



HAL
open science

Coastal strip of the Levantine Corridor for the Calabrian (late Early Pleistocene) hominin migration

N. Öğretmen, M. Bylinskaya, D. Biltekin, L. Golovina, S. Sari, S. El Zaatari, S. Mclin, F. Nader

► **To cite this version:**

N. Öğretmen, M. Bylinskaya, D. Biltekin, L. Golovina, S. Sari, et al.. Coastal strip of the Levantine Corridor for the Calabrian (late Early Pleistocene) hominin migration. *Palaeogeography, Palaeoclimatology, Palaeocology*, 2026, 693, pp.113811. <10.1016/j.palaeo.2026.113811>. <hal-05597782>

HAL Id: hal-05597782

<https://ifp.hal.science/hal-05597782v1>

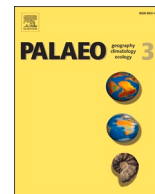
Submitted on 21 Apr 2026

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons CC BY 4.0 - Attribution - International License



Coastal strip of the Levantine Corridor for the Calabrian (late Early Pleistocene) hominin migration

N. Ögretmen^{a,b,*}, M. Bylinskaya^c, D. Biltekin^d, L. Golovina^c, S. Sari^e, S. El Zaatari^f, S. McLin^f, F. Nader^{g,h}

^a Centro de Ciências do Mar do Algarve (CCMAR/CIMAR LA), Universidade do Algarve, Faro and Instituto Português do Mar e da Atmosfera (IPMA), Algés, Portugal

^b Aarhus Institute of Advanced Studies (AIAS) and Department of Geoscience, Aarhus University, Aarhus, Denmark

^c Russian Academy of Sciences, Moscow, Russia

^d Eurasia Institute of Earth Sciences, Istanbul Technical University, Istanbul, Türkiye

^e Department of Sciences, Roma Tre University, Rome, Italy

^f Paleoanthropology, Senckenberg Center for Human Evolution and Paleoenvironment, Eberhard Karls Universität Tübingen, Tübingen, Germany

^g Earth Simulation Lab, Utrecht University, Utrecht, the Netherlands

^h IFP Energies Nouvelles (IFPEN), Geosciences Division, Lyon, France

ARTICLE INFO

Editor: Laura Sadori

Keywords:

Foraminifers, biostratigraphy
Eastern Mediterranean Sea
Paleoshoreline
Palynology
Paleoclimate

ABSTRACT

As a geographical bridge across continents, the Levantine Corridor has played an important role in the migration and dispersal of hominins throughout the Pleistocene. Archaeological sites along and around this corridor provide evidence of these movements dating back to the Early Pleistocene, in the form of artefacts and, to a lesser extent, fossils, which attest to the presence of hominins in the region. Interestingly, younger sites (i.e., Calabrian) are located along the coastal strip of the Levantine Corridor while older sites (i.e., Gelasian sites such as Zarqa, Yiron and El-Kowm Oasis) are found further inland. In this study, we revise the foraminiferal biostratigraphy of marine deposits exposed on land in Latakia, Syria, in order to track sea-level and coastal line changes. We demonstrate that the coastal strip of the Levantine Corridor was inaccessible to hominins as a migration pathway prior to 1.28 Ma, as evidenced by the presence of biomarker planktic (*Neoglobobulimina pachyderma*, *Globobulimina rubescens*, *Globigerinoides tenellus*, *Globigerinoides obliquus obliquus*) and benthic foraminifers (*Bulimina marginata* and *Hyalinea baltica*). We also document the governing climate conditions and sea-levels during the Calabrian times in this region, more specifically between Marine Isotope Stage (MIS) 53 and MIS 40, where foraminifers and detailed dinoflagellate data point to frequent short-term oscillations before the Early-Middle Pleistocene Transition (EMPT; ~1.2–0.7 Ma) with shifts between warm and cold temperatures and between saline and freshwater environments with varying nutrient input linked to riverine inflow. Pollen data reveal that the prevailing climate was typically Mediterranean climate during the Calabrian (late Early Pleistocene).

1. Introduction

The Levantine Corridor is believed to have been a crucial land bridge for hominins that facilitated their migration across the Old-World continents (El Zaatari, 2018; Eppelbaum and Katz, 2022; Rolland, 2013). However, effects of tectonics, climatic shifts and associated changes in sea-level and vegetation, and natural disasters, such as earthquakes and landslides would also have played a key role in shaping hominin pathways across this bridge (Bailey and King, 2011; Ben-Avraham et al., 2005; Eppelbaum and Katz, 2022, 2023, 2024, 2025; Foerster et al.,

2022). Several archaeological sites along the Levantine Corridor, spanning almost the duration of the entire Pleistocene, provide significant insights into the hominin migratory pathways (Bradley, 1937; Carbonell et al., 2008; Carotenuto et al., 2016; Jagher et al., 2015; El Zaatari, 2018; Le Tensorer, 2017; Rosenfeld et al., 2004). The earliest evidence of hominin presence in the region comes from the hinterland of the coastal part of the Levantine Corridor, particularly from the Zarqa Valley in Jordan, dating as back as 2.48 Ma (Parenti et al., 2024; Scardia et al., 2019) and Yiron in Israel, dating to 2.0 Ma (De Lumley et al., 2009; Ronen, 2006). The coastal part itself, i.e., the narrow strip of land

* Corresponding author at: Centro de Ciências do Mar do Algarve (CCMAR/CIMAR LA), Universidade do Algarve, Faro and Instituto Português do Mar e da Atmosfera (IPMA), Algés, Portugal.

E-mail address: nog@aias.au.dk (N. Ögretmen).

<https://doi.org/10.1016/j.palaeo.2026.113811>

Received 30 December 2025; Received in revised form 9 March 2026; Accepted 13 April 2026

Available online 15 April 2026

0031-0182/© 2026 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

between the Mediterranean Sea to the west and the highlands to the east of the coast, which are particularly steeply inclined in the central and northern parts of the Levant, starts to present evidence of hominin presence somewhat later, i.e., with industry identified as Acheulean dating as far back as ~ 1.6 – 1.4 Ma as the Ubeidiya site suggests (Belmaker et al., 2002; Belmaker and O'Brien, 2018; Eppelbaum and Katz, 2022). In agreement with earlier insights by Winder et al. (2015), determining whether this is related to paleoshoreline development becomes crucial to assessing the role this region played in hominin migrations.

The location of the coastal strip of the Levantine Corridor is intriguing. It is the easternmost part of the Mediterranean Sea, which is a semi-enclosed basin that responds to climate and sea-level variation more rapidly than the global ocean (Abbate and Sagri, 2012; An-Ming, 1982; Azibeiro et al., 2023; Anderson et al., 1984; Derricourt, 2005; Gaffney, 2021; Rohling et al., 2013; Rolland, 2013). From a tectonics perspective, it is bounded by the Dead Sea Transform Fault Zone to the east, and the Cyprus Trench to the west, which trigger subsidence and uplift dynamics of the region (Fig. 1). Also, the tectonic restraining bend that resulted in regional uplift of the Lebanon Mountains in the region extends from Lebanon to southern Syria (Fig. 1A) (Gomez et al., 2006; Wetzler et al., 2022). In such a complex geological setting, paleoshoreline development along the coastal strip of the Levantine Corridor would have also been influenced by these uplift dynamics, in addition to sea-level fluctuations (Bridgland et al., 2024; Winder et al., 2015). In the eastern Mediterranean region, revisiting onland marine sections following the most recent biostratigraphical charts (Lirer et al., 2019) revealed an important update in age constraints. For example, some marine deposits of so-called Late Pliocene age proved to be of Calabrian age (e.g., Kanbur and Ögretmen, 2022), bringing forward the necessity of re-evaluation of sea-level stands and paleogeography of the coastlines. Thus, accurate age constraints, which requires identifying and dating available onland marine deposits, are crucial to understand paleoshoreline development and the availability of the coastal strip of the Levantine Corridor as a pathway for hominins' crossings (Abbate and Sagri, 2012; Bailey and King, 2011; Derricourt, 2005; Gaffney, 2021; Rohling et al., 2013; Rolland, 2013).

This present study concentrates on the easternmost Mediterranean onshore marine deposits found in Latakia, northwest Syria, that were previously studied by Devyatkin et al. (1996) and assigned an age to the upper Pliocene-lower Pleistocene based on the available foraminifer and nannofossil biostratigraphic charts at the time of their study (Colalongo et al., 1981; Rio et al., 1991), and magnetostratigraphy. By integrating new foraminiferal, nannofossil, and palynological data, we refine the biostratigraphic framework of the Msherpheh section and reconstruct the depositional environments and coastal paleogeography of the Levantine Corridor during the Calabrian (late Early Pleistocene). Particular emphasis is placed on sea-level oscillations, shoreline shifts, and their broader paleoenvironmental context. These findings allow us to reassess the role of the Levantine coastal strip within the framework of early hominin migration out of Africa via the Levantine Corridor.

2. Geology of the study area

In this study, we concentrate on the coastal strip of the Levantine Corridor that lies between the eastern Mediterranean Sea and the mountain ranges of Syria (Al-Ansariyyah Mountains) and Lebanese Mountains (Fig. 1A), stretching from north to south (El Zaatari, 2018).

The study area is located at the easternmost part of the Mediterranean Sea along the Syrian coastline, in the Neogene El-Kabir Depression in the Latakia area (Fig. 1B). The sampled section (Msherpheh Section) is found within the Latakia Ridge Basin, extensions of which reach offshore and are bounded by the NE-trending Nahr-El-Kabir Fault on the eastern part onshores (Babbo, 2020; Hardenberg and Robertson, 2013). The depression formed as a half-graben basin under transtensional tectonics during the Neogene and was filled with terrigenous carbonate and gypsum deposits during the Miocene under a fault-controlled sedimentation process (Eppelbaum and Katz, 2024; Hardenberg and Robertson, 2013; Hardenberg and Robertson, 2007). Pliocene-Pleistocene clays and siltstones unconformably overlie the Miocene deposits, reaching up to 300–400 m in thickness (Devyatkin et al., 1996) and even up to ~ 2 km thickness in some parts (Hardenberg and Robertson, 2013), deposition of which was possibly coupled with regional subsidence during the Calabrian under the influence of the Dead Sea Transform Fault System

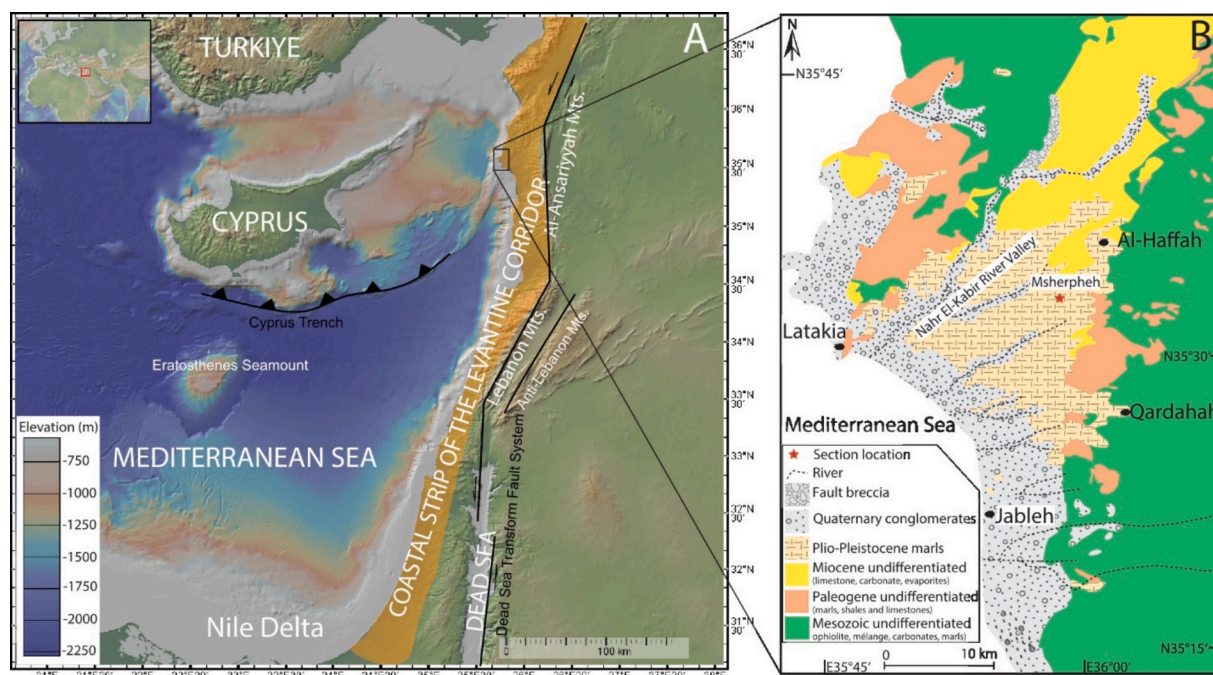


Fig. 1. A. Base map showing the extension of the coastal strip of the Levantine Corridor and important geographic markers of the region (from Hardenberg and Robertson, 2013). B. Simplified geological map of the study area showing the location of the studied Msherpheh section. Base map (A) was prepared using Geo-MapApp. The geological map is modified and revised after Devyatkin et al. (1996) and Hardenberg and Robertson (2013) based on the new findings of this study.

which affected the entire Levantine Corridor coastal strip (Fig. 1A; Eppelbaum and Katz, 2022, 2025) and due to regional uplift, they are at ~200 m above sea level today (Devyatkin et al., 1996). Regional uplift has been recognized through the exposed late Quaternary staircase river terraces and raised beaches that yield uplift rates of ~0.4 mm/yr in the Latakia region (Bridgland et al., 2017; Bridgland et al., 2024; Trifonov et al., 2014). During the Middle Pleistocene, a gradual regressional phase replaced the transgressional phase of the Pliocene; the former is represented by shallow-marine sandy-clayey deposits in western Syria (Devyatkin et al., 1996) (Fig. 1B). Accordingly, the studied Msherpheh Section is located ~180 m above sea level and consists of marine sandy marls, reaching a total thickness up to ~110 m (Fig. 2A).

3. Material and methods

Sediment samples were collected from the exposed marly Msherpheh section (Fig. 2A and B) during the field study of 1990–1992 in collaboration between the Academy of Sciences and Moscow State University in Russia, and the General Establishment of Geology and Mineral Resources of Syria. The results were published by Devyatkin et al. (1996). Later, raw whole-rock samples were archived at the Russian Academy of Sciences. In the current study, these samples were revisited. Accordingly, 17 whole-rock samples, corresponding to the lower 48 m of the section, were studied (Figs. 2A, B). Preparation and processing of the

samples for foraminiferal investigation were conducted according to a standard technique: they were soaked in water, washed through a 100-µm sieve and dried (Saraswati and Srinivasan, 2016). The residues were studied under a light microscope and SEM Tescan 2300 at the Russian Academy of Sciences. In identifying planktic foraminifers, the classification of Wade et al. (2011) was followed. For biostratigraphical age constraints, we followed Cita et al. (2008) and Lirer et al. (2019) as they presented integrated biozonations in the Mediterranean Region in combination with astronomical tuning and magnetostratigraphy that produced high-resolution biochronology. Given that some biomarker species of the eastern Mediterranean (i.e., *Globocanella inflata* and *Globoturborotalita truncatulinoides*) were reported in rare frequencies or as absent (Azibeiro et al., 2023), to capture all the relevant biomarker species, we performed a qualitative relative abundance approach where we scanned a larger quantity of sediment and marked only common species and rare but present biomarker species. We also used a smaller mesh-sized sieve (i.e., 100-µm) as some important biomarker species (e.g., *Globoturborotalita rubescens*, *Globigerinoides tenellus*) in the eastern Mediterranean marine outcrops are reported to be found more abundantly when a smaller fraction is used compared to a larger fraction (i.e., >125-µm) (Kanbur, 2025; Ögretmen et al., 2022). The results are displayed in Figs. 2C and 3, and reported in Table 1.

Nannofossils were studied in smear slides in light and polarization modes with a magnification of x1600 under a JenaLumar Carl Zeiss

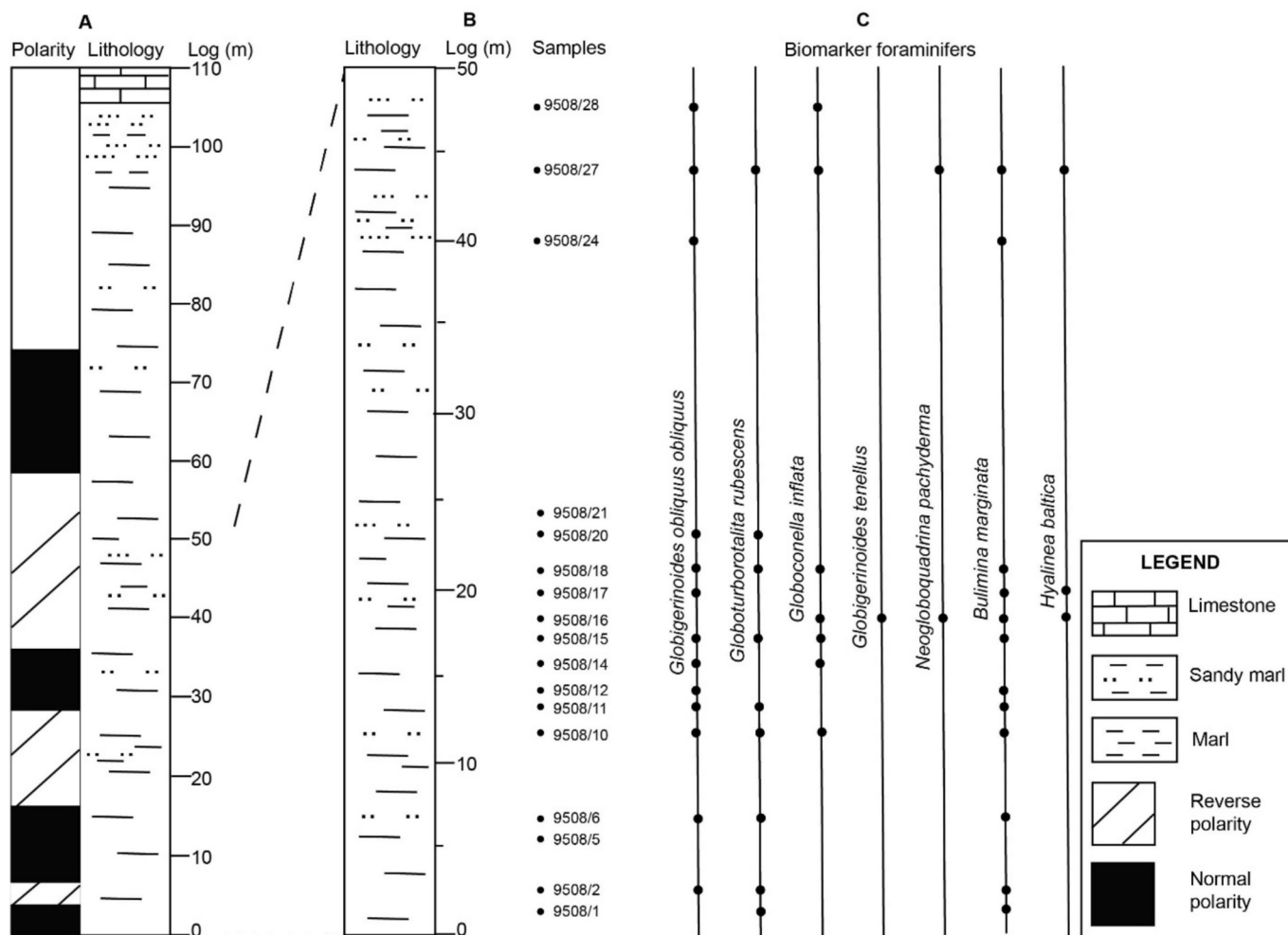


Fig. 2. A. Complete lithological log and polarity of Msherpheh section (modified after Devyatkin et al., 1996). Polarity annotations were adapted according to the modern use where black refers to normal polarity and oblique hatching is reverse polarity, contrary to the original study of Devyatkin et al. (1996) (details of their magnetostratigraphic framework linked to the scientific practice of that era [Khramov and Tarling, 1987] were explained in the Supplementary Material, Text S2) along with B. the lithological log of the lower half of the section, studied samples, and C. their biomarker foraminifers.

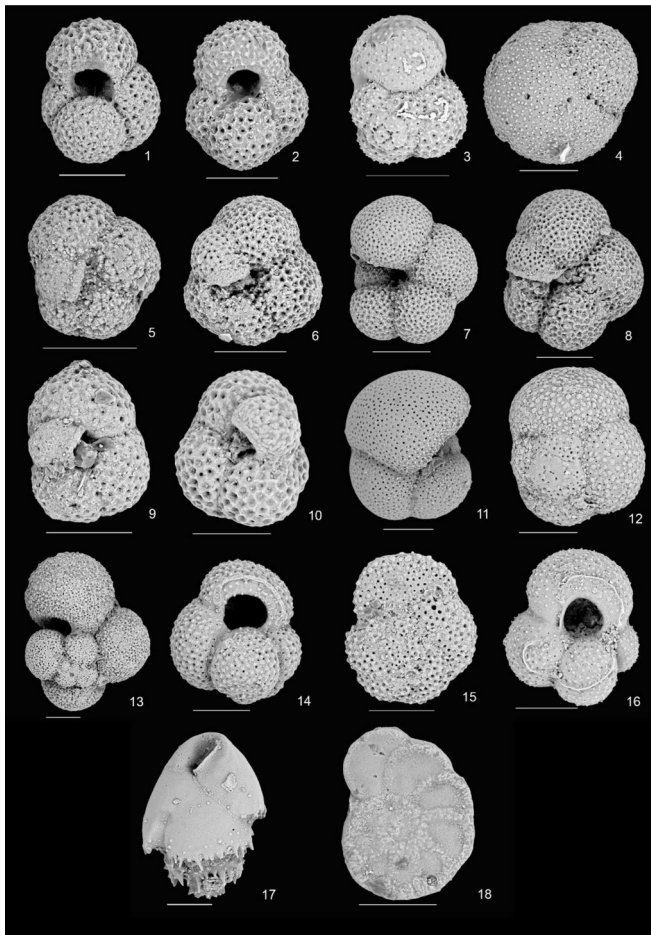


Fig. 3. SEM photos of the most common and biostratigraphically important planktic and benthic foraminifer species of the Msherpheh section. 1–3 *Globoturborotalita rubescens*, (1) Sample 9508/1; (2) Sample 9508/2; (3) Sample 9508/6. 4 – *Orbulina suturalis*, Sample 9508/10. 5–9 *Neogloboquadrina incompta* (5) Sample 9508/2; (6, 7) Sample 9508/10; (8) Sample 9508/10; (9) Sample 9508/2. 10 – *N. pachyderma*, Sample 9508/27. 11, 12 – *Globoconella inflata*, (11) Sample 9508/10, (12) Sample 9508/27. 13 – *Globigerinella calida*, Sample 9508/11. 14 – *Globigerinoides obliquus obliquus*, Sample 9508/11. 15 – *Globorotalia crassaformis*, Sample 9508/20. 16 – *Globigerinoides tenellus*; Sample 9508/27. 17 - *Bulimina marginata*; Sample 9508/11. 18 – *Hyalinea baltica*; Sample 9508/27. Scale bars: 100 μ m.

microscope. At least 300 fields of view were examined in each sample. Smear slides were prepared following a standard method of sample preparation (Muzylev, 1980) at the Russian Academy of Sciences. Taxonomic identifications are based on Bown and Young (1998), Galović and Young (2012), Perch-Nielsen (1985), and the Nannotax website (Young et al., 2013). The most recent study by Raffi et al. (2020) was used for biostratigraphical age constraints in the Mediterranean Region. The results are displayed in Table 2.

For pollen analysis, approximately 20 g of sediment was used. The samples were prepared according to the standard pollen preparation method (Cour, 1974). First, 35% cold HCl acid and 47% cold HF acid were added to eliminate carbonate and silica, respectively. Then, $ZnCl_2$ (density > 2.0) was used to separate the palynomorphs. The resting sediments were sieved using 200 μ m and 10 μ m nylon sieves. The final residue was mounted on a glass slide with one drop of glycerine and fixed with a cover glass. Palynological slides were analyzed under a light transmission microscope (Leica) in the Microscope Laboratory facilities at the Eurasia Institute of Earth Sciences at Istanbul Technical University, using immersion oil and different objectives (X63 and X100). The palynomorphs were counted with a minimum of 300 pollen grains,

except for *Pinus* (pine tree), due to its prolific nature and long-distance transportation (Heusser, 1988; Suc and Drivaliari, 1991; Cambon et al., 1997; Beaudouin, 2003). Three samples from the Msherpheh section were low in pollen grain amounts (samples: 9508/15, 9508/16, and 9508/28), and thus were not included in the distribution chart of palynomorphs. A pollen atlas (Reille, 1992) and pollen photographs were used for pollen identification. Non-pollen palynomorphs (NPPs) are commonly encountered during routine pollen counting (Shumilovskikh and Van Geel, 2020). The percentage of NPPs was calculated based on the overall pollen count. For palynomorph identifications, descriptions and illustrations of Wolf (1966, 1967a, 1967b); Van Geel and Van der Hammen, 1978, Van Geel, 2002; Ellis-Adam and Van Geel (1978); Ellis and Ellis (1997); Van Geel and Van der Hammen (1978); Van Geel et al. (1989); Van Geel and Aptroot (2006); Van Geel et al. (2011); Cugny et al. (2010); and Miola (2012) were used. The counts can be found in Excel format as Supplementary Material.

4. Results and discussion

In this section, we present and discuss the results of each micropaleontological data according to their environmental setting (i.e., marine and terrestrial), linking them to each other and to the collective biostratigraphic age constraints in subsection 4.1. Then, in subsection 4.4, we discuss our data collectively in relation to hominin migration during the Calabrian along the coastal strip of the Levantine Corridor.

4.1. New age constraints from foraminifers and calcareous nannofossils

Planktic foraminifers in the bottom-Msherpheh section (at 1.5 m, 9508/1) are dominated by *Globigerinoides ruber*, with additional presence of *Globigerinoides extremus*, *Trilobatus trilobus*, *Orbulina universa*, *Globigerinella siphonifera*, *Globigerinita glutinata*, *Turborotalita quinqueloba*, *Globoturborotalita rubescens*, *Globoconella inflata*, *Globigerina falconensis* and *G. obliquus obliquus*. Among those, *G. rubescens* and *G. inflata* point to an age younger than 2.09 Ma (Table 1) (Lirer et al., 2019). The rare occurrence of *Globigerinoides tenellus* and *Neogloboquadrina pachyderma* at 17 m should also be noted, as these species mark the Calabrian age (First Occurrence, FO, at 1.79 Ma for both species) (Table 1; Fig. 2; Lirer et al., 2019). The continuous presence of *G. obliquus obliquus* throughout the section is suggestive of an age older than 1.28 Ma (Last Occurrence, LO, at 1.28 Ma) (Table 1; Lirer et al., 2019). The occurrence and reliability of *Globigerinella calida* as a biomarker are discussed separately in the Supplementary Material (Text S3) based on our synthesis following the previous studies of Parker (1962), Bolli and Premoli Silva (1973), Selli et al. (1977), Kennett and Srinivasan (1983), Bylinkskaya and Golovina (2004), Wade et al. (2011), Carotenuto et al. (2016), and Lirer et al. (2019).

Benthic foraminifers are tools for assessing ecological conditions, especially water depth, oxygenation and food availability (Murray, 2006), while some of them are biostratigraphic markers. Reliability of *Bulimina marginata* has been documented in detail from epibathyal depths in the Mediterranean Region (Di Bella, 1999) and has been considered an important datum event for Calabrian times (Cita et al., 2008). Accordingly, because of the continuous presence of the modern morphotype of *Bulimina marginata* (Di Bella, 1999) starting from the bottom of the section (Table 1; Figs. 2C and 3), we can assume that the age of the section is younger than 1.54 Ma (Cita et al., 2008). The presence of *Hyalinea baltica* in sample 16 (Table 1; Figs. 2C and 3), points to an age younger than 1.43 Ma (Cita et al., 2008).

It is important to note that this study is based on the first half (48 m) of the 110-m-thick Msherpheh section described by Devyatkin et al. (1996). Our results from foraminiferal micropaleontology indicate that the lower part of the section, which was deposited during the Calabrian, aligns well with the previous magnetostratigraphic data that mostly revealed reverse polarity in this part of the section (Devyatkin et al., 1996) (Fig. 2).

Table 1

Foraminifers in section 9508, Syria, Msherpheh (samples 9508/1–9508/28). C – common occurrence; x – present.

Sample (9528/)	1	2	5	6	10	11	12	14	15	16	17	18	20	21	24	27	28
Depth in log (m)	1.5	2.5	5.5	6.5	12	13	14	16	17	18	20	21	23	24	40	44	48
Planktics																	
<i>Gs.ruber</i>	C	C	C	C	C	C	C	x	C	C	C	x	C	x	x	C	x
<i>Gs.extremus</i>	x	x	x	x	x	x	C	x	x	x	x	x	x	x	x	x	x
<i>Trilobatus trilobus</i>	x	x	x		C	C		x	x	x	x	x	x		x	x	
<i>T.sacculifer</i>					C	C		x		x		x	x				
* <i>Gs.obliquus</i>		C		C	x	x	C	x	x	x	x	x	x		x	x	x
<i>Gs.conglobatus</i>								x		x							
* <i>Gs.tenellus</i>										x							?
<i>O.universa</i>	x	x	x	x	C	x	x	x	x	x		x	x	x	x	x	x
<i>O.suturalis</i>					x										x		
<i>G.siphonifera</i>	x	x	x		x	x	x	x	x	x	x	x	x	x			
<i>G.glutinata</i>	x	C		C	x	x	x		x	x	C	x	C	x	x	x	
<i>G.uvula</i>																	x
<i>G.hexagonus</i>																	x
<i>T.quinqueloba</i>	x	x		x		x	x		x	x	x	x	x				x
* <i>G.rubescens</i>	x	x		x	x	?			x			x	x				x
<i>G.falconensis</i>	x	x		x	x	x		x	x	x	x	x		x			x
<i>G.bulloides</i>					x	x	x			x	x		x	x	x	x	x
* <i>G.calida</i>					x	x	x			x	x						
<i>G.crassaformis</i>		x		x									x	x			x
<i>G.viola</i>		x		x													
<i>G.hirsuta</i>																	x
* <i>G.inflata</i>					x			x	x	C		x					x
* <i>N.pachyderma</i>										x							?
<i>N.incompta</i>		x			x		x			C		x		x	x		
Benthics																	
* <i>Hyalinea baltica</i>										x	x						x
<i>Ammonia</i> sp.										x	x	C	x	x	C	C	C
* <i>B.marginata</i>	x	x		x	x	x	x		x	x	x	x			x	x	

Table 2

Calcareous nannoplankton of the Msherpheh section.

Age	Depth (m)	Sample	Nannoplankton species
Calabrian	44	27	Barren
	23	20	<i>P. lacunosa</i> , <i>B. bigelowii</i> , <i>C. macintyreii</i> , <i>Scyphosphaera apsteinii</i> , <i>C. leptoporus</i> , redeposited species
	20	17	<i>C. macintyreii</i> , <i>Gephyrocapsa caribbeanica</i>
	17	15	<i>P. lacunosa</i> , <i>C. pelagicus</i> , <i>Gephyrocapsa</i> aff. <i>caribbeanica</i> , <i>H. carteri</i> , <i>Pontosphaera multipora</i> , <i>Thoracosphaera</i> sp. (fragments) and redeposited species
Gelasian	13	11	<i>H. sellii</i> , <i>H. carteri</i> , <i>C. leptoporus</i> , <i>Rhabdosphaera clavigera</i>
	12	10	<i>Scyphosphaera</i> , redeposited species
	6.5	6	<i>D. asymmetricus</i> , <i>Rhabdosphaera clavigera</i> , <i>D. brouweri</i>
	5.5	5	<i>H. carteri</i> , <i>P. lacunosa</i> , <i>Rhabdosphaera clavigera</i> , <i>Reticulofenestra minutula</i> , <i>Scyphosphaera apsteinii</i> , redeposited species
	2.5	2	<i>H. carteri</i> , <i>P. lacunosa</i> , <i>Pontosphaera</i> , <i>Rhabdosphaera</i> , <i>D. asymmetricus</i> , <i>Calcidiscus leptoporus</i> , <i>C. macintyreii</i> , <i>D. brouweri</i> , <i>D. triradiatus</i> , <i>Scyphosphaera apsteinii</i> , <i>Reticulofenestra minutula</i>
1.5	1	<i>Discoaster brouweri</i> , <i>D. variabilis</i> , <i>D. triradiatus</i> , <i>Discoaster</i> sp., <i>Coccolithus pelagicus</i> , <i>Pseudoemiliania lacunosa</i> , <i>Helicosphaera sellii</i> , <i>Rhabdosphaera clavigera</i> , <i>Reticulofenestra minutula</i> , <i>Scyphosphaera apsteinii</i> , <i>Thoracosphaera</i> sp. (fragments), redeposited species	

The contribution of calcareous nannofossils to our age constraints is relatively limited because all samples contain a poor nannofossil assemblage. *Discoaster* species are either rare or represented by a single individual, and their preservation is often unsatisfactory (rays are broken off or the ray-tips are deformed), which makes accurate

taxonomic identification difficult. The previous conclusion that “the lower beds of the Msherpheh section correlate with the upper part of the *Discoaster surculus* Zone (NN 16)” (Devyatkin et al., 1996) can be considered erroneous since no reliable findings of *D. surculus* were encountered in the studied samples. However, studies in 1996 were carried out according to the “sediment enrichment” method, meaning that, for the analysis, a sample of at least 100 g of rock was taken, and was then elutriated by decantation, resulting in the concentration of nannofossils. Currently, studies are carried out by preparing smear slides by scraping from a small piece of rock. Thus, a direct comparison of these results is not entirely correct. Based on the occurrence of *Discoaster asymmetricus* (5-ray variety of *D. brouweri*) and *Reticulofenestra minutula*, the interval from sample 9508/1 (at 1.5 m) to 9508/6 (at 6.5 m) (Table 2) can be attributed to the Gelasian, since their disappearance is recorded in the upper Gelasian [LO: within NN18 zone (2.39–1.93 Ma, top in Gelasian stage)] (Bown and Young, 1998; Raffi et al., 2020).

The continuous occurrence of *D. brouweri* and its three-ray variety, *D. triradiatus*, would point to the interval from sample 9508/1 to 9508/6 (Table 2) is not younger than 1.93 Ma (Raffi et al., 2020), unless these individuals were reworked, considering the unsatisfactory preservation condition in general. Therefore, the position of the upper boundary of the Gelasian and the base of the Calabrian cannot be determined based on nannofossil data, and it is drawn conditionally, considering the age constraints that foraminifers indicate. The continuous presence of *B. marginata* throughout the section marks an age younger than 1.54 Ma, and is supported by the presence of *H. baltica*, which points to an age younger than 1.43 Ma (Table 1; Cita et al., 2008). However, the presence of *D. asymmetricus* and *D. triradiatus* is contradictory to this finding, given that until sample 9805/6, the section cannot be younger than 1.93 Ma (Raffi et al., 2020), unless they are reworked.

At this point, we consider the preservation condition of the specimens investigated in this study. Some enrichment of the assemblage (possibly due to increased seawardness) is recorded in sample 9508/15 at 17 m, where *Gephyrocapsa* aff. *caribbeanica* was found. However, rare *D. asymmetricus* also occurs there (Table 2), which may indicate both reworking of the underlying weakly consolidated sediments and a

possibly longer existence of *D. asymmetricus*. Non-pollen palynomorphs (see sec. 4.3) indicate the presence of *Glomus* and *Pseudoschizaea* at several levels. They are known to be strong indicators of reworking. Therefore, some inconsistencies in nanoplankton findings can be attributed to reworking.

Dinoflagellates are also biostratigraphic tools. In the study carried out by Versteegh (1997) in the North Atlantic and the central Mediterranean, the Last Appearance Datum (LAD) of *Invertocysta lacrymosa* was identified as a potentially valuable biostratigraphic marker for Marine Isotope Stage (MIS) 110. This suggests an age in the latest Pliocene, of approximately 2.74 Ma. However, given that the foraminiferal data suggest the Msherpheh section is younger than this age, the presence of *I. lacrymosa* in the section can be due to reworking. The presence and abundance of certain dinoflagellate cyst species further support the Calabrian age interpretation (Fig. 4). The occurrence of *Lingulodinium machaerophorum* has been found in the Early Pleistocene sediments in the North Atlantic and the North Delta Basin of the Nile Delta (De Schepper et al., 2011; Zakaria et al., 2025). Furthermore, the Early Pleistocene interval is characterized by the predominance of gonyaulacoid dinocysts such as *Operculodinium centrocarpum*, *Impagidinium* sp., and various *Spiniferites* species (McCarthy and Mudie, 1996). The presence of *Spiniferites elongatus* alongside other dinocysts such as *Bitectatodinium tepikiense* and *I. lacrymosa* may be due to the reworking of older sediments (Fig. 4). This is also supported by the presence of *Glomus* fungi in the samples (Fig. 4). *Glomus* is a genus of arbuscular mycorrhizal (AM) fungi and is frequently found in association with plant roots. Its presence in the sedimentary record indicates that materials have been transported and deposited through erosional processes (Anderson et al., 1984; Biltekin et al., 2024). Algal spores, specifically *Pseudoschizaea* (also known as the *Concentricystes* group), may also indicate soil erosion, as with *Glomus* (Milanesi et al., 2006) in the Msherpheh section. Indeed, reworking is also evident among the calcareous nannofossils (Table 2, sec. 4.1).

4.2. Paleoclimate and paleoenvironmental insights from the marine micropaleontological data

Foraminifers of the Msherpheh section consist of various environmental indicators. The section is predominated by species that represent transitional conditions and subtropical conditions, pointing to relatively warm climatic conditions (Kučera, 2007; Lourens et al., 1992; Schiebel and Hemleben, 2017). The taxa that represent transitional conditions in the section include *Globigerina bulloides*, *Globigerinita glutinata* (most frequent and common) and *Globoconella inflata*. Subtropical conditions were represented by *Gs. conglobatus*, *Gs. extremus*, *Orbulina universa*, *G. falconensis*, *Globoturborotalita rubescens*, *Globigerinita siphonifera*, and *Gs. ruber*, which is the most common species in the entire section, and by some scattered *Globorotalia crassaformis* (Table 1). The sediments also include tropical *Trilobatus sacculifer* and *T. trilobus*. Some specific cooling events can be detected by the presence of subpolar species. *N. incompta* (Schiebel and Hemleben, 2017) is present in several levels throughout the section (levels 2.5, 12, 14, 21, 24, and 40 m) with common occurrence at 18 m and is accompanied by *Turborotalita quinqueloba*, which is present almost at all levels (Table 1). The presence of these species is most likely linked to cooler water inflow to the Mediterranean Sea from the Atlantic Ocean (Lourens et al., 1992; Serrano and Guerra-Merchán, 2012). Polar species *N. pachyderma* (Schiebel and Hemleben, 2017) is also found at levels 18 and 44, and probably at 40 m (Table 1, Fig. 5). In particular, the presence of *N. pachyderma* and *N. incompta* in the Mediterranean Sea is considered an indicator of glacial periods or very cold climate episodes (Lourens et al., 1992; Serrano and Guerra-Merchán, 2012). Despite strong reworking in the nannofossil assemblage as explained earlier, the presence of *Coccolithus pelagicus* (at 1.5 m and 17 m; Table 2) can also be considered indicative of cool surface waters, which could be linked to riverine plumes, upwelling zones or meltwater with high productivity (Cachão and Moita, 2000; Trotta et al., 2025).

In general, the Msherpheh section corresponds to a pre-Early-Middle Pleistocene Transition (EMPT), which occurred more predominantly in the Northern Hemisphere between 1.2 and 0.7 Ma (Clark et al., 2006;

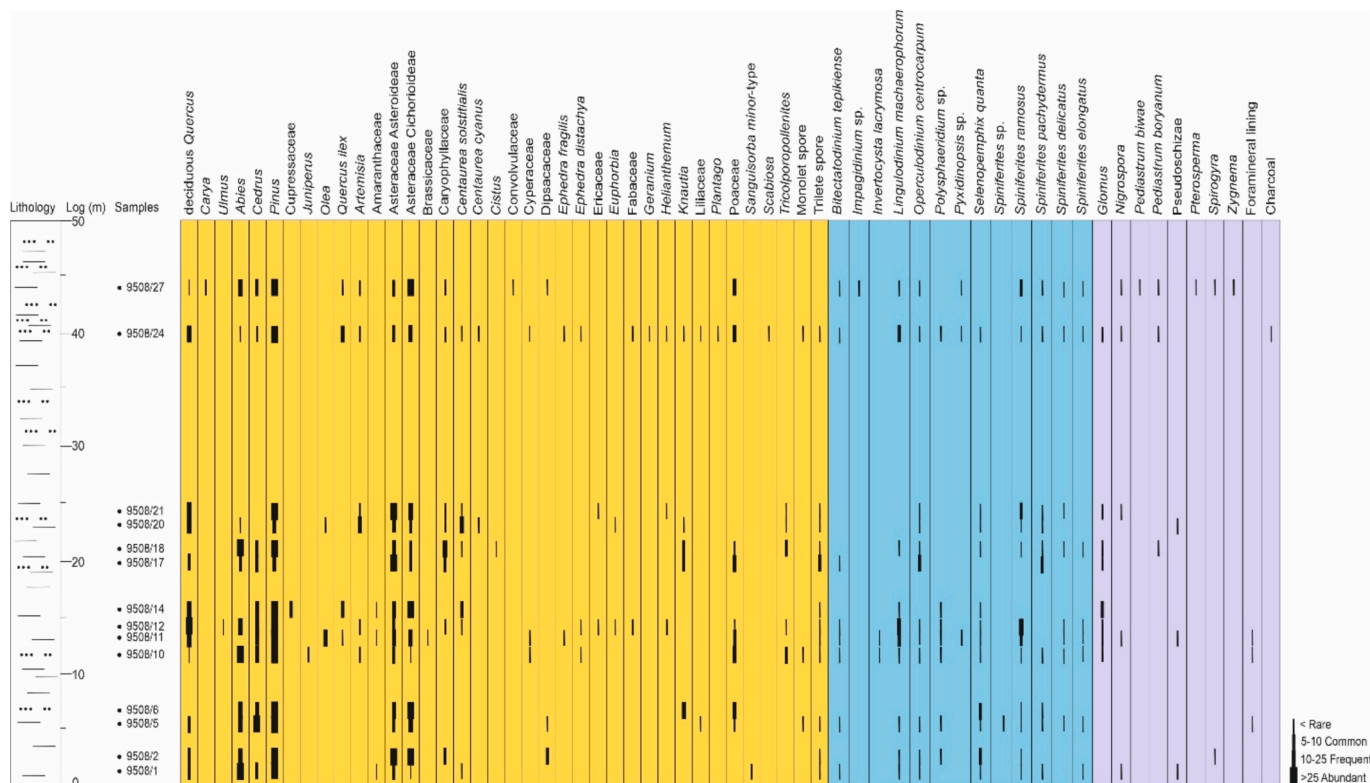


Fig. 4. Distribution chart of the Calabrian-aged palynomorphs of the Msherpheh section.

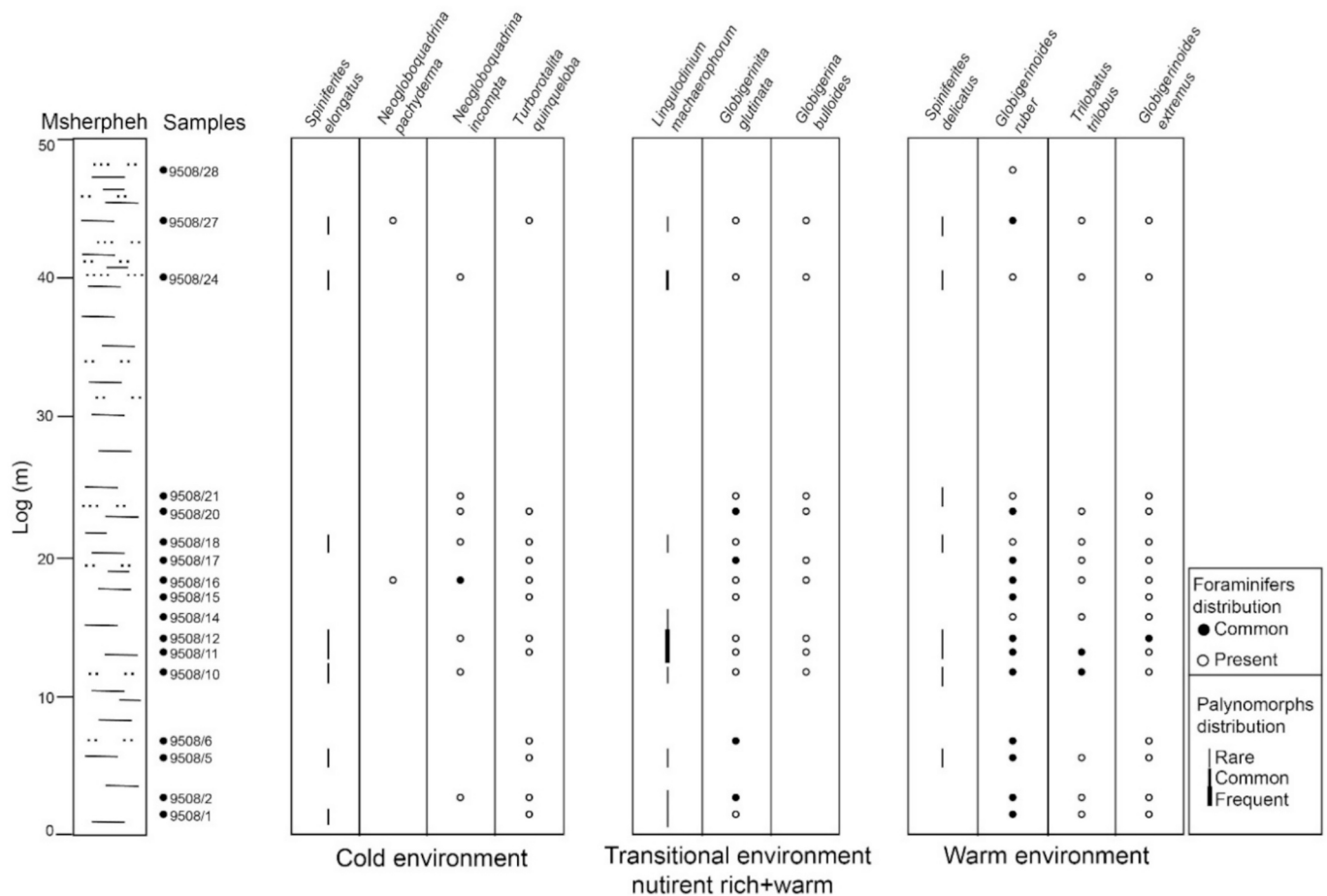


Fig. 5. Integrated distribution chart of foraminifers and palynomorphs as environmental indicators from Msherpheh section during the Calabrian in the easternmost Mediterranean Region.

Head et al., 2008; Head and Gibbard, 2005, 2015). The EMPT marks a shift from warm global conditions with 41-kyr symmetrical climate cycles to 100-kyr cycles with abrupt shifts and long glacial periods. This is presumably linked to the interplay between orbital forcing and global ice volume changes (Head and Gibbard, 2015). This shift is suggested to have been gradual, starting from 2 Ma with a gradual increase in the periodicity of deglaciations (Legrain et al., 2023; Lisiecki and Raymo, 2005), contrary to the scenarios that suggested a progressive preconditioning linked to the sudden expansion of Antarctic ice volume during the glacial stage MIS 22 (~900 ka) (Elderfield et al., 2012; Head and Gibbard, 2015). Despite the lack of continuous data in our study section and, keeping in mind the semienclosed nature of the study region, the strong influence of river input, varying foraminiferal taxa with the co-occurrence of subpolar/polar species and subtropical species can be suggestive of progressive change with, short-term, intermittent oscillations before EMPT rather than gradual as the subpolar/polar forms can reach the Mediterranean realms only from the Atlantic Ocean. The results of this study are consistent with previous findings. Intermittent and varying climatic conditions between 1.72 and 1.08 Ma were also recorded in southern Türkiye from planktic foraminifers reflected in fluctuating nutrient input and temperature (Ögretmen, 2022) and from benthic foraminifers as sapropel deposition marking changing oxygenation due to water column stratification presumably controlled by freshwater input (Ögretmen et al., 2018b). Such conditions, indicative of high nutrient input through rivers and varying bottom water oxygenation, were also registered by foraminifers of uplifted marine sediments of ~1.72–1.32 Ma found in southeast Rhodes Island in the western section of the eastern Mediterranean Sea (Milker et al., 2019). In

addition to our insights on varying climate conditions, the continuous presence of planktic foraminifer *G. bulloides* and benthic foraminifer *B. marginata* supports each other in representing nutrient-rich environments (Table 1; Jonkers and Kučera, 2015; Jorissen et al., 1992; Murray, 2006; Ögretmen, 2022; Vénec-Peyré and Caulet, 2000). Although the Mediterranean Sea is known to be oligotrophic, the proximity to land and, hence, a sustained riverine source with nutrient-rich waters arriving at the depositional setting of the section can explain the common presence of taxa that thrive in nutrient-rich waters. Similarly, calcareous nannoplankton *H. carteri* is also recorded in regions with high river input (Savannah et al., 2024); and it is found at levels 2.5 m, 5.5 m, 13 m, and 17 m (Table 2). Indeed, the section is located within an incision of Nahr El-Kabir, i.e., El-Kabir River (Fig. 1B). Significant percentages of *Lingulodinium machaerophorum* among the dinoflagellates, indicating warm, stratified conditions in transitional environments between inshore upwelling and warmer, offshore waters, are found at depths of 13 m (8%), 14 m (13.8%) and 40 m (6.5%), further supporting the foraminiferal findings with continuous presence of *G. bulloides* (Table 1, Fig. 5), a common species in nutrient-rich environments (Schiebel and Hemleben, 2017).

Spiniferites species among the dinoflagellates (*S. ramosus*, *S. pachydermus*, *S. delicatus* and *S. elongatus*) are also present. The genus *Spiniferites* is generally abundant throughout the section and is a very common genus in marine sediments. *Spiniferites delicatus* is present at various levels (e.g., 0.6% at 1.5 m, 1% at 5.5 m, 0.5% at 14 m and 2.8% at 40 m). This species is typically associated with warm-temperate to tropical conditions, which are often characterized by relatively low salinity and minimal seasonal temperature contrasts. *Spiniferites*

elongatus is also present at various levels, including 0.5% at 5.5 m, 0.3% at 12 m, 0.8% at 13 m, 0.5% at 14 m, at 0.4% 21 m, 1.3% at 40 m, and 0.9% at 44 m. In contrast to *S. delicatus*, *S. elongatus* is considered an Arctic-subarctic indicator and is typically abundant in nutrient-poor environments with winter sea ice and large seasonal temperature contrasts (de Vernal et al., 2018). Indeed, the presence of *S. elongatus* aligns well with the presence of polar/subpolar foraminifers, *N. pachyderma* and *N. incompta* (at 40 m and 44 m, respectively, which co-occur with transitional and subtropical taxa (Table 1, Fig. 5), and calcareous nanoplankton *Coccolithus pelagicus* (Table 2, at 1.5 m), pointing to a cool water source to the easternmost Mediterranean Sea during the Calabrian. The co-occurrence of *Spiniferites delicatus* (a warm-temperate/tropical indicator species) and *Spiniferites elongatus* (an Arctic/subarctic indicator species) at various depths (e.g., 1.5 m, 5.5 m, 13 m and 40 m) suggests that the marine environment at the study site is located in a predominantly transitional zone where warm and cold-water masses mix. Alternatively, the sediment layers may represent an integration of signals over time, capturing rapid, short-term fluctuations in sea-surface temperature, or they may contain reworked older sediments with cold-water species. However, *N. pachyderma* is not abundant in the eastern Mediterranean waters and is not found in deposits older than 1.79 Ma. Thus, the presence of cold-water foraminifer taxa (*N. pachyderma* and *N. incompta*) supports these findings (Table 1, Fig. 5), and the study site could be capturing short-term fluctuations under the influence of Atlantic water inflow. Other dinocyst taxa, such as *Bitectatodinium tepikiense* and *Operculodinium centrocarpum*, also show peaks (Fig. 4). While *O. centrocarpum* (at 3.9% at 13 m, 3.2% at 14 m, 9.1% at 20 m and 1% at 23 m) can be found in a variety of environmental settings from temperate to subpolar, estuarine to oceanic (Poulsen and Kuijpers, 2002); *Bitectatodinium tepikiense*, with significant percentages at 1.1% at 13 m, 1.5% at 14 m and 3% at 20 m, may indicate stratified waters and strong seasonality (Harland et al., 2016).

Freshwater algae further contribute to our overall understanding of riverine input or varying sea-levels in the study area. The presence of *Pediastrum* species, such as *Pediastrum biwae* (0.6% at 40 m) and *Pediastrum boryanum* (2% at 6.5 m; 2.1% at 23 m; 2.2% at 44 m), provides clear evidence of freshwater environments. *Pediastrum* is a genus of green algae that exclusively inhabits freshwater bodies such as lakes, ponds and rivers (Komárek and Jankovská, 2001) and is resistant to diagenesis. Its presence could signal a shift towards an increased fluvial discharge, which would effectively dilute or counteract marine influence. In a dynamic coastal or estuarine setting, this would imply a period of reduced marine influence, perhaps due to a lower sea level or increased terrestrial runoff leading to the dilution of saline waters. The presence of other freshwater green algae, such as *Pterosperma*, *Spirogyra* and *Zygnema*, further reinforces the freshwater signal. This finding agrees with the foraminiferal data, with *Ammonia* sp. appearing at levels 23 m, 40 m and 44 m (Table 1) as it is a species that can tolerate various salinities and predominantly lives in infralittoral depths (Murray, 2006).

4.3. Paleoclimate and paleoenvironmental insights from the palynological data

The palynological record from the Msherpheh section is characterized by the consistent co-occurrence of terrestrial pollen and other non-pollen palynomorphs. A striking and consistent feature throughout most of the samples is the overwhelming dominance of *Pinus* pollen, which frequently comprises the vast majority of the total pollen count in the lithological log (e.g., 91.2% at 1.5 m, 86.5% at 12 m, and 82.2% at 21 m) (Fig. 4). This high abundance is partly due to the ecological characteristics of *Pinus*, which is known for its prolific pollen production and efficient wind dispersal, and can be overrepresented in pollen assemblages (Heusser, 1988; Suc and Drivaliari, 1991; Cambon et al., 1997; Beaudouin, 2003). Nevertheless, such consistently high percentages strongly suggest a substantial regional presence of pine forests. Other arboreal taxa also exhibit notable fluctuations, providing more

prominent climatic signals. *Abies* (fir) pollen shows significant peaks at depths such as 71.1% at 1.5 m, 50% at 12 m, 32.1% at 21 m, and 19.4% at 44 m, intercalated with periods of low or absent representation (e.g., 13 m, 16 m, 24 m). *Abies* is known to be sensitive to moisture changes and is generally an indicator of cold and/or humid conditions (Bledý et al., 2004). Deciduous *Quercus* (oak) pollen, including *Quercus ilex* (Holm Oak), also shows varying trends. General *Quercus* peaks are observed at 30.2% at 14 m and 24.1% at 40 m, with *Quercus ilex* specifically present at 9.4% at 16 m and 10.7% at 40 m. *Quercus* pollen, particularly from evergreen species, is often associated with warm and humid climates. *Quercus ilex* is characteristic of Mediterranean climates with warm, dry summers and mild, wet winters. The co-occurrence and fluctuating dominance of *Abies* (suggesting cooler/humid conditions) and *Quercus* (suggesting warmer/humid conditions; *Q. ilex* specifically indicating Mediterranean-type dry summers) suggest significant shifts in regional temperature and precipitation regimes over time (Combourieu-Nebout et al., 1998). *Cedrus* (cedar) and *Olea* (olive) pollen, with peaks such as *Cedrus* at 42.1% at 5.5 m and *Olea* at 22.6% at 13 m, can suggest specific regional forest types or influences typical of Mediterranean or temperate environments (Biltekin et al., 2015; Combourieu-Nebout et al., 1998). *Carya* is a warm-temperate tree recorded with a frequency of 2.8% in the section's upper part at 44 m. The *Carya* genus, comprising trees that thrive in warm-temperate, highly humid conditions, and is now found in two separate parts of the world: northeastern America and eastern China (An-Ming, 1982; Thompson et al., 2000). *Carya* was once present in Europe, but it faced extinction during repeated cooling periods during the Middle Pleistocene. This decline occurred earlier in Northern Europe due to temperature drops, and in Northern Africa due to increasing dryness (Fauquette et al., 1998; Klotz et al., 2006; Feddi et al., 2011). Another significant refuge existed in northern Anatolia, enabling the *Carya* to survive there until the Holocene (Biltekin et al., 2015).

Non-Arboreal Pollen (NAP) taxa also provide critical information on open landscapes and environmental conditions (Frenzel et al., 1992). Significant peaks in Asteraceae (Asteroideae and Cichorioideae) are observed at depths of 2.5 m (37.5% Asteroideae, 31.3% Cichorioideae), 24 m (56.8% Asteroideae, 13.5% Cichorioideae), and 44 m (8.3% Asteroideae, 38.9% Cichorioideae). Poaceae (grass family) also shows notable percentages, for instance, 22.2% at 6.5 m, 17.6% at 40 m, and 11.1% at 44 m. Significant increases in NAP, particularly when accompanied by decreases in AP, signify periods of cold and dry climate that favored the expansion of herbaceous vegetation over forests (Frenzel et al., 1992).

4.4. A (paleo)shoreline restriction for hominin migration via the Levantine Corridor?

Based on the new age constraints, the Msherpheh section represents an interval between 2.09 Ma (maximum possible) and 1.54 Ma (minimum possible) for the bottom-section, and > 1.28 Ma for the top-section, corresponding to roughly between MIS 79 and 40 (based on maximum possible age; *G. rubescens* FO at 2.09 Ma); more likely between MIS 53 and MIS 40 (based on minimum possible age; *B. marginata* FO at 1.54 Ma) (Lisiecki and Raymo, 2005). The eustatic sea-level variations recorded between MIS 79 and 40, also encompassing MIS 53, are in the range of 50 m (Miller et al., 2005). Such variation alone is insufficient to explain the onshore Msherpheh marine sediments.

The section is found ~15 km inland (Fig. 1), and the topmost part of the deposit unit is found at 110 m above sea level. Considering the presence of globorotalids, a group planktic foraminifers that prefer outer neritic water depths (Table 1; BouDagher-Fadel, 2013; Hart, 1980) and the frequent presence of *B. marginata*, we can suggest that the depositional environment represents upper epibathyal depths ~200–300 m (Milker and Schmiedl, 2012) until the common presence of *Ammonia* sp. at the upper parts of the section (Table 1). *Ammonia* sp. points to lowered water depths of maybe circalittoral-upper epibathyal boundaries

varying from 50 to 200 m (Milker and Schmiedl, 2012; Sgarrella and Moncharmont Zei, 1993). This change is also supported by palynology data, with non-arboreal pollen taxa representative of open landscapes and green algae representative of increased freshwater input (Fig. 4). Therefore, we can estimate that during the Early Pleistocene, the paleoshoreline, presumably more pronounced in incised valleys such as Nahr El-Kabir (Fig. 1B), was approximately 15 km inland. This finding aligns well with previous studies in the neighboring localities along the Turkish coasts (Kanbur and Ögretmen, 2022; Ögretmen et al., 2018b, Ögretmen et al., 2018a; Tari et al., 2018) and Rhodes Island (Moissette et al., 2024; Quillévére et al., 2019, Quillévére et al., 2016) in the eastern Mediterranean region. Furthermore, Clark and BouDagher-Fadel (2020) reported *Globoconella inflata* from the Beirut harbor area sediments in Lebanon. This species marks an age younger than 2.09 Ma according to Lirer et al. (2019), supporting our results pointing to the prevailing Calabrian epibathyal marine conditions along the Levantine Corridor coastal strip, even when ± 50 m of global sea-level variations are considered.

The earliest hominin expansions out of Africa seem to be associated with Mode I (Oldowan) industries with simpler technologies (Barash et al., 2022; Carbonell et al., 2008; Le Tensorer, 2017). Evidence for such expansions, even though present in the Levant area and dating as early as 2.48 Ma, has not been documented from the coastal strip of the Levantine Corridor, but rather at sites that are located more inland (Fig. 6). For the coastal strip, the available archaeological record to date does not present any industry older than Mode II (Carbonell et al., 2008; El Zaatari, 2018) (Fig. 6). Our age constraints of the marine deposits of the Msherpheh section in Latakia, on the coastal strip of Syria of older than 1.28 Ma might suggest, at least for this part of the Levant, that before this time, with shorelines extending around 15 km inland, the narrow coastal strip was completely submerged and thus unavailable for hominins to use during their initial expansions out of Africa. Indeed, the oldest archaeological sites, e.g., Berzine, Sitt Markho and Cheikh Mohammed, located around our studied Msherpheh section, i.e., around the Nahr El Kabir in Syria, have presented Lower Paleolithic material

attributed to the Acheulean industry and dated to 1.3–0.7 Ma (Le Tensorer, 2017) (Fig. 6). Additionally, this region might have continued to be a marine environment even until later. This is evident at the sites of Cheikh Mohammed and Samouk where archaeological artefacts were found in marine deposits dated to lower Quaternary (Le Tensorer, 2017; Sanlaville, 1979), which were later revised as younger than MIS 11, i.e. ~ 424 ka (Bridgland et al., 2024) (Fig. 6, see SI).

The limited accessibility of the relatively narrow coastal strip of the Levant Corridor for early hominin dispersals is also evident further south. Evidence of marine conditions was reported in the area of Beirut harbor prevailing post-2.09 Ma (Clark and BouDagher-Fadel, 2020; Lirer et al., 2019). Furthermore, in the Galilee Coastal Plains, which are located ~ 5 km inland, where Acheulean artefacts were also discovered, particularly at the Evron quarry, a Pliocene-Middle Pleistocene marine environment seems to have persisted until 500 ka (Sivan et al., 1999).

In terms of climate and environmental conditions, previous studies suggest that suitable conditions for hominin migration were open lands, and emerged land-bridges coincide with the major global sea-level drawdown of MIS 22 (~ 866 –900 ka) by ~ 110 m below modern-day sea-level during the EMPT (Muttoni and Kent, 2024). Paleoceanographic data from the Gulf of Cadiz at the exit point of the Mediterranean waters from the Mediterranean Sea suggest that previous glacial stages did not yield “full glacial” conditions in terms of temperatures and sea-level stands except for MIS 34 (~ 1.11 –1.14 Ma) with a prolonged cooling (Voelker et al., 2015). MIS 34 recorded a significant global sea-level drop by ~ 80 m (Miller et al., 2005) and was a significantly cool and arid period in the central Mediterranean Region (Girone et al., 2013; Tzedakis et al., 2006). Thus, overall, it seems that in the easternmost Mediterranean Sea, it was not until a major sea level drawdown that the coastal strip of the Levantine Corridor was fully exposed for hominins to utilize it as a pathway across Africa, Asia, and Europe (Muttoni et al., 2018; Muttoni and Kent, 2024), which probably was coupled with a regional uplift (Bridgland et al., 2017, 2024; Eppelbaum and Katz, 2022, 2025; Trifonov et al., 2014). Up until this point, they would have probably been using a more eastern, today more inland, route, supporting the findings of Eppelbaum and Katz (2025).

5. Conclusion

In this study, we used the latest biostratigraphy of benthic and planktic foraminifers and nannoplankton to update the age constraints of marine deposits (Msherpheh section) found in Latakia, Syria. These deposits are dated to the early-middle Calabrian period (bottom-section age being around 2.09–1.54 Ma), but older than 1.28 Ma. They fall conservatively between MIS 79 and MIS 40, and most likely between MIS 53 and MIS 40 (1.54–1.28 Ma).

The consistent co-occurrence of terrestrial pollen, marine dinoflagellate cysts, and freshwater algae indicated that the depositional site was a highly dynamic interface zone, and it predominantly had typical characteristics of a Mediterranean climate. It was probably a coastal or an estuarine environment with fluctuating connectivity to marine and terrestrial hydrological systems. The consistent dominance of *Pinus* in the terrestrial vegetation suggests a resilient regional ecosystem. Fluctuations in other arboreal taxa, particularly the alternating dominance of *Abies* and *Quercus*, indicated an oscillating paleoclimate with significant shifts in temperature and precipitation in the region linked to pre-EMPT conditions. This points to a gradual shift in the regional climate dynamics with short-term variations, parallel to foraminiferal findings with taxa representative of cold-waters such as *Neoglobobadrina incompta*, *Turborotalita quinqueloba*, and *N. pachyderma*. The increased presence of non-arboreal pollen, particularly from Asteraceae families and ruderal species such as *Centaurea solstitialis* and *C. cyanus*, suggests a transition to more open landscapes, potentially driven by increased aridity. Strong dominance by *Lingulodinium machaerophorum* indicated robust marine connections with warm, stratified waters. Conversely, the sporadic but distinct presence of freshwater algae, such as *Pediastrum*,



Fig. 6. Major sites and findspots with evidence of hominin presence during different migration time slices are represented by yellow circles referring to Mode II, and blue stars referring to Mode I. Orange rectangle refers to the location of Msherpheh section. The full list of sites can be found in Supplementary Material. Basemap created using QGIS. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

indicated periods of significant freshwater input, implying an increased fluvial discharge, which effectively diluted marine influence, aligning well with *Ammonia* sp. results, pointing to a dynamic marine setting with frequent contributions from the continent.

We also showed that the Early Pleistocene paleo-shoreline of the easternmost Mediterranean region was approximately 15 km inland, yet, studies on regional tectonics and geodynamics that translate into subsidence/uplift are necessary to refine this finding. Our analysis revealed that paleoshoreline development might have played an important role in shaping the distribution of hominin migration pathways across different time slices, as the coastal strip of the Levantine Corridor emerged only after 1.28 Ma, most likely as a consequence of a major sea-level drop in tandem with tectonic uplift.

Author Contribution

NÖ: conceptualization, writing, data collection and visualization; MB: conceptualization, writing, data collection and visualization; DB: writing, data collection and visualization; LG: writing, data collection; SS: data collection and visualization; SZ: conceptualization, writing and data collection. SM: data collection. FN: conceptualization and data collection. All authors contributed to the discussion and finalization of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

We thank Prof. Dr. Alexsey Tesakov for his contributions to facilitating this collaboration. NÖ received support from TÜBITAK 2221 Visiting Scientists Fellowship Program, EU-MSCA Postdoctoral Fellowship Program (grant no 101104537), and the Aarhus University Research Foundation. The work of MB and LG was carried out in the framework of the state topic of the Geological Institute of RAS. SEZ and SM were supported by the European Research Council (ERC-CoG-101001889). This study was also supported by Istanbul Technical University, Scientific Research Projects Coordination Unit (İTU BAP), with project number MGA-2023-44653. SS was fully funded by the Italian Ministry of University and Research. This study did not receive any specific research funding. Thanks are also due to the handling editor, Laura Sadori, and two anonymous reviewers whose constructive comments helped improve our manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2026.113811>.

Data availability

Quantitative data of palynomorphs are provided as Supplementary Material in Excel format.

References

Abbate, E., Sagri, M., 2012. Early to Middle Pleistocene *Homo* dispersals from Africa to Eurasia: geological, climatic and environmental constraints. *Quat. Int.* 267, 3–19. <https://doi.org/10.1016/j.quaint.2011.02.043>.
Zakaria, A., Kassab, W.G., Helmy, R.Y., Hamed, M.S., Raafat, A., 2025. Pliocene–Pleistocene bioevents, sequence biostratigraphy and paleoenvironment of the Mediterranean North Delta Basin, Egypt. *Mar. Pet. Geol.* 178, 107428. <https://doi.org/10.1016/j.marpetgeo.2025.107428>.

Anderson, R.S., Homola, R.L., Davis, R.B., Jacobson Jr., G.L., 1984. Fossil remains of the mycorrhizal fungal *Glomus fasciculatum* complex in postglacial lake sediments from Maine. *Can. J. Bot.* 62 (11), 2325–2328. <https://doi.org/10.1139/b84-316>.
An-Ming, L., 1982. On the geographical distribution of the Juglandaceae. *Acta Phytotaxon. Sin.* 20 (3), 257–274 (in Chinese).
Azibeiro, L.A., Kucera, M., Jonkers, L., Cloke-Hayes, A., Sierro, F.J., 2023. Nutrients and hydrography explain the composition of recent Mediterranean planktonic foraminiferal assemblages. *Mar. Micropaleontol.* 179, 102201. <https://doi.org/10.1016/j.marmicro.2022.102201>.
Babbo, I., 2020. Soft-Sediment Deformation Structures and Depositional Environment of the Middle Eocene Carbonates, Al-Kornish Al-Janoubi section, Latakia Ridge Basin, Syria. *EIMJ* 8, 1–24.
Bailey, G.N., King, G.C.P., 2011. Dynamic landscapes and human dispersal patterns: tectonics, coastlines, and the reconstruction of human habitats. *Quat. Sci. Rev.* 30 (11–12), 1533–1553. <https://doi.org/10.1016/j.quascirev.2010.06.019>.
Barash, A., Belmaker, M., Bastir, M., Soudack, M., O'Brien, H.D., Woodward, H., Prendergast, A., Barzilai, O., Been, E., 2022. The earliest Pleistocene record of a large-bodied hominin from the Levant supports two out-of-Africa dispersal events. *Sci. Rep.* 12 (1). <https://doi.org/10.1038/s41598-022-05712-y>.
Beaudouin, C., 2003. Effets du dernier cycle climatique sur la végétation vall Rhone et sur a sédimentation de la plate-forme du golfe du Lion d'apr' es la palynologie. PhD thesis. Université Claude Bernard Lyon-1, France, p. 403.
Belmaker, M., O'Brien, H.D., 2018. Mesowear study of ungulates from the Early Pleistocene site of 'Ubeidiya (Israel) and the implications for early *Homo* dispersal from Africa. *Quat. Int.* 480, 66–77. <https://doi.org/10.1016/j.quaint.2017.03.052>.
Belmaker, M., Tchernov, E., Condem, S., Bar-Yosef, O., 2002. New evidence for hominid presence in the Lower Pleistocene of the Southern Levant. *J. Hum. Evol.* 43, 43–56. <https://doi.org/10.1006/jhev.2002.0556>.
Ben-Avraham, Z., Lazar, M., Schattner, U., Marco, S., 2005. The dead sea fault and its effect on civilization. In: Wenzel, F. (Ed.), *Perspectives in Modern Seismology*. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 145–167. https://doi.org/10.1007/978-3-540-31563-6_9.
Biltekin, D., Popescu, S.-M., Suc, J.-P., Quézel, P., Jiménez-Moreno, G., Yavuz, N., Çagatay, M.N., 2015. Anatolia: a long-time plant refuge area documented by pollen records over the last 23 million years. *Rev. Palaeobot. Palynol.* 215, 1–22.
Biltekin, D., Güzel, A., Özcanlı, M., Gökgöz, D.D., Akbıyık, M., 2024. Exploring pre-neolithic environmental dynamics: Paleoeecology around the Göbekli Tepe based on a multiproxy approach in southeastern Türkiye. *Plant Soil* 502, 297–313. <https://doi.org/10.1007/s11104-024-06548-3>.
Bledý, M., Vacek, S., Brabec, P., Vacek, Z., Cukor, J., Černý, J., Ševčík, R., Brynychová, K., 2004. Silver fir (*Abies alba* Mill): review of ecological insights, forest management strategies, and climate changes impact on European forests. *Forests* 15 (6), 998. <https://doi.org/10.3390/f15060998>.
Bolli, H.M., Premoli Silva, I., 1973. Oligocene to Recent planktonic foraminifera and stratigraphy of the Leg 15 sites in the Caribbean Sea. *DSDP Initial Rep.* 15, 578–584.
BouDagher-Fadel, M.K., 2013. Biostratigraphic and Geological Significance of Planktonic Foraminifera (Second edition). UCL Press.
Bown, P.R., Young, J.R., 1998. Chapter 2: Techniques. In: Bown, P.R. (Ed.), *Calcareous Nannofossil Biostratigraphy*. Kluwer Academic Publisher, pp. 16–28.
Bradley, W.H., 1937. Mediterranean sediments and Pleistocene sea levels. *Science* 88 (2286), 376–379.
Bridgland, D.R., Demir, T., Seyrek, A., Daoud, M., Abou Romieh, M., Westaway, R., 2017. River terrace development in the NE Mediterranean region (Syria and Turkey): patterns in relation to crustal type. *Quat. Sci. Rev.* 166, 307–323. <https://doi.org/10.1016/j.quascirev.2016.12.015>.
Bridgland, D.R., Shaw, A.D., Westaway, R., Daoud, M., Romieh, M.A., 2024. The Quaternary sequence of the Nahr el Kebir, NW Syria: an important repository for evidence of Palaeolithic occupation and landscape evolution in the eastern Mediterranean. *Geomorphology* 458. <https://doi.org/10.1016/j.geomorph.2024.109229>.
Bylinskaya, M.E., Golovina, L.A., 2004. Correlation of the Pliocene–Quaternary foraminiferal and nannofossil zonations in the North Atlantic. *Stratigr. Geol. Correl.* 12, 309–319.
Cachão, M., Moita, M.T., 2000. *Coccolithus pelagicus*, a productivity proxy related to moderate fronts off western Iberia. *Mar. Micropaleontol.* 39, 131–155.
Cambon, G., Suc, J.-P., Aloisi, J.-C., Giresse, P., Monaco, A., Touzani, A., Duzer, D., Ferrier, J., 1997. Modern pollen deposition in the Rhone delta area (lagoon and marine sediments) France. *Grana* 36, 105–113.
Carbonell, E., Mosquera, M., Rodríguez, X.P., Bermúdez de Castro, J.M., Burjachs, F., Rosell, J., Sala, R., Vallverdú, J., 2008. Eurasian gates: the earliest human dispersals. *J. Anthropol. Res.* 64, 195–228.
Carotenuto, F., Tsikaridze, N., Rook, L., Lordkipanidze, D., Longo, L., Condem, S., Raia, P., 2016. Venturing out safely: the biogeography of *Homo erectus* dispersal out of Africa. *J. Hum. Evol.* 95, 1–12. <https://doi.org/10.1016/j.jhevol.2016.02.005>.
Cita, B., Capraro, L., Ciaran, N., Di Stefano, E., Lirer, F., Maiorano, P., Marino, M., Raffi, I., Rio, D., Sprovieri, R., 2008. The Calabrian stage redefined. *Episodes* 31, 408–419.
Clark, G.N., BouDagher-Fadel, M., 2020. Insights into the Cenozoic geology of North Beirut (harbour area): biostratigraphy, sedimentology and structural history. *UCL Open Environ.* 2. <https://doi.org/10.14324/111.444/ucloe.000004>.
Clark, P.U., Archer, D., Pollard, D., Blum, J.D., Rial, J.A., Brovkin, V., Mix, A.C., Pisias, N.G., Roy, M., 2006. The middle Pleistocene transition: characteristics, mechanisms, and implications for long-term changes in atmospheric pCO₂. *Quat. Sci. Rev.* 25, 3150–3184.

- Colalongo, M.L., Pasini, G., Sartoni, S., 1981. Remarks on the Neogene/Quaternary boundary and the Vrica section (Calabria, Italy). *Boll. Soc. Paleontol. Ital.* 20, 99–120.
- Combourieu-Nebout, N., Paterne, M., Turon, J.-L., Siani, G., 1998. A high-resolution record of the last deglaciation in the central Mediterranean sea: palaeovegetation and palaeohydrological evolution. *Quat. Sci. Rev.* 17 (4), 303–317. [https://doi.org/10.1016/S0277-3791\(97\)00039-5](https://doi.org/10.1016/S0277-3791(97)00039-5).
- Cour, P., 1974. Nouvelles techniques de detection des flux et des retombees polliniques: Etude de la sedimentation des pollens et des spores a la surface du sol, 16. *Pollen et Spores*, pp. 103–141.
- Cugny, C., Mazier, F., Galop, D., 2010. Modern and fossil non-pollen palynomorphs from the basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. *Veg. Hist. Archaeobotany* 19, 391–408.
- De Lumley, H., Barsky, D.R., Cauche, D., 2009. Archaic stone industries from east Africa and southern Europe Pre-Oldowan and Oldowan. In: Schick, K., Toth, N. (Eds.), *The Cutting Edge: New Approaches to the Archaeology of Human Origins*, pp. 55–92. Stone Age Institute Publication series number 3.
- De Schepper, S., Fischer, E.I., Groeneveld, J., Head, M.J., Matthiessen, J., 2011. Deciphering the palaeoecology of Late Pliocene and Early Pleistocene dinoflagellate cysts. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 309 (1–2), 17–32.
- de Vernal, A., Eynaud, F., Henry, M., Limoges, A., Londeix, L., Matthiessen, J., Marret, F., Pospelova, V., Radi, T., Rochon, A., Van Nieuwenhove, N., Zaragosi, S., 2018. Distribution and (palaeo)ecological affinities of the main *spiniferites* taxa in the mid-high latitudes of the Northern Hemisphere. *Palynology* 42, 182–202. <https://doi.org/10.1080/01916122.2018.1465730>.
- Derricourt, R., 2005. Getting “Out of Africa”: sea crossings, land crossings and culture in the hominin migrations. *J. World Prehist.* 19, 119–132. <https://doi.org/10.1007/s10963-006-9002-z>.
- Devyatkin, E.V., Dodonov, A.E., Gablina, S.S., Golovina, L.A., Kurenkova, V.G., Simakova, A.N., Trubikhin, V.M., Yasamanov, N.A., Khatib, K., Nseir, H., 1996. Upper Pliocene-lower Pleistocene marine deposits of Western Syria: stratigraphy and paleogeography. *Stratigr. Geol. Correl.* 4, 67–77.
- Di Bella, L., 1999. Biostratigraphical and paleoecological evidences in non-costate *Bulimina* group of Pliocene-Pleistocene sediments (Latium-Southern Umbria, Central Italy). *Boll. Soc. Paleontol. Ital.* 38, 23–38.
- El Zaatari, S., 2018. The central Levantine corridor: The Paleolithic of Lebanon. *Quat. Int.* 466, 33–47. <https://doi.org/10.1016/j.quaint.2017.06.047>.
- Elderfield, H., Ferretti, P., Greaves, M., Crowhurst, S.J., McCave, I.N., Hodell, D., Piotrowski, A.M., 2012. Evolution of ocean temperature and ice volume through the mid-pleistocene climate transition. *Science* 337, 704–709. <https://doi.org/10.1126/science.1221294>.
- Ellis, M.B., Ellis, P., 1997. *Microfungi on Land Plants*. Richmond Publishing, Slough.
- Ellis-Adam, A., Van Geel, C.B., 1978. Fossil zygosporae of *Debarya glyptosperma* (De Bary) Witt. (Zygnemataceae) in Holocene sandy soils. *Acta Bot. Neerl.* 27, 389–396.
- Eppelbaum, L.V., Katz, Y.I., 2022. Combined zonation of the African-Levantine-Caucasian areal of ancient hominin: review and integrated analysis of paleogeographical, stratigraphic and geophysical-geodynamical data. *Geosciences* 12 (1), 21. <https://doi.org/10.3390/geosciences12010021>.
- Eppelbaum, L.V., Katz, Y.I., 2023. Multidisciplinary geological-geophysical analysis unmasks anthropological site structure in the northern part of the Levantine corridor. *J. Anthropol. Archaeol. Sci.* 8 (11), 1056–1078. <https://doi.org/10.32474/JAAS.2023.08.000286>.
- Eppelbaum, L.V., Katz, Y.I., 2024. African-Levantine areal of ancient hominin dispersal: a new look derived from comprehensive geological-geophysical integration. In: Yousef, A.F. (Ed.), *Emerging Issues in Environment, Geography, and Earth Science*, 7. BP International, London, pp. 151–222.
- Eppelbaum, L.V., Katz, Y.I., 2025. Combined Geophysical-Geodynamic Analysis of the Plio-Pleistocene Hominin Dispersal Through the Levantine Corridor. *Appl. Sci.* 15 (21), 11554. <https://doi.org/10.3390/app152111554>.
- Fauquette, S., Guiot, J., Suc, J.-P., 1998. A method for climatic reconstruction of the Mediterranean Pliocene using pollen data. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 144, 183–201.
- Feddi, N., Fauquette, S., Suc, J.-P., 2011. Histoire plio-pléistocène des écosystèmes végétaux de Méditerranée sud-occidentale: apport de l'analyse pollinique de deux sondages en mer d'Alboran. *Geobios* 44, 57–69.
- Foerster, V., Asrat, A., Bronk Ramsey, C., Brown, E.T., Chapot, M.S., Deino, A., Duesing, W., Grove, M., Hahn, A., Junginger, A., Kaboth-Bahr, S., Lane, C.S., Opitz, S., Noren, A., Roberts, H.M., Stockhecke, M., Tiedemann, R., Vidal, C.M., Vogelsang, R., Cohen, A.S., Lamb, H.F., Schaebitz, F., Trauth, M.H., 2022. Pleistocene climate variability in eastern Africa influenced hominin evolution. *Nat. Geosci.* 15, 805–811. <https://doi.org/10.1038/s41561-022-01032-y>.
- Frenzel, B., Pécsi, M., Velichko, A.A., 1992. Atlas of paleoclimates and paleoenvironments of the Northern Hemisphere: Late Pleistocene, Holocene. Geographical Research Institute, Hungarian Academy of Sciences.
- Gaffney, D., 2021. Pleistocene water crossings and adaptive flexibility within the *homo* genus. *J. Archaeol. Res.* 29, 255–326. <https://doi.org/10.1007/s10814-020-09149-7>.
- Galović, I., Young, J., 2012. Revised taxonomy and stratigraphy of Middle Miocene calcareous nannofossils of the Paratethys. *Micropaleontology* 58, 305–334.
- Girone, A., Capotondi, L., Ciaran, N., Di, P., Lirer, F., Maiorano, P., Marino, M., Pelosi, N., Pulice, I., 2013. Paleoenvironmental changes at the lower Pleistocene Montalbano Jonico section (southern Italy): global versus regional signals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 371, 62–79. <https://doi.org/10.1016/j.palaeo.2012.12.017>.
- Gomez, F., Khawlie, M., Tabet, C., Nasser Darkal, A., Khair, K., Barazangi, M., 2006. Late Cenozoic uplift along the northern Dead Sea transform in Lebanon and Syria. *Earth Planet. Sci. Lett.* 241, 913–931. <https://doi.org/10.1016/j.epsl.2005.10.029>.
- Hardenberg, M.F., Robertson, A.H.F., 2007. Sedimentology of the NW margin of the Arabian plate and the SW-NE trending Nahr El-Kabir half-graben in northern Syria during the latest Cretaceous and Cenozoic. *Sediment. Geol.* 201, 231–266. <https://doi.org/10.1016/j.sedgeo.2007.02.009>.
- Hardenberg, M.F., Robertson, A.H.F., 2013. Role of the Palaeogene–Recent sinistral El-Kabir Lineament and the associated transtensional Neogene–Recent El-Kabir Basin (northern Syria) in distributed deformation between the African and Eurasian plates. *Geol. Soc. Spec. Publ.* 372, 447–471. <https://doi.org/10.1144/SP372.18>.
- Harland, R., Polovodova, I., Morley, A., Morris, A., 2016. Latest Quaternary palaeoceanographic change in the eastern North Atlantic based upon a dinoflagellate cyst event ecostratigraphy. *Heliyon* 2 (5), e00114. <https://doi.org/10.1016/j.heliyon.2016.e00114>.
- Hart, M.B., 1980. A water depth model for the evolution of the planktonic Foraminiferida. *Nature* 286, 252–254.
- Head, M.J., Gibbard, P.L., 2005. Early–Middle Pleistocene transitions: an overview and recommendation for the defining boundary. In: Head, M.J., Gibbard, P.L. (Eds.), *Early–Middle Pleistocene Transitions: The Land–Ocean Evidence*, 247. Geological Society of London, p. 0. <https://doi.org/10.1144/GSL.SP.2005.247.01.01>.
- Head, M.J., Gibbard, P.L., 2015. Early-Middle Pleistocene transitions: linking terrestrial and marine realms. *Quat. Int.* 389, 7–46. <https://doi.org/10.1016/j.quaint.2015.09.042>.
- Head, M.J., Pillans, B., Farquhar, S.A., 2008. The Early-Middle Pleistocene transition: characterization and proposed guide for the defining boundary. *Episodes* 31 (2), 255–259.
- Heusser, L., 1988. Pollen distribution in marine sediments on the continental margin off northern California. *Mar. Geol.* 80 (1988), 131–147. [https://doi.org/10.1016/0025-3227\(88\)90076-X](https://doi.org/10.1016/0025-3227(88)90076-X).
- Jagher, R., Elsuède, H., Le Tensorer, J.M., 2015. El Kowm Oasis, human settlement in the Syrian Desert during the Pleistocene. *L'anthropologie* 119 (5), 542–580. <https://doi.org/10.1016/j.anthro.2015.10.003>.
- Jonkers, L., Kučera, M., 2015. Global analysis of seasonality in the shell flux of extant planktonic foraminifera. *Biogeosciences* 12, 2207–2226. <https://doi.org/10.5194/bg-12-2207-2015>.
- Jorissen, F.J., Barmawidjaja, D.M., Puskaric, S., van der Zwaan, G.J., 1992. Vertical distribution of benthic foraminifera in the northern Adriatic Sea: the relation with the organic flux. *Mar. Micropaleontol.* 19, 131–146.
- Kanbur, S., 2025. Neglected small foraminifers of the eastern Mediterranean and their paleoecological importance. *J. Foraminif. Res.* 55, 218–232.
- Kanbur, S., Ögretmen, N., 2022. Revised late Cenozoic foraminifer biostratigraphy of the Eskiköy Formation (Aksu Basin), SW Turkey and its paleoenvironmental conditions. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 591, 110883. <https://doi.org/10.1016/j.palaeo.2022.110883>.
- Kennett, J.P., Srinivasan, S.M., 1983. *Neogene Planktonic Foraminifera: A Phylogenetic Atlas*. Hutchinson Ross Publishing Company, Pennsylvania.
- Khrumov, A.N., Tarling, D.H., 1987. *Paleomagnetology*. Springer-Verlag, Berlin.
- Klotz, S., Fauquette, S., Combourieu-Nebout, N., Uhl, D., Suc, J.-P., Mosbrugger, V., 2006. Seasonality intensification and long-term winter cooling as a part of the Late Pliocene climate development. *Earth Planet. Sci. Lett.* 241, 174–187.
- Komárek, J., Jankovská, V., 2001. Review of the green algal genus *Pediastrum*; implications for pollen-analytical research. *Bibl. Phycol.* 108, 1–127.
- Kučera, M., 2007. Chapter six planktonic foraminifera as tracers of past oceanic environments. *Dev. Mar. Geol.* 1 (07), 213–262. [https://doi.org/10.1016/S1572-5480\(07\)01011-1](https://doi.org/10.1016/S1572-5480(07)01011-1).
- Le Tensorer, J.-M., 2017. The lower palaeolithic of syria. In: *Quaternary of the Levant*. Cambridge University Press, pp. 567–576. <https://doi.org/10.1017/9781316106754.062>.
- Legrain, E., Parrenin, F., Capron, E., 2023. A gradual change is more likely to have caused the Mid-Pleistocene transition than an abrupt event. *Nat. Commun. Earth Environ.* 4 (1), 1–10. <https://doi.org/10.1038/s43247-023-00754-0>.
- Lirer, F., Foresi, L.M., Iaccarino, S.M., Salvatorini, G., Turco, E., Cosentino, C., Sierro, F. J., Caruso, A., 2019. Mediterranean Neogene planktonic foraminifer biozonation and biochronology. *Earth Sci. Rev.* 196, 102869. <https://doi.org/10.1016/j.earscirev.2019.05.013>.
- Lourens, L.J., Hilgen, F.J., Gudjonsson, L., Zachariasse, W.J., 1992. Late Pliocene to Early Pleistocene astronomically forced sea surface productivity and temperature variations in the Mediterranean. *Mar. Micropaleontol.* 19, 49–78. [https://doi.org/10.1016/0377-8398\(92\)90021-B](https://doi.org/10.1016/0377-8398(92)90021-B).
- McCarthy, F.M.G., Mudie, P.J., 1996. Palynology and dinoflagellate biostratigraphy of Upper Cenozoic sediments from Sites 898 and 900, Iberia Abyssal Plain. In: Whitmarsh, R.B., Sawyer, D.S., Klaus, A., et al. (Eds.), *Proceedings of the Ocean Drilling Program, Scientific Results*, 149. Ocean Drilling Program, College Station, Texas, pp. 241–265.
- Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}O$ records. *Paleoceanogr* 20, 1–17. <https://doi.org/10.1029/2004PA001071>.
- Milanesi, C., Vignani, R., Ciampolini, F., Faleri, C., Cattani, L., Moroni, A., Arrighi, S., Scali, M., Tiberi, P., Sensi, E., Wang, W., Cresti, M., 2006. Ultrastructure and DNA sequence analysis of single *Concetricystis* cells from Alta Val Tiberina Holocene sediment. *J. Archaeol. Sci.* 33 (8), 1081–1087. <https://doi.org/10.1016/j.jas.2005.11.014>.
- Milker, Y., Schmiechel, G., 2012. A taxonomic guide to modern benthic shelf foraminifera of the western Mediterranean Sea. *Palaeontol. Electron.* 15, 134. <https://doi.org/10.26879/271>.

- Milker, Y., Jorissen, F.J., Riller, U., Reicherter, K., Titschack, J., Weinkauff, M.F.G., Theodor, M., Schmiedl, G., 2019. Paleo-ecologic and neotectonic evolution of a marine depositional environment in SE Rhodes (Greece) during the Early Pleistocene. *Quat. Sci. Rev.* 213, 120–132. <https://doi.org/10.1016/j.quascirev.2019.04.021>.
- Miller, K.G., Kominz, M.A., Browning, J.V., Wright, J.D., Mountain, G.S., Katz, M.E., Sugarman, P.J., Cramer, B.S., Christie-Blick, N., Pekar, S.F., 2005. The Phanerozoic record of global sea-level change. *Science* 310 (1293), 1293–1298. <https://doi.org/10.1126/science.1116412>.
- Miola, A., 2012. Tools for Non-Pollen Palynomorphs (NPPs) analysis: a list of Quaternary NPP types and reference literature in English language (1972–2011). *Rev. Palaeobot. Palynol.* 186, 142–161.
- Moissette, P., Quillévéré, F., Kontakiotis, G., Thivaoui, D., Koskeridou, E., Antonarakou, A., Drinia, H., Melinte-Dobrinescu, M., Cornée, J.J., 2024. Early Pleistocene upper bathyal communities in fault-bounded paleovalleys of the island of Rhodes (Greece). *Quat. Res.* 1–21. <https://doi.org/10.1017/qua.2024.19>.
- Murray, J., 2006. *Ecology and Applications of Benthic Foraminifera*. Cambridge University Press, Cambridge.
- Muttoni, G., Kent, D.V., 2024. Hominin population bottleneck coincided with migration from Africa during the Early Pleistocene ice age transition. *Proc. Natl. Acad. Sci.* 121 (13), e2318903121. <https://doi.org/10.1073/pnas.2318903121>.
- Muttoni, G., Scardia, G., Kent, D.V., 2018. Early hominins in Europe: the Galerian migration hypothesis. *Quat. Sci. Rev.* 180, 1–29. <https://doi.org/10.1016/j.quascirev.2017.10.031>.
- Muzylev, N.G., 1980. *Stratigrafiya paleogena Yuga SSSR po nannoplanktonu (Severnyy Kavkaz i Krym)* (The Paleogene Nannoplankton Stratigraphy of the Southern USSR (Northern Caucasus and Crimea)). Nauka, Moscow [in Russian].
- Ögretmen, N., 2022. Quantitative analysis of Calabrian-Chibanian planktic foraminifer assemblages and paleoecology of the eastern Mediterranean Sea from the onshore epibathyal sedimentary archives (Mersin, Turkey). *Yerbilimleri* 43, 18–36.
- Ögretmen, N., Cipollari, P., Frezza, V., Faranda, C., Karanika, K., Gliozzi, E., Radeff, G., Cosentino, D., 2018a. Evidence for 1.5 km of Uplift of the Central Anatolian Plateau's Southern Margin in the Last 450 kyr and Implications for Its Multiphased Uplift History. *Tectonics* 37, 359–390. <https://doi.org/10.1002/2017TC004805>.
- Ögretmen, N., Frezza, V., Hudácková, N., Gliozzi, E., Cipollari, P., Faranda, C., Radeff, G., Cosentino, D., 2018b. Early Pleistocene (Calabrian) marine bottom oxygenation and palaeoclimate at the southern margin of the Central Anatolian Plateau. *Ital. J. Geosci.* 137, 452–464. <https://doi.org/10.33011/IJG.2018.19>.
- Ögretmen, N., Kanbur, S., Gönülal, O., 2022. Preliminary results from the Finike seamounts foraminifer assemblages, Eastern Mediterranean Sea. *J. Black Sea/Mediterr. Environ.* 28 (2), 139–165.
- Parenti, F., Varejão, F.G., Scardia, G., Okumura, M., Araujo, A., Ferreira Guedes, C.C., Neves, W.A., 2024. The Oldowan of Zarqa valley, Northern Jordan. *J. Paleolith. Archaeol.* 7 (1). <https://doi.org/10.1007/s41982-023-00168-6>.
- Parker, F.L., 1962. Planktonic foraminiferal species in pacific sediments. *Micropaleontology* 8 (2), 219–254.
- Perch-Nielsen, K., 1985. Cenozoic calcareous nannofossils. In: Bolli, H., Saunders, J., Perch-Nielsen, K. (Eds.), *Plankton Stratigraphy*. Cambridge University Press, Cambridge, pp. 427–554.
- Poulsen, N.E., Kuijpers, A., 2002. Dinoflagellate Cyst Evidence of Holocene Ocean Circulation Variability on the Hebrides Shelf, UK.
- Quillévéré, F., Cornée, J.J., Moissette, P., López-Otálvaro, G.E., van Baak, C., Münch, P., Melinte-Dobrinescu, M.C., Krijgsman, W., 2016. Chronostratigraphy of uplifted Quaternary hemipelagic deposits from the Decadense island of Rhodes (Greece). *Quat. Res.* 86, 79–94. <https://doi.org/10.1016/j.yqres.2016.05.002>.
- Quillévéré, F., Nouailhat, N., Joannin, S., Cornée, J.J., Moissette, P., Lécuyer, C., Fouré, F., Agiadi, K., Koskeridou, E., Escarguel, G., 2019. An onshore bathyal record of tectonics and climate cycles at the onset of the Early-Middle Pleistocene Transition in the eastern Mediterranean. *Quat. Sci. Rev.* 209, 23–39. <https://doi.org/10.1016/j.quascirev.2019.02.012>.
- Raffi, I., Wade, B.S., Pälke, H., Beu, A.G., Cooper, R., Crundwell, M.P., Krijgsman, W., Moore, T., Raine, I., Sardella, R., Vernyhorova, Y.V., 2020. The Neogene Period. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), *Geologic Time Scale 2020*. Elsevier B.V., pp. 1141–1215. <https://doi.org/10.1016/b978-0-12-824360-2.00029-2>.
- Reille, M., 1992. *Pollen et spores d'Europe et d'Afrique du Nord*. Laboratoire de botanique historique et de palynologie, Marseille, France, p. 543.
- Rio, D., Sprovieri, R., Thunell, R., 1991. Pliocene-lower Pleistocene chronostratigraphy: a re-evaluation of Mediterranean type sections. *Geol. Soc. Am. Bull.* 103, 1049–1058. [https://doi.org/10.1130/0016-7606\(1991\)103<1049:PLPCAR>2.3.CO;2](https://doi.org/10.1130/0016-7606(1991)103<1049:PLPCAR>2.3.CO;2).
- Rohling, E.J., Grant, K.M., Roberts, A.P., Larrasoña, J.C., 2013. Paleoclimate variability in the Mediterranean and Red Sea regions during the last 500,000 years: implications for hominin migrations. *Curr. Anthropol.* 54. <https://doi.org/10.1086/673882>.
- Rolland, N., 2013. The Early Pleistocene human dispersals in the Circum-Mediterranean basin and initial peopling of Europe: single or multiple pathways? *Quat. Int.* 316, 59–72. <https://doi.org/10.1016/j.quaint.2013.06.028>.
- Ronen, A., 2006. The oldest human groups in the Levant. *Comptes Rendus - Palevol.* 5 (1–2), 343–351. <https://doi.org/10.1016/j.crpv.2005.11.005>.
- Rosenfeld, A., Nathan, Y., Feibel, C.S., Schilman, B., Halicz, L., Goren-Inbar, N., Siman-Tov, R., 2004. Palaeoenvironment of the Acheulian Gesher Benot Ya'aqov Pleistocene lacustrine strata, Northern Israel - lithology, ostracod assemblages and ostracod shell geochemistry. *J. Afr. Earth Sci.* 38 (2), 169–181. <https://doi.org/10.1016/j.jafrearsci.2003.10.008>.
- Sanlaville, P., 1979. Étude géomorphologique de la basse-vallée du Nahr el Kébir. In: Sanlaville, P. (Ed.), *Quaternaire et Préhistoire Du Nahr El Kébir Septentrional. Les Débuts de l'occupation Humaine Dans La Syrie Du Nord et Au Levant*. Travaux de La RCP 438, pp. 7–28. Sous La Direction de Paul Sanlaville. Collection de la Maison de l'Orient méditerranéen. Série géographique et préhistorique, 9, Lyon.
- Saraswati, P.K., Srinivasan, M.S., 2016. *Micropaleontology*. Springer Cham. https://doi.org/10.1007/3-540-31078-9_85.
- Savannah, M., Elco, R., Timme, D., Katharine, G., Jörg, K., Marino, G., Francesca, S., Caridi, F., Caterina, M., Sabbatini, A., Negri, A., 2024. The “glacial” sapropel S6 (172 ka; MIS 6): A multiproxy approach to solve a Mediterranean “cold case.” *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 650, 112384. <https://doi.org/10.1016/j.palaeo.2024.112384>.
- Scardia, G., Parenti, F., Miggins, D.P., Gerdes, A., Araujo, A.G.M., Neves, W.A., 2019. Chronologic constraints on hominin dispersal outside Africa since 2.48 Ma from the Zarqa valley, Jordan. *Quat. Sci. Rev.* 219, 1–19. <https://doi.org/10.1016/j.quascirev.2019.06.007>.
- Schiebel, R., Hemleben, C., 2017. *Planktic Foraminifers in the Modern Ocean*. Springer, Berlin.
- Selli, R., Accordi, C., Bandini Mazzanti, M., Bertolani Marchetti, D., Bigazzi, G., Bonadonna, F., Borsetti, A., Catì, F., Colalongo, M., Mezzetti, R., Pasini, G., Savelli, C., Tampieri, R., 1977. The Vrica Section (Calabria, Italy). A potential Neogene/Quaternary boundary stratotype. *Giorn. Geol.* 42, 181–204.
- Serrano, F., Guerra-Merchán, A., 2012. Sea-surface temperature for left-coiling *Neoglobobulimina* populations inhabiting the westernmost Mediterranean in the middle Pleistocene and the Pleistocene-Pliocene transition. *Geobios* 45, 231–240. <https://doi.org/10.1016/j.geobios.2011.04.003>.
- Sgarrella, F., Moncharmont Zei, M., 1993. Benthic foraminifera of the Gulf of Naples (Italy): systematics and autoecology. *Boll. Soc. Paleontol. Ital.* 32, 145–264.
- Shumilovskikh, L.S., Van Geel, B., 2020. Non-Pollen palynomorphs. In: Henry, A.G. (Ed.), *Handbook for the Analysis of Micro-Particles in Archaeological Samples*. Interdisciplinary Contributions to Archaeology. Springer, pp. 65–94. https://doi.org/10.1007/978-3-030-42622-4_4.
- Sivan, D., Gvirtzman, G., Sass, E., 1999. Quaternary Stratigraphy and Paleogeography of the Galilee Coastal Plain, Israel. *Quat. Res.* 51, 280–294.
- Suc, J.-P., Drivaliari, A., 1991. Transport of bisaccate coniferous fossil pollen grains to coastal sediments: an example from the earliest Pliocene Orb Ría (Languedoc, Southern France). *Rev. Palaeobot. Palynol.* 70, 247–253. [https://doi.org/10.1016/0034-6667\(91\)90006-0](https://doi.org/10.1016/0034-6667(91)90006-0).
- Tari, U., Tüysüz, O., Blackwell, B.A.B., Mahmud, Z., Florentin, J.A., Qi, J., Genç, C., Skinner, A.R., 2018. Sealevel change and tectonic uplift from dated marine terraces along the eastern Mediterranean coast, southeastern Turkey. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* <https://doi.org/10.1016/j.palaeo.2018.07.003>, 51180–102.
- Thompson, R.S., Anderson, K.H., Bartlein, P.J., 2000. Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America —Hardwoods. *U.S. Geol. Surv. Prof. Pap.* 1650 (B), 1–423.
- Trifonov, V.G., Bachmanov, D.M., Simakova, A.N., Trikhunkov, Y.I., Ali, O., Tesakov, A. S., Belyaeva, E.V., Lyubin, V.P., Veselovsky, R.V., Al-Kafri, A.M., 2014. Dating and correlation of the Quaternary fluvial terraces in Syria, applied to tectonic deformation in the region. *Quat. Int.* 328–329, 74–93. <https://doi.org/10.1016/j.quaint.2013.10.063>.
- Trotta, S., Duque-Castaño, M., Rodrigues, T., Voelker, A.H.L., Maiorano, P., Balestra, B., Flores, J.A., Siniscalchi, A., Addante, M., Marino, M., 2025. High-frequency glacial climate instability during the Early Pleistocene: insights from IODP site U1387 (Gulf of Cadiz). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 674. <https://doi.org/10.1016/j.palaeo.2025.113041>.
- Tzedakis, P.C., Hooghiemstra, H., Pälike, H., 2006. The last 1.35 million years at Tenaghi Philippon: revised chronostratigraphy and long-term vegetation trends. *Quat. Sci. Rev.* 25 (23–24), 3416–3430. <https://doi.org/10.1016/j.quascirev.2006.09.002>.
- Van Geel, B., 2002. Non-Pollen palynomorphs. In: Smol, J.P., Birks, H.J.B., Last, W.M., Bradley, R.S., Alverson, K. (Eds.), *Tracking Environmental Change Using Lake Sediments. Developments in Paleoenvironmental Research*, 3. Springer, Dordrecht. https://doi.org/10.1007/0-306-47668-1_6.
- Van Geel, B., Aptroot, A., 2006. Fossil ascomycetes in Quaternary deposits. *Nova Hedwigia* 82 (3), 313–330.
- Van Geel, B., Van Der Hammen, T., 1978. Zygnetmataceae in Quaternary Columbian sediments. *Rev. Palaeobot. Palynol.* 25 (5), 377–391.
- Van Geel, B., Coope, G.R., Van Der Hammen, T., 1989. Palaeoecology and stratigraphy of the Late-Glacial type section at Usselo (the Netherlands). *Rev. Palaeobot. Palynol.* 60 (1–2), 25–129.
- Van Geel, B., Gelorini, V., Lyaruu, A., Aptroot, A., Rucina, S., Marchant, R., Verschuren, D., 2011. Diversity and ecology of tropical African fungal spores from a 25,000-year palaeoenvironmental record in southeastern Kenya. *Rev. Palaeobot. Palynol.* 164 (3–4), 174–190.
- Vénec-Peyré, M.T., Caulet, J.P., 2000. Paleoproductivity changes in the upwelling system of Socotra (Somali Basin, NW Indian Ocean) during the last 72,000 years: evidence from biological signatures. *Mar. Micropaleontol.* 40, 321–344. [https://doi.org/10.1016/S0377-8398\(00\)00044-X](https://doi.org/10.1016/S0377-8398(00)00044-X).
- Versteegh, G.J.M., 1997. The onset of major Northern Hemisphere glaciations and their impact on dinoflagellate cysts and acritarchs from the Singa section, Calabria (southern Italy) and DSDP holes 607/607A (North Atlantic). *Mar. Micropaleontol.* 30 (4), 319–343. [https://doi.org/10.1016/S0377-8398\(96\)00052-7](https://doi.org/10.1016/S0377-8398(96)00052-7).
- Voelker, A.H.L., Salgueiro, E., Rodrigues, T., Jimenez-Espejo, F.J., Bahr, A., Alberto, A., Loureiro, I., Padilha, M., Rebotim, A., Röhl, U., 2015. Mediterranean Outflow and surface water variability off southern Portugal during the Early Pleistocene: A

- snapshot at Marine Isotope Stages 29 to 34 (1020-1135ka). *Glob. Planet. Chang.* 133, 223–237. <https://doi.org/10.1016/j.gloplacha.2015.08.015>.
- Wade, B.S., Pearson, P.N., Berggren, W.A., Pälike, H., 2011. Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. *Earth Sci. Rev.* 104, 111–142. <https://doi.org/10.1016/j.earscirev.2010.09.003>.
- Wetzler, N., Segev, A., Lyakhovskiy, V., 2022. Uplift and subsidence at the periphery of the Lebanese Restraining Bend, Northern Dead Sea Fault. *Tectonophysics* 830. <https://doi.org/10.1016/j.tecto.2022.229292>.
- Winder, I.C., Devès, M.H., King, G.C.P., Bailey, G.N., Inglis, R.H., Meredith-Williams, M., 2015. Evolution and dispersal of the genus *Homo*: a landscape approach. *J. Hum. Evol.* 87, 48–65. <https://doi.org/10.1016/j.jhevol.2015.07.002>.
- Wolf, F.A., 1966. Fungus spores in East African lake sediments. *Bull. Torrey. Bot. Club* 93 (2), 104–113.
- Wolf, F.A., 1967a. Fungus spores in East African lake sediments. IV. *Bull. Torrey Bot. Club* 94 (1), 31–34.
- Wolf, F.A., 1967b. Fungus spores in East African lake sediments. VII. *Bull. Torrey. Bot. Club* 94 (6), 480–486.
- Young, J.R., Bown, P.R., Lees, J.A., 2013. Nannotax Website.