12–10 ka. Each of these peaks coincides with peaks in the T:A ratio, in large part because most of the terrestrial grasses are Pooideae, the main terrestrial C₃ grass family. The Fs declines steadily over the section, with a modest increase between 18 and 11 ka before declining again afterwards.

4.5. BULLIFORM Size and Types

The calculation of BULLIFORM type frequencies and measurements of length and width on 25 random BULL_FLA per sample shows interesting patterns along the profile (Figure 9; Table 7). First, it is evident that Type 2 (BUL_FLA_LON) is the BULLIFORM type along the profile, while the other type remains below 20%, except in one sample (around 19–20 ka), where Type 1 dominates (Figure 9a). Second, the length and width of all three types combined show a steady increase through time (Figure 9b). This same pattern occurs in the same measurements of Type 2 alone (Figure 9c; Table 7).

Interestingly, length and width tend to increase with time, which is opposite to the declining trend of the Fs index (Figure 9d). The latter is influenced by the number of BULLIFORM in relation to other morphotypes in its calculation (Table 4). Moreover, when comparing the number of BUL_FLA_LON to SAD_PLA (both associated to *P. australis*), BULLIFORM morphotypes are overabundant (Figure 9e).

4.6. Pollen and Spores in Section SM-6

The appearances and frequencies of pollen taxa through the sequence exhibit marked changes (Figure 10). Notably, tree pollen is absent before 20 ka, coinciding with high frequencies of Poaceae and *Artemisia* (Figure 10a) and low frequencies of aquatic taxa (Figure 10b). Although the frequency of spores is relatively low, frequencies of ascospores are high, though very few of them are coprophilous fungi ascospores (Figure 10b).

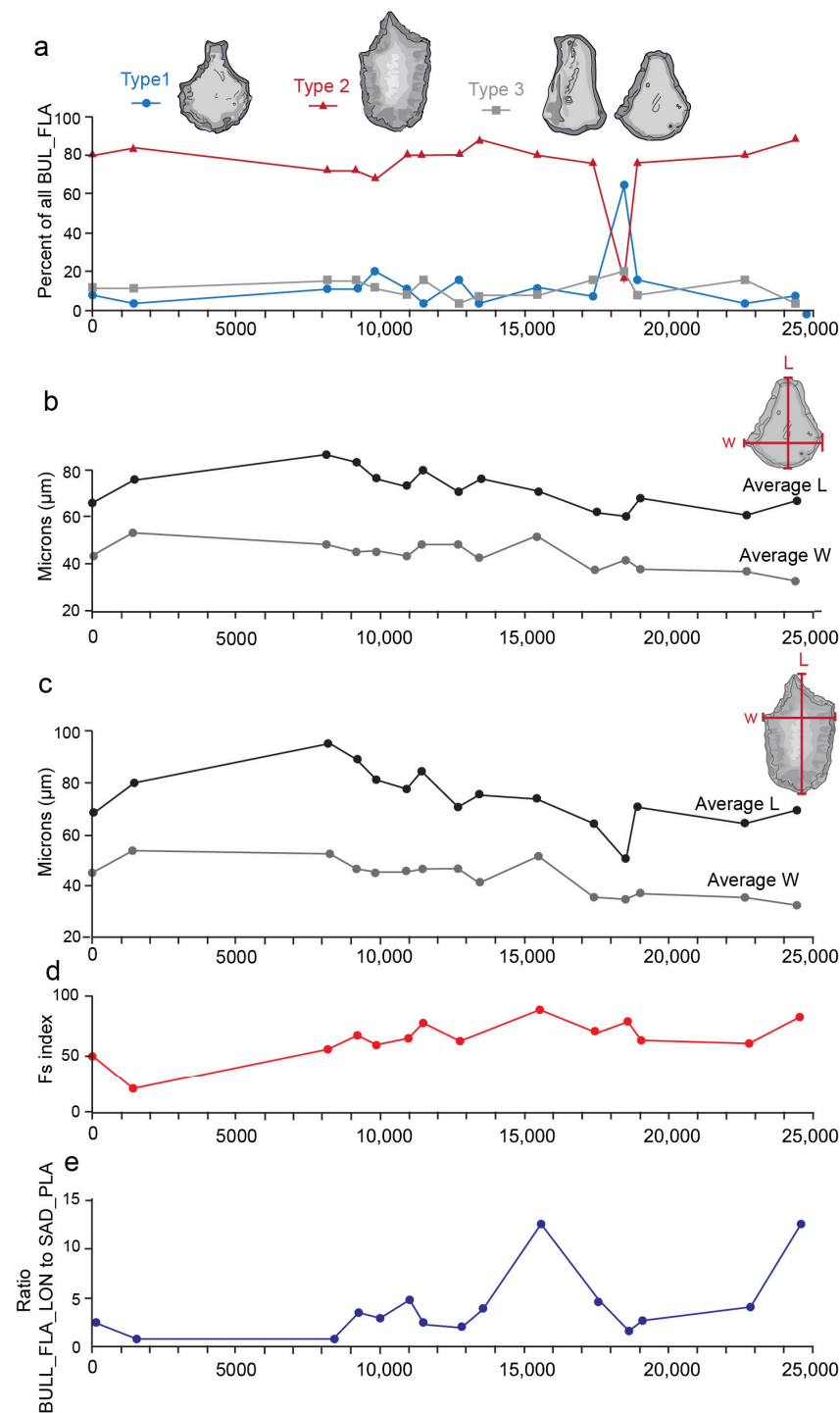


Figure 9. Bulliform shape and morphometrics in relation to GSSCP and Fs Index. (a) Percent of Types 1, 2, and 3 within the phytolith class BULLIFORM, where Type 2 is BULL_FLA_LON; (b) average length and width for all BULLIFORM morphotypes, (c) average length and width for all BULLIFORM Type 2; (d) Fs index, and (e) ratio between all BULL_FLA_LON (Type 2) and all SAD_PLA.

A notable change occurs from c. 17 ka to 11 ka, when Mediterranean tree pollen appears and Poaceae dominance changes toward aquatic grasses ($<22\ \mu\text{m}$), coinciding also with an increase in other aquatic taxa (Figure 10b). Other taxa that increase during this period are *Pinus*, *Tamarix*, *Ephedra*, *Nitraria*, Brassicaceae, Geraniaceae, Umbelliferae, and Asteraceae. Another notable change occurs at c. 17 ka, when *Artemisia*, *Tamarix*, *Nitraria*, and ascospores all spike before declining to low values.

Table 7. Average length and width in μm on samples of BULLIFORM morphotypes *.

All Types				Type 2 Only		
Cal yr BP	Avg L	Avg W	N	Avg L	Avg W	N
0	65.68	44.32	25	68.9	44.9	20
1433	76	53.68	25	79.9	53.85	21
8174	86.52	49.12	25	94.74	52.42	18
9183	84.25	45.66	25	89.66	46.83	18
9860	76.96	46.12	25	81.53	45.58	17
10,933	73.32	44.2	25	78.2	44.85	20
11,465	80.72	47.4	25	84.7	46.65	20
12,711	71.16	48.76	25	71.25	46.1	20
13,474	75.52	41.72	25	75.91	41.26	22
15,462	70.92	51.88	25	74.35	51.75	20
17,427	62.04	37.36	25	64.68	35.68	19
18,500	61.12	42.08	25	50	35	4
18,967	66.96	37.68	25	71.11	36.77	19
22,689	61.16	37.08	25	64.35	35.55	20
24,467	67.08	33.12	25	69.18	32.72	22

N: Number of counts. * Full counts in Supplementary Material.

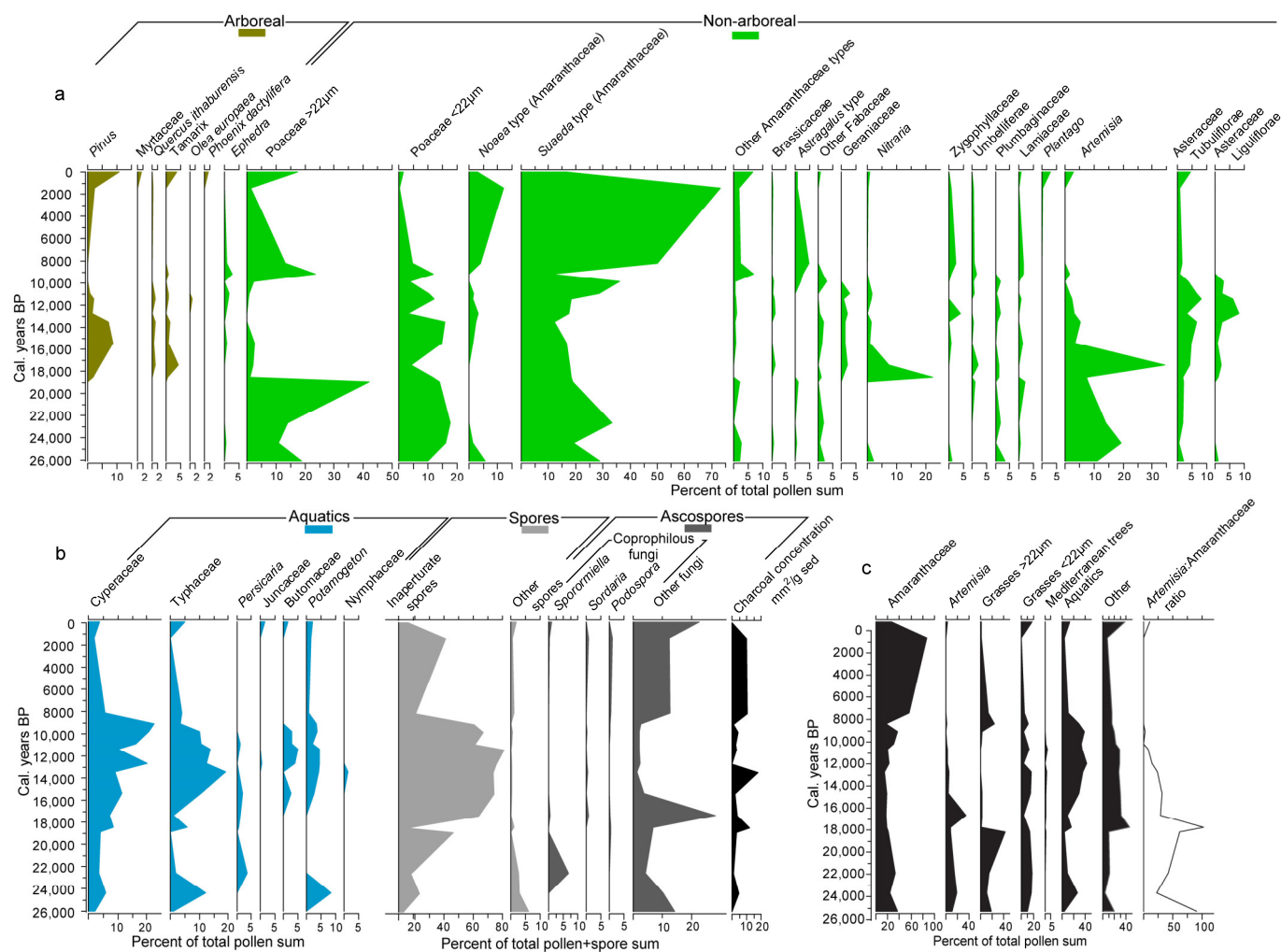


Figure 10. Section SM-6 pollen and spores; (a) Tree, shrub, and herb pollen taxa, (b) aquatic pollen taxa and spores, and (c) percentage by pollen groups and A:C ratio.

After 11 ka trees decline, Poaceae > 22 µm quickly decline, and Poaceae < 22 µm, although still important, also decline. Other taxa that decline or disappear during this period are *Artemisia*, Plumbaginaceae, Asteraceae, and most aquatic taxa. Only the Amaranthaceae exhibits a considerable increase, resulting in the decline of the A:C ratio. Finally, during this period, ascospore concentrations increase.

5. Discussion

5.1. Comparison Between Phytolith and Pollen Records

While phytolith and pollen records provide different information about paleovegetation, comparison of proxy summaries, indices, ratios, and selected taxa provide a more thorough vegetation reconstruction (Figure 11).

The T:A (terrestrial-to-aquatic grasses) ratio shows some parallels with the incidence of phytolith morphotypes produced by *Phragmites australis* (i.e., SAD_PLA and BUL_FLA_LON) (Figure 11c,d). However, when compared to the Poaceae pollen classes that differentiate *P. australis* from other grasses (i.e., > 22 µm and < 22 µm), there are some inconsistencies with the phytolith record, particularly between c. 17 and 11 ka (Figure 11h). These inconsistencies are understandable in terms of transport characteristics of phytoliths and pollen, with the former being heavier and less aerodynamic than the latter. Thus, phytoliths often reflect the local presence of certain floristic groups, while pollen the regional spectrum of vegetation. Accordingly, pollen shows that between c. 17 and 11 ka, there are almost no terrestrial grasses contributing to the counts of pollen spectra from the broader region, but phytoliths show that there are some terrestrial grasses growing immediately around the wetland. A similar situation occurs with the SPHEROID (SPH) morphotypes, which through the record show a virtual absence of woody plants, but pollen shows that they grow within the pollen source regionally (Figure 8a).

Phytolith indices such as the Ic show the proportions of grasses that grow in cold environments versus those that grow in hot deserts, an aspect that resonates in the proportion of *Artemisia* and Amaranthaceae pollen or the A:C ratio indicating cold or warm conditions (Figure 11b,g). However, despite the cold or warm climatic background, *P. australis* dominates through the sequence, as attested by the abundance of SAD_PLA and FLA_BUL_LON, a fact supported by modern samples and by the persistent presence of <22 µm grass pollen. This fact suggests an almost continuous wetland environment dominated by *P. australis* through the entire time of the sequence, particularly from c. 20 ka to present.

5.2. The Water Stress Index (Fs) and Bulliform Phytoliths

According to tests in tropical Africa, the Fs index increases with water stress [46]. Thus, the expectation here would be that under the lower temperatures during the LGM, the index would be lower than in the early Holocene, when temperatures were higher because of high summer insolation. However, the results show the opposite trend (Figure 11a,e).

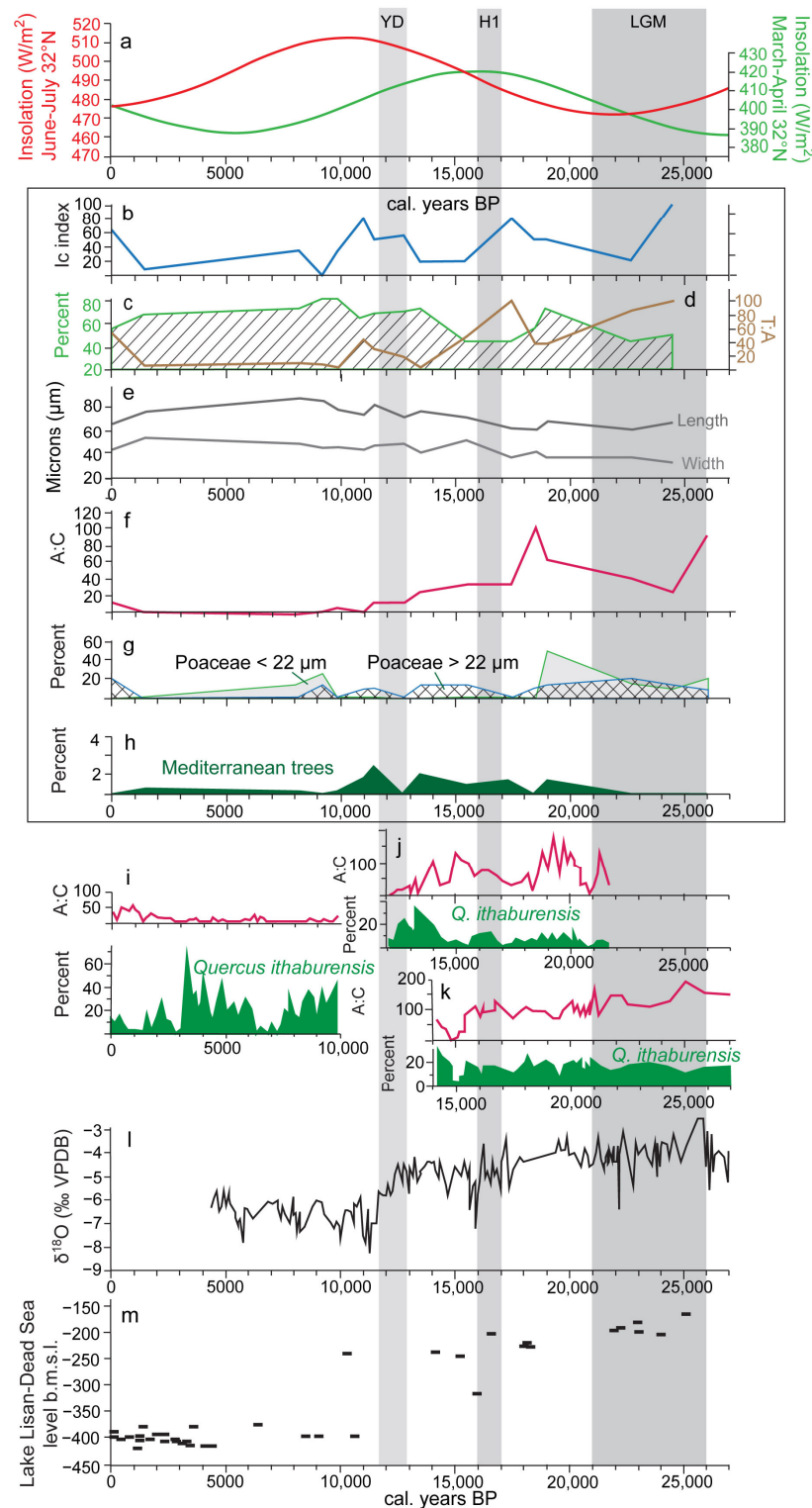


Figure 11. Phytolith and pollen summaries from the SM-6 section (inside box) in relation to insolation and regional paleoclimatic records; (a) Summer and spring insolation curves for 32° N [53]. Section SM-6 phytolith and pollen summary data (b–i): (b) climatic index (Ic), (c) percent of SAD_PLA, (d) terrestrial to aquatic ratio (T:A), (e) water stress index (Fs), (f) BULLIFORM length and width, (g) *Artemisia*–*Amaranthaceae* ratio (A:C), (h) percentage of two different classes of Poaceae pollen, and (i) percent of Mediterranean trees. *Artemisia*:*Amaranthaceae* ratio (A:C) and percent of *Quercus ithaburensis* from (j) Ein Gedi [54], (k) JRD site in the Hulah Basin [10], and (l) Dead Sea core 5017-1-A [8]. Other paleoclimatic data: (m) $\delta^{18}O$ (‰ VPDB) from Soreq Cave [55] and Lake Lisan-Dead Sea levels [6,56]. Background gray bands: YD, Younger Dryas; H1, Heinrich Stage 1; and LGM, Last Glacial Maximum.

There are several possible reasons for the unexpected Fs index trend in the SM-6 sequence. One is that this index was created and tested using terrestrial grasses [45], while here the environment is dominated by aquatic grasses, which may respond to water stress differently. Another reason is that it was implemented in tropical Africa in an area of summer rainfall [46], which contrasts with the winter rainfall regime of the study area. A third reason could be that grasses in aquatic environments tend to produce more BULLIFORM phytoliths [44], which overwhelm the other morphotypes used to calculate the index. Finally, differential preservation may work in favor of BULLIFORM phytoliths, which are larger and more resistant to dissolution than other phytoliths, a problem that often leads to misinterpretation in phytolith assemblages [57].

Usually, the production of BULLIFORM morphotypes is strongly related to aquatic environments, where silica production is relatively high, especially under conditions of high evapotranspiration [45,58,59]. Accordingly, it is possible to assume that when silica deposition is high, not only should BULLIFORM production be higher, but their size should be greater. For this reason, in this study, length and width measurements were tested against the Fs index (Figure 9). Although this approach is often applied to specific grass taxa, such as wild versus domesticated rice and other cereals [44,60–62], it may also apply to BULLIFORM phytoliths produced by wild grasses such as *P. australis*.

The results show that BULLIFORM length and width (Figure 9b,c) are more consistent with an increase in water stress, or increased evapotranspiration, as temperatures increase at the end of the deglaciation and the early Holocene. This pattern is consistent with data showing increasing silica deposition in relation to high temperatures caused by increased summer insolation, as tested elsewhere [61]. Nevertheless, the morphometric approach used here, though it appears to work for the case of the glacial–interglacial transition in this wetland, may need more research. Therefore, at this point, interpretations should be considered provisional.

5.3. Local Vegetation and Climate in a Regional Context

5.3.1. Comparison with Regional Records

Unfortunately, there are no complete high-resolution records in Jordan's Eastern Desert or from any other part of the country to compare with the sequence studied here. Therefore, most of the paleoclimatic and paleovegetation records available for comparison are in the western part of the southern Levant, mostly the Dead Sea–Jordan Valley and caves in the west-flanking highlands (Figure 1a). These records have a higher resolution than the SM-6 phytolith and pollen record and encompass the period studied here (c. 26 ka), allowing comparison of possible regional similarities and differences in climate and vegetation change across the glacial cycle.

We compare the phytolith and pollen results from section SM-6 with combined pollen records from the Dead Sea and Ein Gedi [8,54] and the JRD Hulah Basin [10], which together cover most of the LGM, the deglaciation period, and the Holocene (Figure 11j–l). The hydro-climatic proxies discussed here include the $\delta^{18}\text{O}$ record from speleothems in Soreq Cave [55], Lake Lisan, and Dead Sea stands [6,55] (Figure 11m,n) against the background of summer and spring insolation curves (Figure 11a,b). Summer insolation is usually a factor used in assessing hydro-climatic aspects that affect vegetation, though in this case, the spring insolation curve has been added to compare with vegetation at the end of the rainy season.

5.3.2. The LGM: c. 26 ka to c. 18 ka

The high T:A and A:C ratios suggest a landscape dominated either by steppe or cold desert vegetation, at least from 26 ka to 20 ka (Figure 11d,g). The incidence of terrestrial

grasses is also evident by the relatively high frequency Poaceae > 22 μm pollen and the high incidence of C_3 grasses apparent in the Ic index (Figure 11b,h), suggesting that the landscape outside the wetland was dominated by *Artemisia* and grasses typical of the modern cold steppes and cold deserts in other parts of Asia [42,63]. Other herbs in that steppe or desert landscape include Plumbaginaceae, Lamiaceae, and Asteraceae Tubuliflorae (Figure 10).

The high A:C ratio and low or lack of Mediterranean tree pollen in the SM-6 record correlates with a similar trend in the Dead Sea pollen record (Figure 11l), both suggesting cold and dry conditions. However, despite the apparent dry conditions, low $\delta^{18}\text{O}$ values and high Lake Lisan levels suggest more effective precipitation (Figure 11m), probably due to low evapotranspiration resulting from low summer insolation and moderate spring insolation (Figure 11a). This extra moisture perhaps permits the dominance of *Artemisia* over Amaranthaceae and a higher incidence of C_3 grasses.

Pollen and phytolith data suggest a more reduced, though stable, wetland, as the proportions of aquatic grasses and aquatic vegetation do not vary considerably (Figure 11b,d,h). The small sizes of BULLIFORM morphotypes (Figure 11f) suggest less evapotranspiration because of low summer insolation (Figure 11a). The high percentage of burnt grass phytoliths suggests fires in the wetland grasses, which could be human-induced, given the presence of Early Epipaleolithic occupation has been reported in the Shishan Marsh area at this time [20,26]. Although natural fires could occur, they are less likely to represent an important amount of burnt grass phytoliths, given the presence of humans in an area surrounded by a rather dry environment.

5.3.3. Deglaciation Period: 18 ka to 11 ka

The surrounding landscape in the deglaciation period experienced a change in vegetation characterized by a slow but sustained decline in the A:C ratio and the appearance of Mediterranean tree pollen, which is consistent with pollen records in the western Southern Levant during that period (Figure 11k,l) [7,8]. The T:A ratio and Poaceae pollen suggest the decline of terrestrial grasses in favor of aquatic grasses (i.e., *P. australis*). Other changes during this period include the appearance of the sand-loving *Tamarix* and *Nitraria* and herbs of the Brassicaceae, Umbelliferae, and Asteraceae families. Although the pollen record indicates almost no terrestrial grasses, the phytolith T:A ratio suggests that some terrestrial grasses grew near section SM-6, probably around the wetland.

Although ascospores decline, the coprophilous fungi ascospores increase, which suggests a higher incidence of herbivores. Grass burning (burnt grass phytoliths) declines, but some peaks in the graph suggest that it happens occasionally. Burning is likely related to human influence, as supported by the archaeological record of the Shishan Marsh area ('Ayn Qasiyya) and other parts of Azraq [16,20,26]. As in the previous period, although natural fires can occur, the overwhelming presence of human activity suggests human-led fires.

BULLIFORM size increases, probably in association with increased summer and spring insolation, which results in higher evapotranspiration in the wetland. This hydro-climatic change is evident in the increase in $\delta^{18}\text{O}$ values in Soreq Cave and a water level drop at Lake Lisan (Figure 11m). Although these records show changes associated with Heinrich 1 event (H1), Bolling Allerod, and Younger Dryas, such changes are not apparent in SM-6 given its low time resolution.

5.3.4. The Holocene

Although better resolution of the SM-6 record occurs in the early Holocene, it is evident that vegetation and climate attain conditions like the present by this time. The A:C ratio declines with a higher incidence of Amaranthaceae over *Artemisia*, thus paralleling the trend in the southwestern Levant (Figure 11g,j,k). Mediterranean tree pollen in section SM-6 declines,

though at Ein Gedi, arboreal pollen (i.e., *Q. ithaburensis*) increases [54] (Figure 11i,j), as recorded in other parts of the southern Levant [8,54]. Other vegetation changes in the landscape around the wetland include the decline and disappearance of Plumbaginaceae, Geraniaceae, and Asteraceae Liguliflorae, as well as the appearance of Fabaceae producing the *Astragalus*-type of pollen. The T:A ratio and Poaceae pollen size classes suggest the expansion of terrestrial grasses, but not like any period before, though it is possible that this is not a climatic influence but the rise of pastoralism. However, the Ic index suggests that despite the dominance of C₃ grasses, a few C₄ grasses appear, likely responding to warmer temperatures. Thus, the information provided by phytoliths and pollen suggests that the area around the wetland is becoming as hot a desert as it is at the present.

The wetland seems to be reduced and dominated by *P. australis*, though still with many of the other aquatic species present. This wetland reduction is concurrent with the increase in BULLIFORM phytolith size, likely caused by an accelerated evapotranspiration consistent with high summer insolation. This hydro-climatic change parallels the decrease in effective moisture in the $\delta^{18}\text{O}$ records of the Soreq cave and the drop in the level of the Dead Sea (Figure 11m). The percentage of burnt phytoliths declines, signaling fewer fires in the wetland, perhaps signaling a shift to different patterns of aquatic resource procurement. Ascospore frequencies increase, with a higher diversity of those of coprophilous fungi (*Podospora*, *Sporormiella* and *Sordaria*), suggesting more herbivores, although in this case it could be the result of domesticated goats and sheep.

6. Conclusions

The combined record of phytoliths and pollen from section SM-6 shows that during the LGM (c. 26–18 ka), the Shishan wetland was surrounded by steppe or cold-desert vegetation, with important presence of *Artemisia*, grasses, and minor proportions of Lamiaceae and Plumbaginaceae. At the beginning of the Deglaciation Period, c.18 ka, *Artemisia* and grasses begin to be replaced by Amaranthaceae, Asteraceae, and other taxa, but with high variability through this time. During the Holocene, this landscape becomes dominated by Amaranthaceae and most of the taxa that characterize the region today.

The wetland experiences a few changes, but it has been always dominated by *Phragmites australis*. During the LGM, conditions seem to indicate a very stable wetland environment, with less water loss through evapotranspiration despite low precipitation, but with increasing incidence of herbivores and human-led fire. After c. 18 ka, previous conditions prevail, though the proportions of *P. australis* and other aquatics vary, with a notable incidence of salt-tolerant taxa (*Tamarix* and *Nitraria*) and variable incidence of fire and herbivores. After 11 ka, the wetland changes to a dominance of *P. australis*, with fewer fires but a higher incidence of herbivores.

The water stress index (Fs index) shows an opposite trend than expected, being higher in the LGM and lower in the Holocene. This may be due to (i) the overproduction of BULLIFORM phytoliths by *Phragmites australis* and (ii) the overall humid environment of the area, different from the summer-rainfall tropical parts of Africa, where the index was created. However, BULLIFORM length and width have the opposite trend, paralleling summer insolation trends, suggesting that in this kind of aquatic environment, BULLIFORM size could be a better indicator of evapotranspiration, although this is an aspect that needs additional research.

Finally, this study provides a reconstruction of the stages of vegetation change in this part of Jordan's Eastern Desert at the end of the Pleistocene and its transition to the Holocene, thus constituting an understanding of the environmental context of adaptations and cultural change of the local cultures. Thus, it seems that during full glacial conditions, humans adapted to a cold desert/steppe and wetlands, both offering important resources

for their subsistence, and then to relatively rapid changes during the deglaciation that led to the establishment of a hot desert and wetlands modified by climatic shifts to warm conditions and human pressure. Similar adaptive strategies may have occurred in previous glacial–interglacial transitions, which makes this study a foundation to examine the environmental context of adaptations in the Paleolithic of Azraq.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/quat9010018/s1>, Excel sheet.

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Abbreviations

The following abbreviations are used in this manuscript:

LGM	Last Glacial Maximum
GAOA	Greater Azraq Oasis Area
AMAPP	Azraq Marshes Archaeological and Paleoecological Project
GSSCP	Grass silica short cell phytoliths
OSL	Optically stimulated luminescence
RSCN	Royal Society for the Conservation of Nature
T:A	Terrestrial-to-aquatic grass ratio
A:C	Artemisia-to-Amaranthaceae pollen ratio
Fs	Water stress index
Ic	Phytolith climatic index
Iph	Phytolith aridity index

Appendix A

Appendix A.1. Phytolith Processing

Phytolith samples were first decalcified using 10% hydrochloric acid (HCl) and then neutralized by adding distilled water, centrifuging in 50-mL tubes, and decanting several times. Clay removal was achieved by adding 5 g of potassium hydroxide (KOH) and

sonicating it for 10 min and leaving the sample to settle for 40 min in 100-mm beakers and finally decanting supernatant liquid. Subsequently, organics were removed using 10% potassium hydroxide solution for 3 min, stirred, centrifuged in 50-mL tubes, and decanted. The stirring, centrifuging, and decanting was repeated until neutrality was reached. The sample was again sonicated and let stand for 50 min to remove excess clay and other small particles. Once the liquid was clear, the residue at the bottom was transferred to 15-mL tubes and centrifuged at 3000 rpm. Once the water was removed, sodium polytungstate (Polygee) heavy liquid at density 2.3 was added to the sample in the tube, which was then stirred with a vortex genie. The tubes were centrifuged at 1200 rpm for 10 min. The supernatant residue was pipetted out and placed in clean 15-mL tubes, which were filled with water and centrifuged at 3000 rpm 3 times. The residue was then placed on a coverslip, dried on a hot plate, and mounted on a slide using Entellan as a medium.

Appendix A.2. Pollen Processing

Pollen samples were processed by removing carbonates using HCl, removing clays by letting silts and sand settle in 120 mL layers and decanting every 45 min. Organics, which in general were low but variable, were removed by a 15 min bath in 10% KOH. Pollen and other microfossils were recovered from the sediment by flotation using Poly Gee heavy liquid at 2.0 density. Phytolith samples were processed similarly, but the density used for flotation was 2.3. The residues were collected and placed in slides using Entellan as a medium.

Although phytoliths were more abundant, the counts fluctuated between 150 and 250 per sample, depending on the concentration per sample, but most of the counts were above 150. They were classified following the taxonomy described in Section 3.3. The number of pollen grains counted under the microscope varied, as generally the samples contained low concentrations. Those with less than 100 grains were not used in this study.

Appendix A.3. Radiocarbon Dating

Plant remains radiocarbon dating: Seived plant remains underwent standard acid-base-acid (ABA) pretreatment with sequential HCl-NaOH-HCl at the Center for Accelerator Mass Spectrometry (CAMS) of the Lawrence Livermore National Laboratory, USA.

Pollen concentrate radiocarbon dating: sediment samples underwent standard acid-base-acid (ABA) pretreatment with sequential HCl-NaOH-HCl to remove carbonates, humic acids, and fluvic acids liberated during NaOH wash. Organic fractions were then isolated from the dominant inorganic mineral component using sodium polytungstate heavy liquid flotation at a specific gravity of 2 g/cm³. Sequential sieving of remaining samples was undertaken at 100 µm, 70 µm and 15 µm to concentrate pollen fraction [47]. Pre-treated samples were freeze dried and converted to graphite by reduction with hydrogen over an iron catalyst at 600 °C. Accelerator Mass Spectrometry (AMS) measurements were conducted on the MICADAS accelerator at [48]. Blank samples of MIS5 peat sediment [48] were processed alongside pollen concentrates.

Hydrogen Pyrolysis (HyPy) radiocarbon dating: Sediment samples were pre-treated using hydrogen pyrolysis (at up to ~600 °C) to remove labile organic matter. HyPy was conducted at the Advanced Analytical Centre, James Cook University, alongside blank MIS5 peat sediments. HyPy residues were subject to a hot HCl wash prior to being converted to graphite at the Chronos 14C radiocarbon facility, UNSW.

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