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The Main Nile Valley at the End of the Pleistocene (28–15 ka): Dispersal Corridor or Environmental Refugium?

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Under present environmental conditions, the Nile Valley acts as a 'natural' route between Africa and Eurasia, and is often considered as a corridor for dispersals out of and back into Africa in the past. This review aims to address the role played by the Nile Valley at the end of the Pleistocene (28-15 ka) in the context of post-'Out of Africa' modern human dispersals. Genetic studies based on both modern and ancient DNA suggest pre-Holocene dispersals 'back into Africa' as well as genetic interactions between modern humans across Africa and the Levant. During the Last Glacial, the lowering, or even complete desiccation of major eastern African lakes, including Lake Victoria, reduced the White Nile to a highly seasonal river, depriving the main Nile from its most important tributary in the dry season. This had major consequences, the specifics of which are still debated, on the behavior of the main Nile and the landscape around the Nile Delta. Despite this shift to more arid conditions, there is abundant evidence for human occupation in the main Nile Valley. Combining available geological, palaeoenvironmental, anthropological, genetic and archaeological data, this article discusses problems encountered when trying to reconcile results from different fields, the current limitations of the available data and research perspectives to further address the role of the Nile Valley as a dispersal corridor or an environmental refugium at the end of the Pleistocene.

Keywords: North-Eastern Africa, prehistory, human dispersals, late palaeolithic, human-environment interactions

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INTRODUCTION

The Last Glacial (Marine Isotope Stages (MIS) 4-2, 73.5-14.7 ka) is marked by abrupt climatic oscillations of irregular periodicity. In particular, MIS 2 (27.8-14.7 ka – Sanchez Goñi and Harrison, 2010), which includes the Last Glacial Maximum (LGM, 23-19 ka – Waelbroeck et al., 2009) and Heinrich Stadial 1[1] (HS 1, 19-14.6 ka – Stanford et al., 2011), is generally characterized by drier conditions and lower temperatures than the present day, with some abrupt arid-humid transitions in northern and equatorial Africa (Gasse, 2000). The impact of these rapid climatic fluctuations on Palaeolithic hunter-gatherer populations in Africa, although undeniable, remains not well understood. MIS 2 may have been a period of contraction of populations (toward environmental refugia), which may have been significant in shaping the variability in human

[1]In this review paper, Heinrich Stadial is used rather than Greenland Stadial (Rasmussen et al., 2014), as it follows recent regional palaeoenvironmental studies (e.g., Stager et al., 2011; Revel et al., 2015; Castañeda et al., 2016).

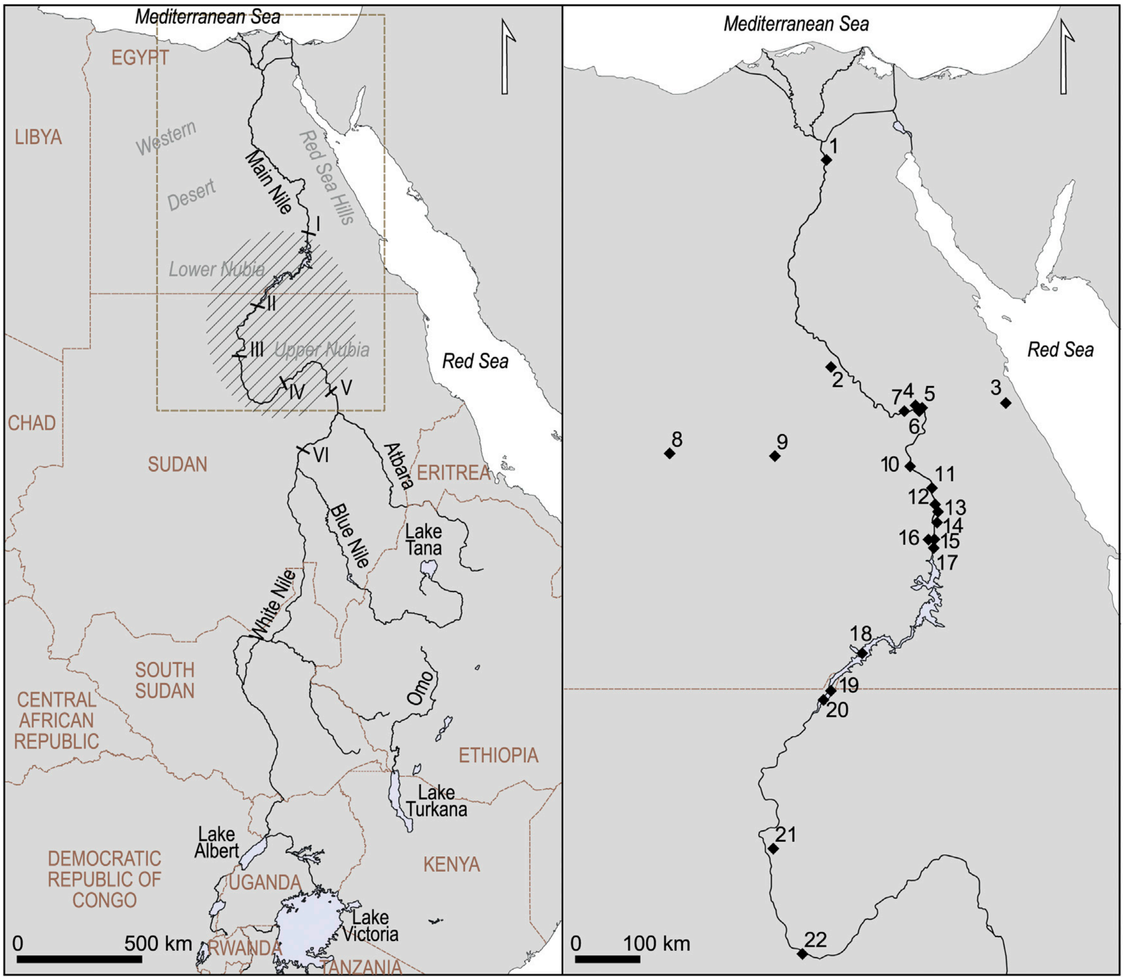

FIGURE 1 | Map of the Nile Basin **(left)** and the Main Nile Basin **(right)**. Created in QGIS v. 3.15 (QGIS Development Team, 2017) using Natural Earth Data. Hatched area: broad geographical extent of Nubia. Numbers: geographical locations discussed in the text; 1, Helwan; 2, Nazlet Khater; 3, Sodmein Cave; 4, Makhadma; 5, Qena; 6, Taramsa; 7, Dishna; 8, Dakhleh Oasis; 9, Kharga Oasis; 10, Esna; 11, Edfu; 12, El Hosh; 13, Qurta; 14, Kom Ombo; 15, Wadi Abu Subeira; 16, Wadi Kubbaniya; 17, Aswan; 18, Tushka; 19, Jebel Sahaba; 20, Wadi Halfa; 21, El Barga; 22, Ed-Debba.

populations that we know today (e.g., Mirazón Lahr, 2016). However, at the same time, genetic data indicate the occurrence of gene flow between human populations in northern Africa, the Levant and south of the Sahara before 15 ka BP (Van de Loosdrecht et al., 2018).

This paper investigates the role that the main Nile Valley (i.e., the northern end of the Nile Valley corresponding to the main Nile, **Figure 1**) may have had for human populations during MIS 2. In the context of a hyper-arid Sahara (e.g., Pachur and Hoelzmann, 2000), the Nile Valley may have constituted an environmental refugium for human populations and / or it may have acted as a dispersal corridor. Numerous archaeological sites dating to MIS 2 are known in the Nile Valley in southern Egypt and northern Sudan. While several reviews of the archaeological record already exist (e.g., Schild and Wendorf, 2010; Vermeersch and Van Neer, 2015; Usai, 2019; Garcea, 2020; Vermeersch, 2020), the aim here is to take a multidisciplinary approach and review recent advances in palaeoenvironmental, anthropological, genetic and archaeological research in order to shed new light on human-environment interactions and in particular the potential role of the main Nile Valley as an environmental refugium or dispersal corridor during MIS 2.

This article focuses on the northern end of the Nile Valley and particularly on southern Egypt, northern (= Lower) and southern (= Upper) Nubia during MIS 2. This geographical focus is mainly guided by the availability of archaeological data for this period. The definition and geographical extent of Nubia has varied through time, in particular regarding its southern boundary. In a broad sense, Nubia is located between the First Cataract near Aswan with a southern boundary fluctuating between the Fourth and the Sixth Cataract north of Khartoum (**Figure 1**). Northern Nubia corresponds to the area between the First and

TABLE 1 | General expectations under a refugium or dispersal corridor model.

	Palaeoenvironmental data	Human fossil and genetic data	Archaeological data
The Nile Valley is an environmental refugium	Suitable environmental conditions for continuous human occupation over the period (e.g., availability of water) Areas adjacent to the Nile Valley unsuitable for human occupation	In a long-term isolation model, development of unique biological characteristics that differ from human remains in other regions and biological continuity over the refugial period	Abundant archaeological evidence (based on archaeological radiocarbon data) in the Nile Valley, but not in adjacent areas
The Nile Valley is a dispersal corridor	Suitable environmental conditions for continuous human occupation over the period (e.g., availability of water), restricted to the Nile Valley Areas at either end of the Nile Valley suitable for human occupation	Evidence for past gene flow between different areas Evidence for biological similarities in all adjacent areas	Abundant archaeological evidence (based on archaeological radiocarbon data) in the Nile Valley, in the Levant, in North and in eastern Africa Possible but not required: Evidence for horizontal cultural transmission in the archaeological record between the Nile Valley, the Levant, North Africa and eastern Africa consistent with contact between populations

Second Cataract, whereas southern Nubia corresponds to the area upstream from the Second cataract (Adams, 1977, 13–17; Hassan, 2007; Auenmüller, 2019).

The concept of 'refugia' comes from the field of biogeography in the context of studies focusing on changing spatial distributions of plant and animal species linked to climatic and environmental fluctuations (Bennett and Provan, 2008; Sommer and Zachos, 2009; Stewart et al., 2010). Refugia therefore refer to areas where, for example, temperate animal or plant species can survive during unfavourable environmental conditions (in this case Glacial periods). Refugia areas are thus necessarily restricted compared to the full range distribution of these species under different environmental conditions (Interglacial). Most of these studies concern Eurasian species during the Last Glacial Maximum, where the distribution range of temperate species was restricted to southern Europe. Because population contraction to refugia often imply reduced population size, the concept of refugia is closely linked to the genetic concept of a 'bottleneck,' a drastic decrease in population followed by a phase of expansion (Bennett and Provan, 2008). Genetic studies have indeed shown for several species that refugia areas during the LGM were the source of subsequent major expansions of the distribution of these species after the LGM and also included speciation processes (see Hewitt, 1996; and review in Bennett and Provan, 2008).

Refugia models have been used in archaeological studies as well, in particular as a possible framework to explain the population history of Western Europe at the end of the Pleistocene (e.g., Gamble et al., 2005), modern human expansions within and out of Africa, as well as population substructure (Basell, 2008; Stewart and Stringer, 2012; Mirazón Lahr and Foley, 2016; Mirazón Lahr, 2016; Scerri et al., 2018). In the context of this paper, a (n environmental) refugium for human populations is defined as an area that human populations inhabited during phases of unfavourable environmental conditions which restricted their distribution range over a given time interval. Refugial phases therefore correspond to periods when populations are in isolation. While some definitions specify that these areas must have been inhabited during an entire glacial / interglacial cycle (e.g., Stewart and Stringer, 2012, or 'long-term refugium' as defined in Stewart et al., 2010), this should not necessarily be the case (Stewart et al., 2010).

A dispersal corridor indicates a restricted geographical area characterized by environmental conditions suitable for allowing movements of faunal or floral species (and specifically in this paper, of human populations) from one region to another.

The definitions used for each of these concepts imply that at a given time the Nile Valley can only be a refugium area or a dispersal corridor. However, the period considered spans nearly 15 millennia and the Nile Valley may have been alternately a refugium area and a dispersal corridor. An alternative scenario to the refugium / dispersal corridor dichotomy is that the Nile Valley may have not been suitable for human occupation at all during periods of MIS 2. Because most of the Sahara was hyper-arid during MIS 2 and there is no evidence for human occupation of the Sahara during MIS 2, we can dismiss the last alternative scenario that the Nile Valley was only part of a wider area occupied by human populations (and not a restricted area) during MIS 2.

The multidisciplinary approach adopted here will address the complex issue of the role that the main Nile Valley may have had for human populations during MIS 2 from different perspectives. General expectations of what we may find from a palaeoenvironmental, human fossil and genetic, and archaeological perspectives under each of the two models (refugium model and dispersal corridor model) are summarized in **Table 1** and will provide a broad framework for the ensuing discussion.

PALAEOENVIRONMENTAL DATA

General Data on the River Nile

The Nile Basin is one of the largest basins in the world–*ca.* 3.3 million km^2, from 4°S to 31°N–with three principal tributaries for the main (or desert) Nile: the White Nile, the Blue Nile and the Atbara (**Figure 1**). It encompasses several climatic zones. In Equatorial East Africa where the White Nile, Blue Nile and

TABLE 2 | Characteristics of cultural entities of the Late Palaeolithic in the Lower Nile Valley.

Cultural entity	Location*	Lithic characteristics**	Other characteristic finds
Idfuan/Shuwikhatian	A	Blade production using opposed platform cores and crested products; denticulates, burins, endscrapers[a]	
Levallois Idfuan	A	Blade production using opposed platform cores, use of Levallois and Halfa methods; notches, denticulates are dominant	
Fakhurian	A	Blade and bladelet production, single and opposed platform cores; backed bladelets largely dominant, retouched pieces and perforators	
Gemaian	B	Halfan and Nubian-like cores; denticulates and notches	Bone tool (N = 1)
Halfan	B	Microlithic aspect; Halfan and Levallois cores; Ouchtata and backed bladelets	
Kubbaniyan	A	Flake and bladelet production, use of single and opposed platform cores, occasional use of Levallois and Halfa methods; Ouchtata and backed bladelets, burins. Egyptian variant of the Halfan?	Grinding implements, bone tools and ostrich eggshell beads
Ballanan-Silsilian	A, B	Sometimes includes the use of exotic raw materials; mainly oriented toward the production of short elongated blanks (blade/let) with single and opposed platform cores; backed pieces, truncations, proximally retouched blade (let)s and notched tools, occasional use of the micro-burin technique[b]	
Qadan	Mostly B, one site in a (Wadi Kubbaniya)	Small dimensions of the artefacts; mainly oriented toward flake production with single and opposed platform cores, several cores reminiscent of the Levallois methods for Qadan point production, bladelet production documented in some but not all sites; Qadan points, burins, small scrapers and backed pieces (the latter only at some sites)[c]	Rare bone tools, grinding implements
Afian	A	Mainly oriented toward the production of wide and small elongated products, planimetric conception of debitage with high frequencies of faceted platforms; truncations, backed bladelets and geometrics[d]	Grinding stones (Kom Ombo area), bone tools (Makhadma 4)
Sebilian	A, B	Discoidal and Levallois cores for the production of flakes; truncated and backed flakes, use of the microburin technique	
Isnan	A	Production of flakes and rare blades from single and opposed platform cores; high percentage of endscrapers, followed by notches and denticulates, rare backed pieces	Grinding implements
Arkinian (excl. El Adam Variant)	B	Bladelet and flake production from single and opposed platform cores, presence of bipolar reduction, stone anvils; numerous backed pieces and endscrapers	Grinding implements, bone spatula

After Schild and Wendorf (2010), A = southern Egypt between Sohag and the first cataract, see also **Figures 1, **3** (N.B. Schild and Wendorf, 2010 use Dishna as the northern limit); B = Egyptian and Sudanese Nubia between the first and the second cataract.*

***After Schild and Wendorf (2010) except when mentioned otherwise.*

[a]*Characteristics after Vermeersch (2020). These characteristics, associated with minimal ages around 25 ka led to an attribution to the later Upper Palaeolithic, rather than the Late Palaeolithic (Vermeersch, 2020).*

[b]*Characteristics after Smith (1966) and Leplongeon (2017).*

[c]*Characteristics after Usai (2020).*

[d]*Characteristics after Leplongeon (2017). Note that in Leplongeon (2017), the attribution of Makhadma 4 to the Afian is questioned.*

Atbara headwaters are located, precipitation is mostly driven by the East African monsoon system, a complex interplay of seasonal migrations of the Intertropical Convergence Zone (ITCZ) and the Congo Air Boundary (CAB) (Gasse, 2000; Gasse et al., 2008). At the northern end of the Nile Valley, a Mediterranean dry-summer climate predominates and precipitation is mostly brought by the Western westerlies in winter (Gasse, 2000; Williams, 2019). Regional environmental responses to global climatic events are thus very diverse across the Nile Basin.

The contribution of tributaries to the main Nile can be divided into two main types: flood discharge and sediment discharge. Regarding flood discharge, two main periods are distinguished: high flow months and low flow months. Prior to the building of the main dams, the Blue Nile and Atbara rivers provided most of the flood discharge during high flow months (respectively 68 and 22%), whereas the White Nile provided most of it (83%) during low flow months. The White Nile flood discharge was therefore critical for maintaining a perennial flow of the Nile (Williams, 2020; Williams, 2019). Regarding sediment discharge, most of the total sediment load of the Nile comes from the Blue Nile (61%) and Atbara (36%) (Williams, 2019).

This brief summary of the characteristics of the Nile Basin shows that reconstructions of past environments along the northern end of the Nile Valley cannot be understood without the support of information on environmental changes in White Nile, Blue Nile and Atbara.

Palaeoenvironments in the Main Nile Valley During MIS 2

General Data on the Late Pleistocene Main Nile and Its Tributaries

Major comprehensive reviews for the late Quaternary environmental changes in the Nile Basin have been recently published (e.g., Woodward et al., 2007; Williams, 2019; Williams, 2020). The aim here is to briefly review the available and most recent palaeoenvironmental data relevant for a study of human occupation and population dynamics in the northern end of the Nile Valley during MIS 2.

MIS 2 was generally drier and colder than present in the Nile Basin, with peaks of aridity during the LGM and HS 1. The Late Pleistocene Blue Nile was a highly seasonal river, similar to the modern Atbara, and was characterized by a reduced annual discharge while keeping a high carrying capacity and transporting coarse sand and gravels until its alluvial fan in Central Sudan (Williams, 2020; Williams, 2019, 93). In the Atbara headwaters region, the small cirque glaciers on the highest mountains associated with lower temperatures caused the river to be even more seasonal than nowadays, transporting coarse debris. Regarding the White Nile, very high floods are documented at *ca.* 27 ka (Williams et al., 2010; Williams, 2019, 113). However, for most of MIS 2 and until 14.7 ka, the White Nile was cut off from its main source, Lake Victoria (Johnson et al., 1996; Talbot et al., 2000; Williams et al., 2006; Williams et al., 2015), and may have virtually ceased to flow during the LGM (Williams, 2020; Williams, 2019, chapter 14). Because the water discharge of the main Nile during low flow months is dependent on the contribution of the White Nile, perennial flow throughout the year of the main Nile during MIS 2, and particularly during the LGM, was probably jeopardised.

At the other end of the Nile Basin, the Nile Delta Project within the Mediterranean Basin (MEDIBA) project has conducted intensive geological coring across the northern Delta and documented subsurface (located from 3 to 45 m deep) Late Pleistocene deposits dated to >35–12 ka (Stanley et al., 1996, **Table 2**). These deposits are interpreted as sands of alluvial, aeolian or shallow marine origins, interfingered with thin and localized floodplain and playa muds (Stanley and Warne, 1993; Warne and Stanley, 1993). While different origins have been identified for these Late Pleistocene muds, most of them are interpreted as relating to deposits occurring in seasonally flooded depressions in the vicinity of the Nile channels, in a context of low sea levels (Chen and Stanley, 1993). Radiocarbon ages (n = 46) associated with Late Pleistocene muds span the entirety of MIS 2 with their deposition generally occurring >34 ka, *ca.* 28-22 ka and *ca.* 16->10 ka uncal BP, whereas evidence for deposition during the interval between 16 and 22 ka uncal BP is limited (Chen and Stanley, 1993, 560 and fig. 12). Similarly, sand deposits dated to >35–11 ka uncal BP are interpreted as braided river deposits (Chen et al., 1992) but the (dis)continuity of their deposition throughout MIS 2 remains difficult to evaluate, as are their implications and relationship with what happens upstream from the Nile Delta (Butzer, 1997, 167). Late Pleistocene deposits have since been identified in drilling projects in northern Egypt focusing on the Holocene (e.g., Hamdan et al., 2019).

Geological cores in the eastern Mediterranean show that sediment input from the Nile during the LGM, while present, is highly reduced compared to previous periods (e.g., Revel et al., 2010). These data are consistent with a Nile that continued to flow during MIS 2, but possibly only seasonally or during major flood events. Element analyses of core sediments from the eastern Mediterranean confirm a negligible input from the White Nile, vs. an input from the Blue Nile and Atbara, and indicates an increase of Saharan dust input during the LGM (Revel et al., 2010; Revel et al., 2015). A recent high-resolution multi-proxy study of a sediment core from the eastern Mediterranean (Castañeda et al., 2016) documents the most severe period of aridity in the Nile Basin in the past 28,000 years, after the LGM, during the second phase of HS 1, ca. 16-14.5 ka (HS 1b).

From 14.5 ka, the Mediterranean sea level starts to rise again and several proxies, such as pollen data and lake levels, indicate wetter conditions over at least some areas of eastern Africa, in two phases *ca.* 14.5 and *ca.* 11.6 ka (e.g., Williams et al., 2006; Gasse et al., 2008; Foerster et al., 2012). In particular, the abrupt return of precipitation over eastern Africa *ca.* 14.5 ka led to an overflow of Lake Victoria into Lake Albert, the Ugandan headwaters of the White Nile, which triggered high floods in the White Nile Valley as well as at the northern end of the Nile Valley (Williams et al., 2006). These data are mirrored by data from the Delta, indicating a marked increase in the sedimentary input of the Blue Nile and Atbara in Delta sediment cores (Ducassou et al., 2009; Revel et al., 2015), with evidence for high floods in the Delta *ca.* 15–10 ka (Ducassou et al., 2007; Ducassou et al., 2009). However, millennial-scale episodes of aridity are noted, such as one *ca.* 13-12 ka before a return to humid conditions *ca.* 12 ka (Revel et al., 2015). Maximum Nile flow is documented in the Delta at that time leading to the deposition of an organic-rich dark layer known as Sapropel 1 in the Delta *ca.* 9.5-7 ka (Ducassou et al., 2007).

The Late Pleistocene Main Nile in Southern Egypt and Nubia

The late Pleistocene geological evolution of the main Nile, in Egypt and Nubia in particular, has been the subject of major work (e.g., Said, 1981; Said, 1993; Hamimi et al., 2020). At the regional scale, research projects conducted in numerous districts of Nubia (Sandford and Arkell, 1929; Sandford and Arkell, 1933; de Heinzelin, 1968), in the mouth of Wadi Kubbaniya (Schild et al., 1989; Wendorf and Schild, 1989), in the Kom-Ombo plain (Butzer and Hansen, 1968; Butzer, 1980), in the El Kihl (north of Edfu) and Esna areas (Wendorf and Schild, 1976) and in the Sohag area in Middle Egypt (Paulissen and Vermeersch, 1989; Vermeersch et al., 1989; Vermeersch, 2000; Vermeersch, 2002a), enabled reconstruction of the geology of the Egyptian Nile Valley during the Pleistocene (see also reviews in Paulissen and Vermeersch, 1987; Wendorf and Schild, 1989; Butzer, 1997). However, the general chronology is not well known, as many radiocarbon dates are considered too young (Wendorf et al., 1979). In addition, correlations between the geological formations of the different parts of the Nile Valley remain problematic (see **Figure 2** and discussions in Paulissen and Vermeersch, 1987; Schild et al., 1989; Butzer, 1997).

Two main models are currently proposed for the Late Pleistocene main Nile based on geological data from southern Egypt. The first model suggests the presence of a slowly aggrading highly seasonal braided river, and is hereafter referred to as the braided river model (Schild et al., 1989; Wendorf and Schild, 1989; Schild and Wendorf, 2010). The second model suggests that

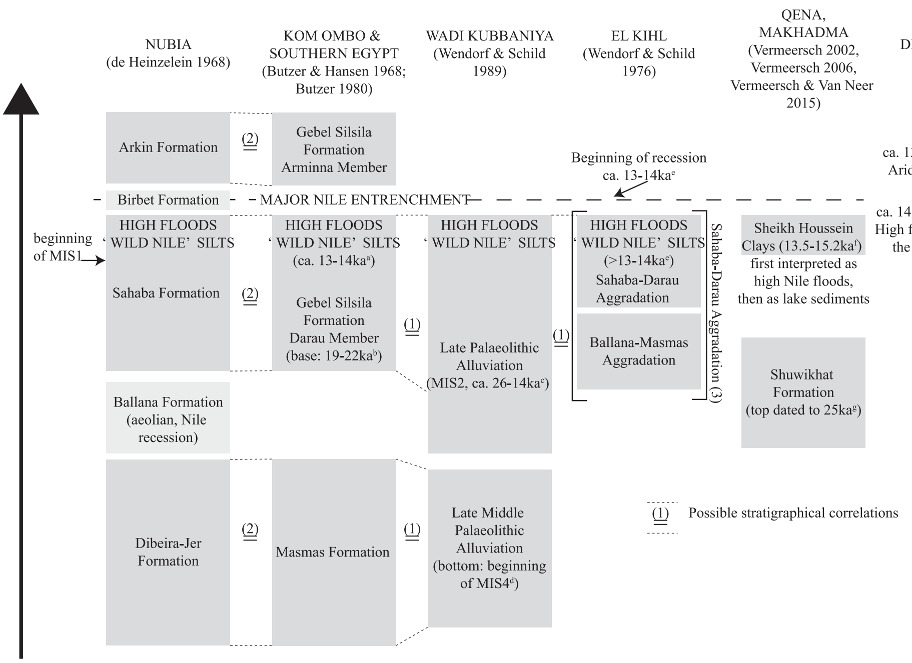

FIGURE 2 | Overview of main geological formations and their proposed correlations in the Lower Egyptian Nile Valley. All dates in the figure are in cal BP and were calibrated with two sigma ranges using Intcal20 (Reimer et al., 2020) for terrestrial or Marine20 (Heaton et al., 2020) for marine samples and Calib v. 8.1.0 (Stuiver and Reimer, 1993) 1) Correlations proposed in Wendorf and Schild (1989) 2) Correlations proposed in Butzer and Hansen (1968) and Butzer (1980) 3) Proposed name in Paulissen and Vermeersch, 1987, 46 [a]Dark silts at New Ballana I dated to 11,720 ± 195 BP (Hv-1264) and 12,000 ± 120 BP (Y-1446) (Butzer and Hansen, 1968), 115) but they are uncorrected for fractionation and may be too young (Butzer, 1997), 161) [b]Date of the base of the Gebel Silsila Formation at Kom Ombo, dated to 17,000 ± 600 BP (I-297) (Butzer and Hansen, 1968), 114) [c]The base of the Late Palaeolithic Alluviation at Wadi Kubbaniya is dated to 20,690 ± 280 BP (SMU-1037) and the top to 12,430 ± 100 BP (SMU-1032) (Haas, 1989) [d]The chronological attribution of the Late Middle Palaeolithic Alluviation is discussed in detail in (Schild et al., 2020) eThe beginning of the recession of the Nile at the site E71P5 (Late Isnan) at El Kihl is dated to 11,560 ± 180 BP (I-3760) (Wendorf and Schild, 1976, 179), which means that the preceding high floods documented at the area must be older [f]The Sheikh Houssein Clays (Paulissen and Vermeersch, 2000; Van Neer et al., 2000) are dated between 12,570 ± 80 BP (GrN-12033) and 12,060 ± 280 BP (GrN-12029). [g]Burnt clay from the Shuwikhat Formation (Paulissen and Vermeersch, 2000) was dated by thermoluminescence (Vermeersch et al., 2000) to 25,000 ± 2500 BP (Ox85TLi), which is considered as a minimum age (Vermeersch, 2020).[h]Isotope data from marine core MS27PT indicating an arid episode between 10,835 ± 40 BP (corrected age, SacA16516) and 11,495 ± 40 BP (corrected age, SacA16517) (Revel et al., 2015). NB: these ages were calibrated using the Marine20 curve. [i]Sedimentary features in cores from the Nile deep-sea turbidite system indicate high Nile floods during early MIS1. The chronological range given is based on two dates from core 84MD637 (Ducassou et al., 2007; Ducassou et al., 2009); 12,670 ± 50 BP (corrected age, SacA004998) and 8,800 ± 35 BP (corrected age, SacA004997). NB: these ages were calibrated using the Marine20 curve.

the Nile was dammed by sand dunes at several places along the Nile Valley, thus creating large lakes favourable for human occupation, hereafter referred to as the lake model (Vermeersch and Van Neer, 2015). These models and their different implications for human groups living in the Nile Valley are briefly summarized below.

The braided river model is extensively described in the second and third volume of *The Prehistory of Wadi Kubbaniya* (Schild et al., 1989; Wendorf and Schild, 1989). The data on which the model relies result from several years of archaeological and geological fieldwork at Wadi Kubbaniya. MIS 2 (or Late Palaeolithic) deposits at Wadi Kubbaniya lie in disconformity above MIS 4 (or Late Middle Palaeolithic) deposits (Schild et al., 2020). MIS 2 deposits in the mouth of Wadi Kubbaniya can be described as follows (after Schild et al., 2020; Schild et al., 1989; Wendorf and Schild, 1989):

- A series of silts (Lower Kubbaniyan silts) interfingering and interstratified with aeolian sands (Dunes). These are interpreted as evidence for a dune encroachment creating a dune barrier across the mouth of the wadi that favored accumulation of Nilotic overbank silts.
- The wadi floor is characterized by a flat silty plain (Fronting Plain), probably made of Lower Kubbaniyan clayey silts and clays. Above these silts and a vertisol, there is a bed of clayey lacustrine silts which is interpreted as having formed in a temporary pond within an interdunal basin.
- At several localities of the mouth of Wadi Kubbaniya (main Dune field, embayment, bay area), a series of white-to-grey silts, marls and diatomites (Upper Lacustrine Series) is observed. They are interpreted as lacustrine sediments, relating to a lake that would have formed when the expansion of the dune field completely closed the wadi mouth before 13 ka BP (or before 15 ka cal BP).
- A series of silts (Upper Kubbaniyan silt) interpreted as Nilotic overbank silts deposited in the context of exceptional high floods overlie the Upper Lacustrine Series. A correlation with the high floods documented at

the beginning of MIS 1 (or 'Wild Nile', Butzer, 1980) is proposed.

- A lack of evidence for wadi run-off during MIS 2 suggests that the wadi was not active and that the desert was hyper-arid during the whole period.

Based on these data, Schild et al. (1989) and Wendorf and Schild (1989) develop a model according to which the main Nile during MIS 2 was a seasonal braided river with a reduced stream competence and an increased sediment load. Renewed precipitation during the rainy season in the Nile headwaters would be responsible for high floods in southern Egypt and would lead to the deposition of the overbank silts identified at Wadi Kubbaniya. This model is consistent with the data available from the Delta, suggesting a continuous albeit very reduced sediment input from the Nile during MIS 2 (Revel et al., 2015). A correlation based on petrological compositions has additionally been proposed between the Late Pleistocene aggradation (Sahaba-Darau corresponding to the Late Palaeolithic Alluviation at Wadi Kubbaniya, see **Figure 2**) and some Late Pleistocene deposits from the Nile Delta, which are interpreted as evidence for the presence of a seasonal braided river in the Delta plain (Chen et al., 1992, 568–569; Stanley and Warne, 1993, 631). However, the exact relationship between the Late Pleistocene Delta sequence and the Nile River system upstream of the Delta is unclear (Butzer, 1997). In particular, sea level variation is an important geological factor in the development of Delta sequences (e.g., Warne and Stanley, 1995), and their relatively coarse chronological resolution for the Late Pleistocene (>35-11 ka uncal BP, see Stanley et al., 1996, **Table 2**) makes direct chronological correlation difficult.

The lake model was first described by Vermeersch and colleagues (2006) and further detailed by Vermeerch and Van Neer (2015). They argue that the aeolian and Nilotic deposits in the main Nile Valley can be interpreted in terms of a lake model. The lake model hypothesizes that enhanced dune activity associated with reduced Nile flow during MIS 2, and especially during the LGM, would have favored the presence of dune dams over the Nile, creating large lakes. Such lakes would have offered a favourable environment for human occupation all-year round (Vermeersch and Van Neer, 2015). The authors' main objections to the braided river model is that there is no evidence for major alluvial deposits in the Nile Valley such as those expected in the braided river model, and that there is no evidence for channel deposits at Wadi Kubbaniya (Schild et al., 1989, 91). Damming of water courses by sand dunes are well-documented in similar contexts (e.g., in the Negev, Goring-Morris and Goldberg, 1990 and see below; or at Wadi Kubbaniya itself, see above and Schild et al., 1989), and satellite images show that similar processes may have occurred at different locations along the Nile Valley (Vermeersch and Van Neer, 2015; **Supplementary Information 3**). Dune activity would have been possible due to strong winds, lack of vegetation and abundant sand supply (e.g.,, from the Delta area, which was at the time a sparsely-vegetated plain, Vermeersch and Van Neer, 2015; or from previous high floods of the Nile, leading to the transport of large quantities of sand and subsequent evaporative events, as is documented in the White Nile Valley, Williams, 2019, 113). Data from fish 'ear-stones' (otoliths) found at the archaeological site of Makhadma 4 indicate that hydroclimatic conditions during MIS 2 were different from both modern and expected pre-Aswan dam Nile conditions and would be consistent with the lake model (Dufour et al., 2018).

In the context of the lake model, deposits in the area of Makhadma (Sheikh Houssein Clays, see **Figure 2**), interpreted as high Nile deposits are re-interpreted as suspension deposits, that would have occurred in the setting of a lake environment. Schild and Wendorf (2010) have objected to this model arguing that deposits at Makhadma are not typical of lacustrine deposits, as they are lacking calcareous marls or diatomites. Vermeersch and Van Neer (2015) responded to this by indicating that their model implies a dynamic landscape. The lakes were not permanent lakes *per se* and the dune dams were occasionally breached by a stronger Nile flood, but would have reformed quickly afterward, recreating a lake at a slightly different location. Such a process is not favourable to the formation of calcareous marls or diatomites. Vermeersch and Van Neer (2015) propose that the geological data at other locations (near Esna, or at Wadi Kubbaniya) may also be reinterpreted in terms of the lake model (Vermeersch and Van Neer, 2015).

This model would also be consistent with available data from the Delta, if we consider that the reduced sediment input documented in geological cores in the eastern Mediterranean (Revel et al., 2015) and part of the Late Pleistocene sequences documented in the Delta (Stanley and Warne, 1993; Warne and Stanley, 1995) were deposited during occasional major floods that would have breached the sand dune dams.

Further field data are thus needed to confirm one or the other model. However, because both models are connected to evidence for human occupation, they imply availability of fresh water and habitability of the main Nile Valley during MIS 2. In addition, both models suggest similar mechanisms of water courses dammed by encroaching sand dunes. They differ in that the braided river model implies that sand dunes did not dam the Nile but rather only specific locations such as the mouth of wadis (e.g., at Wadi Kubbaniya), whereas the lake model implies damming of the Nile itself. The braided river model implies that the floodplain become inaccessible during the flood season, whereas the lake model implies habitability in restricted–but dynamic–zones (lakes) in an overall more stable environment. Nonetheless, because the Nile would have been a seasonal river in the braided river model, or would have resumed its course only during major Nile floods in the lake model, it can be inferred from both models that dammed lakes or seasonally filled depressions on the floodplain would have been attractive and predictable environments for human groups, particularly during the dry season.

After MIS 2, evidence for major floods (or 'Wild Nile', Butzer, 1980) corresponding to the overflow of eastern African lakes *ca.* 14.5 ka cal BP are documented at several locations along the Nile Valley (**Figure 2**). These floods would have created important environmental changes and may have been catastrophic for human populations living in the Nile Valley (Connor and Marks, 1986; Kuper and Kröpelin, 2006; Schild and Wendorf, 2010; Vermeersch and Van Neer, 2015). However, Butzer (1997) suggests that it is the subsequent incision of the Nile (**Figure 2**), broadly coeval with the Younger Dryas (*ca.* 12.8-12 ka), rather than the high floods, that would have presented a major adaptation challenge to human groups living in the Nile Valley.

Palaeoenvironments in the Main Nile Valley and Neighboring Regions During MIS 2: Indirect Evidence for Environmental Refugia or Dispersal Corridor?

In order to consider the hypotheses of the main Nile Valley as an environmental refugium or corridor for dispersals during MIS 2, the palaeoenvironmental data from neighboring regions must also be considered (see **Table 1**). In particular, the available records from northern Egypt, the southern Levant, and the deserts adjacent to the Nile Valley will be reviewed below in order to discuss whether the Delta, Sinai and Negev or eastern Sahara could have been crossed by human populations at the end of the Pleistocene.

When looking at local and regional palaeoenvironmental records, few well-dated records are available but several indicate that some areas were wetter than today during part of MIS 2. For example, fine-grained valley fills in the Sinai suggest that low-energy stream channels during times of prolonged but gentle winter rains existed in the Sinai during the late Pleistocene (Williams, 2019), whereas spring-fed tufa deposits are documented in the Eastern Desert of Egypt and Sinai during the late Pleistocene until *ca.* 22 ka (Hamdan and Brook, 2015). Wetter conditions are also suggested at Sodmein Cave, in the Red Sea Mountains, *ca.* 25 ka (D layer, Moeyersons et al., 2002). The Negev desert was characterized by arid (in the northern part) to hyper-arid (in the southern part) conditions (Enzel et al., 2008). A major phase of dune activity, probably related to the high-velocity winds generated by deep Cyprus Lows over the Eastern Mediterranean (Enzel et al., 2008), is documented in the northwestern Negev in the second part of MIS 2 (23-11.5 ka), with three distinct episodes broadly coeval to the LGM, HS1 and the Younger Dryas (YD) (Goring-Morris and Goldberg, 1990; Roskin and Tsoar, 2017). Dune encroachment sometimes led to damming wadis and the creation of seasonal ponds, creating environments favourable for vegetation growth, attracting animals and thus human groups (Goring-Morris, 2017).

During MIS 2, the lowering of the sea level led to an incision of the Nile starting around Qena (nick point, Sandford, 1936; Wendorf and Schild, 1989). No archaeological evidence dated to MIS 2 is available from the northern part of Egypt (north of Dishna). Geological deposits from this period and associated archaeological remains are thus either absent or buried under several meters of sediments accumulated by the Nile in parallel with the rise of the sea level. One main issue when discussing whether the Nile Valley acted as a corridor during MIS 2 is whether the Nile Delta was habitable. However, it is important to consider that the sea shore during most of MIS 2 was several kilometres northwards, and up to 50 km to the north during the LGM and maximum sea low stand (Stanley and Warne, 1993). Late Pleistocene deposits dated to MIS 2 documented in what is today the Nile Delta, was thus located well upstream from the sea shore. They show evidence for Nile floods and the presence of seasonal ponds, but the evidence is limited for the LGM in particular (Chen and Stanley, 1993; Stanley and Warne, 1993). Based on the characteristics of the mud deposits and their distribution in the Nile Delta, Chen and Stanley (1993) and Stanley and Warne (1993) suggest that the region during the Late Pleistocene was mostly a minimally-vegetated plain with seasonally active braided channels and ephemeral ponds in a generally arid environment. In addition, the composition of the Late Pleistocene Nile deposits in the Delta are consistent with the hypothesis that the Delta constituted the primary source of sand for the Negev-Sinai erg (Muhs et al., 2013). Punctuated human occupation of what is now the Nile Delta in the Late Pleistocene may therefore have been possible but it remains to be confirmed, particularly during the LGM.

West of the Nile Valley, the eastern Sahara was hyper-arid during MIS 2 and until after the Younger Dryas (i.e., after 12.8 ka, Kuper and Kröpelin, 2006). However, at Kharga and Dakhleh, in the Western Desert of Egypt, the presence of tufa deposits and lacustrine sediments where freshwater snails (which can only survive in abundant fresh water lakes) are found, are past evidence for several phases where surface water was present in the now hyper-arid Western Desert of Egypt (Nicoll et al., 1999; Skinner et al., 2013). Tufa deposits were formed during times of alkaline spring discharge, the latter likely linked to a high groundwater table in the Nubian Sandstone Aquifer (Nicoll et al., 1999; Skinner et al., 2013). Electron Spin Resonance (ESR) dates on shells and mammalian teeth suggest the presence of surface water in Kharga and Dakhleh during several phases of the Late Pleistocene, including during MIS 2 (Blackwell et al., 2012; Blackwell et al., 2017; Skinner et al., 2013; Kleindienst et al., 2016; Kleindienst et al., 2020). These MIS 2 dates are consistent with evidence for groundwater recharge of the Nubian Sandstone Aquifer during late MIS 3 / the first part of MIS 2 (pre-LGM) (e.g., Pachur and Hoelzmann, 1991; Abouelmagd et al., 2014). Isotopic composition of older (>MIS 3) fossil water in the Western Desert has been linked to precipitation brought by westerly winds (Sultan et al., 1997). Westerly winds may be dominant across the northern Sahara during glacial periods (Williams, 2019, 244), and a similar origin may be hypothesized for the groundwater recharge of the Nubian Sandstone Aquifer during MIS 2.

Despite a reduced flow and its possible transformation into a more seasonal river, this short review shows that the main Nile never ceased to flow for a long period of time. Survival during the dry season and dry periods of MIS 2 may have been possible around lakes created by the damming of the Nile by sand dunes or interdunal ponds. Favourable conditions for human occupation therefore existed in at least part of the Lower Nile Valley during MIS 2 as well as in several other localized areas over northeastern Africa and the southern Levant (e.g., around lakes fed by wadis or local springs). These localized environmental refugia occur in an otherwise hyper-arid environment, which characterizes the Sahara during MIS 2 as well as probably what is nowadays the Nile Delta. However, based on palaeoenvironmental data alone, the available geographical and chronological resolution of the data does not yet allow us to determine whether the Nile Valley facilitated a free passage to the Sinai-Negev or the rest of northern Africa at that time.

ARCHAEOLOGICAL EVIDENCE FOR HUMAN OCCUPATION OF THE NILE VALLEY DURING MIS 2

General Data on the Late Palaeolithic of the Main Nile Valley

Numerous archaeological sites are dated to MIS 2 in the main Nile Valley, most of which are surface occurrences of bone fragments and lithic artefacts. Based on the characteristics of the lithic artefacts, i.e., the production of flakes and elongated products (blade/lets) of small dimensions associated with a toolkit including high proportions of backed tools, they are attributed to the Late Palaeolithic. The Late Palaeolithic (*ca.* 25-12 ka) in north-eastern Africa follows the Upper Palaeolithic (with scarce sites dated to *ca.* 50-25 ka), and precedes the Epipalaeolithic in the Egyptian Nile Valley and Egyptian Eastern Desert (with sites dated from *ca.* 9 ka cal BP, Vermeersch, 2012), the Early Neolithic in the Western and Eastern Desert of Egypt (from *ca.* 10 ka cal BP, Wendorf et al., 2001; Gatto, 2012) and the Mesolithic in the Sudan (from *ca.* 11 ka cal BP, Honegger, 2019). The Late Palaeolithic in north-eastern Africa is coeval with the Epipalaeolithic in the Levant, the Iberomaurusian/Later Stone Age in northern Africa and the Later Stone Age in other African regions. This constellation of terminologies and the use of the same terms to designate different periods in different regions make comparisons at the macro-regional scale difficult.

Late Palaeolithic sites in north-eastern Africa are located mostly in southern Egypt and Nubia. Most sites were discovered during prehistoric investigations as part of the Nubia Campaign which began in 1961–1962, (Schild and Wendorf, 2002) and archaeological expeditions that followed, until the end of the 1980s. This leads to a record biased toward certain geographical areas (in particular, the location of the Aswan Dam in northern Nubia), although geomorphological reasons also explain why virtually no Late Palaeolithic sites are known north of Qena (see also *The Late Pleistocene main Nile in southern Egypt and Nubia* section). The only possible occurrences of Late Palaeolithic assemblages in northern Egypt are in the region of Helwan, near Cairo, where P. Bovier-Lapierre at the beginning of the 20th century (Bovier-Lapierre, 1926) and F. Debono in 1936 (Debono, 1948; Debono and Mortensen, 1990, 9–11) noted several surface occurrences or 'stations' of material that they attribute to the end of the Palaeolithic. In a later reassessment of Debono's surface collections, Schmidt (1996) attributed Debono site 7 'ostrich' to the Late Upper Palaeolithic and published two dates on ostrich eggshell fragments of *ca.* 18 ka BP (or *ca.* 21–23 ka cal BP). Schmidt (1996) also mentions several localities with microlithic artefacts that he attributes to the Epipalaeolithic, although it is unclear whether this refers to the Epipalaeolithic or Late Palaeolithic. Recent research in the Nile Delta has also reported the presence of Epipalaeolithic assemblages (Rowland and Tassie, 2014; Tassie, 2014). However, with the exception of the two dates on ostrich eggshell fragments which must be considered with caution as these are surface finds, the Late Palaeolithic or Epipalaeolithic surface occurrences in the Nile Delta are poorly dated and may not in fact date to MIS 2 (see discussion below).

In southern Egypt and Nubia, where most Late Palaeolithic sites are found, the archaeological record shows evidence for variability in subsistence behaviors, which may correspond to different seasons of the year. Many sites document subsistence based on fishing, with numerous fish remains, mainly belonging to the Clariidae (e.g., *Clarias* sp.) and Cichlidae (e.g., tilapias) families that prefer shallow waters and could be fished at the beginning and end of the flood season, or even after the flood season when some fish can survive in residual pools that remain on the floodplain (Van Neer et al., 2000). A variety of fishing methods may have been used depending on the season, and in particular there is archaeological evidence for the use of small double-pointed bone hooks (Van Neer and Gautier, 1989; Van Neer et al., 2000). In addition, at Makhadma 4 (Van Neer et al., 2000), the association of high densities of fish bones with black archaeological layers showing an abundance of charcoal and the occurrence of post-holes may suggest the use of curing strategies such as fish smoking at the site. Other sites document subsistence based on large-game hunting. The most common hunted species are hartebeest, aurochs and (Dorcas) gazelles (Linseele and Van Neer, 2010; Coudert, 2013; Yeshurun, 2018). Occasionally, hippopotamus hunting is documented (e.g., on the Kom Ombo plain), and this high-risk hunting may have been related to activities other than strictly subsistence-based ones (Yeshurun, 2018). There is also archaeological evidence for plant (tubers) processing, through the use of grinding implements, e.g., at Wadi Kubbaniya (Roubet, 1989a; Roubet, 1989b).

Beyond subsistence-based behaviors, several rock art panels attributed to the Late Palaeolithic have been documented in localities near Kom Ombo, in Qurta and Abu Tanqura Bahari at el-Hosh (Huyge et al., 2007; Huyge et al., 2011; Huyge, 2009; Huyge and Claes, 2015) and near Aswan, in Wadi Abu Subeira (Storemyr et al., 2008; Kelany, 2012; Graff and Kelany, 2013; Kelany, 2014; Kelany et al., 2015). These rock art panels had previously been noticed in 1962–1963 by the Canadian Prehistoric Expedition (e.g., Smith, 1967; Smith et al., 1985) during the investigation of Late Palaeolithic sites on the Kom Ombo plain. Rock art at these localities comprises a very homogeneous group of panels characterized by the use of hammering and incision to represent large animal figures in a naturalistic style. Bovid (aurochs) figures are dominant, followed by birds, hippopotami, gazelle, fish and hartebeest. Highly stylized human figures are also present in Qurta and Abu Tanqura Bahari (Huyge, 2009; Huyge, 2018). Because these representations are very different in style from what is known for later periods (e.g., Huyge, 2005), and because they are characterized by a dark patina and rock varnish associated with intense weathering, a Late Pleistocene age was proposed (Huyge et al., 2007) and later confirmed by the OSL (Optically-Stimulated Luminescence) dating of sediments covering rock art panels at Qurta II (Huyge et al., 2011). These suggest a minimal age of 15 ka. Due to the vicinity of the Qurta localities to several Late Palaeolithic sites in the Kom Ombo area, Huyge and colleagues (2007, 2011) suggest an association with a particular entity of the Late Palaeolithic, the Ballanan-Silsilian (**Table 2**). It is also interesting to note that these sites are located not far (on the opposite bank of the Nile) from one of the main Late Palaeolithic site clusters, Wadi Kubbaniya (Wendorf et al., 1989).

Finally, several cemeteries are attributed to the end of the Late Palaeolithic; one of the best documented is site 117 in Jebel Sahaba (Wendorf, 1968). These cemeteries are well-known for showing evidence for inter-personal violence, several individuals bearing marks consistent with parry fractures or with lithic artifacts still embedded in their bones (Wendorf, 1968; Greene and Armelagos, 1972). Evidence from these cemeteries is detailed further in *Human fossil and genetic data: evidence for a return to Africa during MIS 2?* section.

Geographical and Chronological Patterns of Human Occupation in the Lower Nile Valley During the Late Palaeolithic

Although a few well-preserved archaeological contexts enable us to have a glimpse of Late Palaeolithic lifeways in the main Nile Valley, most of the archaeological record consists of surface occurrences of stone artefacts. The variability observed in lithic assemblages has led to their grouping into different basic cultural taxonomic entities or industries (see **Table 2** and Schild and Wendorf, 2010). Most of these entities were defined in the 1960s–1970s based on typological characteristics (types of cores and finished tools) and were thought to represent different adaptations by different groups to the Nilotic environment (e.g., Schild and Wendorf, 2010, 116). A few recent studies aiming to study lithic variability in the Late Palaeolithic from a technological perspective have questioned the characteristics of some of these entities or the integrity of the assemblages used to define them (e.g., Paulissen and Vermeersch, 1987; Vermeersch, 2000; Usai, 2008; Usai, 2020; Leplongeon, 2017). However, the validity of the use of this chrono-cultural system for the Late Palaeolithic in the Nile Valley and its implications for reconstructing past human behaviors or human interactions has rarely been called into question. In the current research context aiming to contribute to the reconstruction of past population dynamics both from an archaeological and genetic perspective, evaluating the relevance of the current cultural taxonomic system in use is a fundamental step that remains to be done, as is the case for (most) other regions (e.g., the Upper and Late Palaeolithic in Europe; Reynolds and Riede, 2019; Riede et al., 2019).

Keeping in mind this caveat, a systematic literature review was conducted in order to investigate geographical and chronological patterns of human occupation in the Lower Nile Valley during the Late Palaeolithic, with the aim of creating an inventory of all published sites attributed to this period (**see Supplementary Information 1a–d**). The attribution of sites to specific entities or industries was kept in order to provide an overview of the archaeological record as it is currently classified.

This inventory was undertaken in parallel with the creation of the database for the 'Big Dry' Project, coordinated by Prof. François Bon and funded by the French National Research Agency (ANR). All data used in this paper are presented in the supplementary information (**see Supplementary Information 1a–d**). The definition of a 'site,' particularly when dealing with surface material in desert areas, is a matter of debate (see discussion in Phillips et al., 2017). In the context of this paper, the designation used by the excavators was retained. Only in cases where different areas of a site (localities) were assigned to different taxonomic entities were these areas considered as separate sites. For example, site 8,905 is divided into several localities but all are attributed to the Qadan, and it was thus considered as a single site. Conversely, site E71P1, located in the Edfu area (Wendorf and Schild, 1976), consisted of material collected at four arbitrarily-defined localities, two of which were later attributed to the Kubbaniyan and two others to the Levallois Idfuan, therefore E71P1 is considered here as two sites. Only sites with an–even limited–description of the context (location, geological description) were included in the database. This resulted in the exclusion of the surface occurrences in the Nile Delta surveyed in the first part of the 20th century and mentioned above, since no description of the geological setting of the sites is available. Similarly, and despite the presence of geological descriptions, the seminal work of Vignard (1928); Vignard (1955) on the plain of Kom Ombo could not be included in the database as Vignard's survey methods do not allow the identification of sites. Sites where only surface and limited subsurface material was found (usually less than 10 cm below the surface) were considered as having only one 'archaeological' layer. Only in the case of sites with stratified evidence for multiple layers were sites divided into two or more archaeological layers. Absolute dates associated with the archaeological layers were also systematically collected in the database. All of the steps and arguments used to retain or reject each date are described in the supplementary material (**Supplementary Information 1a–d**).

The detailed literature review shows that a total of 151 sites located in southern Egypt and Egyptian and Sudanese Nubia–corresponding to 168 archaeological layers–are attributed to the Late Palaeolithic (see **Table 3**). Their distribution (see **Figure 3**) shows clear concentrations within southern Egypt and Nubia, which reflect the history of research in the area.

The most common Late Palaeolithic industries (based on the number of archaeological layers attributed to them, see **Table 3**) are the Qadan, Kubbaniyan, Sebilian, Isnan, Ballanan-Silsilian and Halfan. Only a limited number of absolute dates are available (i.e., 120 dates), including 23 dates that are likely minimum or maximum ages, coming from 41 archaeological sites and two geological localities (see **Table 3**). Among the different industries defined for the Late Palaeolithic, only the Kubbaniyan is well-dated, with 47 dates coming from eight archaeological sites. This represents more than a third of all available dates for the Late Palaeolithic in the Nile Valley.

Other reasonably dated industries are the Afian, Isnan and to a lesser extent the Halfan. The Qadan is associated with a relatively

TABLE 3 | Number of sites, archaeological layers and dates for each industry for the Late Palaeolithic of the Lower Nile Valley.

Industry	Number of sites where the industry is represented	Number of archaeological layers	Number of sites with dates (incl. geological locations)	Number of dates (incl. minimum or maximum ages)**	Chronological range (this study)***
Shuwikhatian/Idfuan	6	6	2	4 (4)	Min age of ca. 25 ka
Fakhurian	8	8	4 (1)	4 (1)	23–25.6 ka cal BP
Levallois Idfuan	3	3	1	4	19.7–22 ka cal BP
Gemaian	5	5	0	0	Undated
Kubbaniyan	16	25	8	47	**19.3–23.5 ka cal BP**
Halfan	15	15	5	6	**19–24 ka cal BP**
Ballanan-Silsilian	15	16	3	3 (1)	16.3–20.8 ka cal BP
Qadan[a]	22	22	3	13 (9)	**12–20.2 ka cal BP**
Afian	5	5	2	10	**14–16.8 ka cal BP**[b]
Isnan	19	19	6 (1)	9 (2)	**13.2–16.6 ka cal BP**
Sebilian	18	19	2	5	12.6–16.9 ka cal BP
Arkinian (excl. El Adam)	1	2	1	2	11.9–12.8 ka cal BP
Late Palaeolithic – Miscellaneous	23	23	6	13 (6)	11.2–23.9 ka cal BP
TOTAL	**156***	**168**	**43 (2)***	**120 (23)**	

These totals differ from the total number of archaeological sites. The total of 156 correspond to 151 archaeological sites including five sites where two industries are represented. 43 dated locations correspond to 41 dated sites plus two geological localities. ** the number of dates does not include dates that were rejected by the authors or for which the association with archaeological material was not sustained on stratigraphic grounds. * Only radiocarbon dates with error margins <1,000 and which did not represent minimum or maximum ages were taken into account. In bold are chronological ranges based on more than five dates.*

[a]*Sites 34C, 605 and 621 were removed from the count of Qadan sites since these present clear signs of admixture (see review in Usai, 2008; Usai, 2020). It is probable that other sites attributed to the Qadan also represent mixed contexts (Usai, 2020).*

[b]*Although doubts were cast on the association of the site of Makhadma 4 to the Afian (Leplongeon, 2017), in the absence of detailed comparative analysis that would confirm or refute this association, in the context of this review, the site is attributed to the Afian.*

high number of dates (N = 15), but most of them are minimum ages and come from one site, site 117 (Zazzo, 2014). The association of the cemetery at site 117 with the Qadan industry has been questioned (Usai, 2020). The Qadan lithic assemblages remain poorly described and several doubts have been raised about the mixed nature of some of the sites (e.g., discussion in Usai, 2008; Usai, 2020).

Previous studies (Vermeersch and Van Neer, 2015; Vermeersch, 2020) have shown two main periods of human occupation in the main Nile Valley during MIS 2, *ca.* 23-20 ka cal BP and ca. 16-14 ka cal BP. They correspond to the LGM and the second phase of H1, identified by Castañeda et al., 2016 as the most arid phase of MIS 2 in north-eastern Africa. These studies showed that virtually no human occupation is known after 14 ka cal BP in the Egyptian Nile Valley (Vermeersch and Van Neer, 2015; Vermeersch, 2020), but the picture is less clear in Sudanese Nubia (e.g., Butzer, 1997). The period 14-11 ka cal BP corresponds to major environmental changes that may have been catastrophic for human populations living in the Nile Valley (Butzer, 1997; Kuper and Kröpelin, 2006; Vermeersch and Van Neer, 2015).

To build on these studies (see also Nicoll, 2001, for radiocarbon dates of the Western Desert during the Holocene) and in order to explore the distribution of radiocarbon dates and associated Late Palaeolithic human occupations, a subset of the date database was created, where only dates directly associated with archaeological material were considered (i.e., minimum or maximum ages for human occupations were removed). In addition, dates with an error margin greater than 1,000 years were also removed (e.g., following Vermeersch, 2020 and see **Supplementary Information 1a,c**). The remaining dates (N = 91), all of which are radiocarbon dates, were then calibrated with two sigma ranges using the INTCAL20 calibration curve (Reimer et al., 2020) and Calib 8.1 (Stuiver and Reimer, 1993). To summarize the data and explore the temporal density of the available dates, a Kernel Density Estimate (KDE) was calculated, using the Rowcal package (McLaughlin, 2019) in R (R Core Team, 2020). The Rowcal KDE method uses a bootstrap method in order to take into account the error margin caused by the calibration process (McLaughlin, 2019, 481). KDE is one of the most effective ways to summarize radiocarbon dates and is particularly useful for exploring radiocarbon data when there is little information on the relative stratigraphic locations of the dates (e.g., Bronk Ramsey, 2017; McLaughlin, 2019). Because of the timespan considered (*ca.* 15,000 years) and the fact that the radiocarbon dates included in the dataset are mostly conventional dates with relatively large standard deviations, a bandwidth of 200 years was used in the model.

Figure 4 shows the resulting density graph. Unsurprisingly, as it is based on similar datasets to the ones used in previous studies (compare **Figure 4** with Vermeersch and Van Neer, 2015; **Figure 3**; Vermeersch, 2020; fig. 6.4 and Butzer, 1997; **Figure 2**), it shows similar results, with higher densities of dates during the LGM as well as during the second part of H1 (HS1b). However, it should be noted that the peak in dates corresponding to the LGM is mostly due to the numerous dates available for the Kubbaniyan, which represent more than half of the sample considered here (N = 47/91). The peak in dates between 15 and 14 ka cal BP is mostly associated with Afian and Isnan occupations. Because of the nature of our radiocarbon dataset, which includes an over-representation of the Kubbaniyan, and to a lesser extent the Afian and Isnan

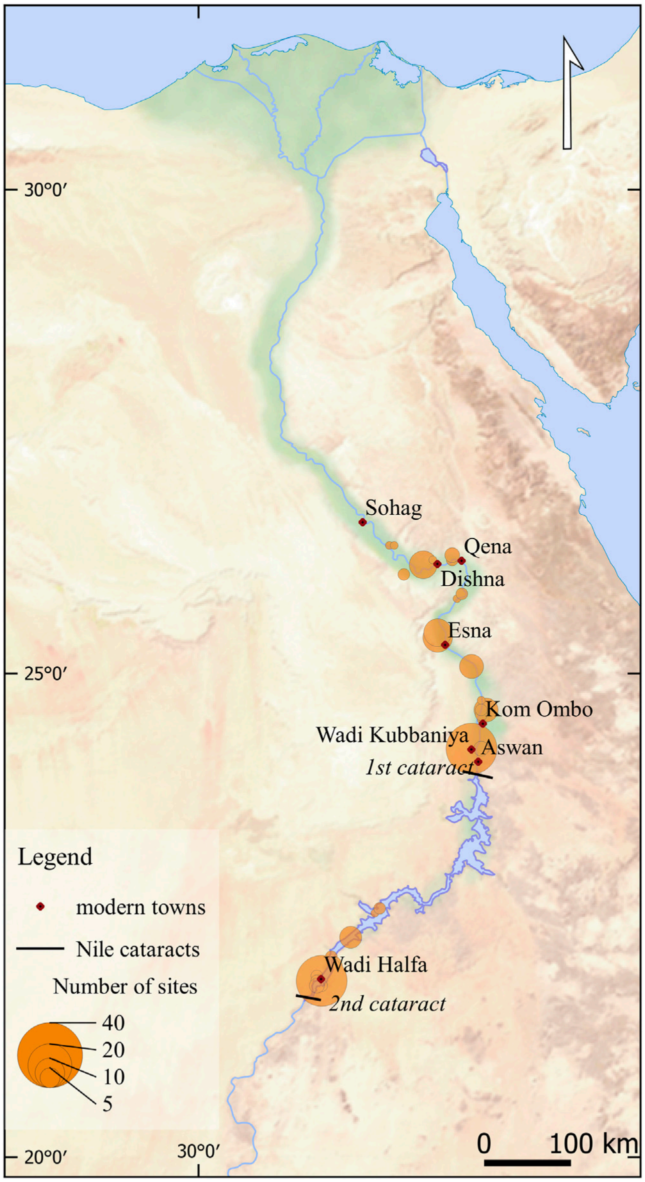

FIGURE 3 | Geographic distribution of Late Palaeolithic sites in the main Nile Valley. Number of sites were counted using a square grid with each square side measuring ca. 5 kms. Created in QGIS v. 3.15 (QGIS Development Team, 2017) using Natural Earth Data.

compared to the other industries (see **Table 3**), and because of the characteristics of the method chosen (KDE), these peaks show evidence for human occupation during these times but the low densities of dates between the two peaks cannot be interpreted as reflecting lower frequencies of human occupation in-between the LGM and the end of H1. Additional dates from other industries are needed in order to test this hypothesis.

In addition, the KDE graph shows that some dates fall within the range of 14-11 ka cal BP. When looking at the raw data (see **Figure 5**), this corresponds to 11 dates, coming from Qadan (8,905 – Tushka), Sebilian (1024A–Wadi Halfa and possibly Sebil VII–Kom Ombo), Isnan (Makhadma 2, El Abadiya 3 – Qena; E71P5 – Edfu) and Arkinian (DIW 1 – Wadi Halfa) sites, plus two sites (Makhadma 1, Qena; WK26, Wadi Kubbaniya) which were attributed to the Late Palaeolithic. In order to interpret the significance of these dates for the presence of human occupation in the Nile Valley in early MIS 1, it is useful to briefly review their geological context.

Only very limited information is available from Sebil VII (Smith, 1967), but most of the calibrated range of the date falls before 14 ka cal BP. The dated material from the sites of Makhadma 1, 2 and El Abadiya come from levels stratigraphically located within the Sheikh Houssein Clays (Paulissen and Vermeersch, 2000; Vermeersch et al., 2006). The site of WK26 (Banks et al., 2015) is located within the Upper Kubbaniyan silts (Schild et al., 1989). Both the Sheikh Houssein Clays and the Upper Kubbaniyan silts may relate to the same phase of high Nile floods at the very beginning of MIS 1. The stratigraphic location of the dated material thus suggests a probable age close to 14 ka cal BP and the date of El Abadiya 3 may be too young. In addition, the charcoal dated to 12,060 ± 50 BP (Beta-319442) at site WK26 was collected during a preliminary survey of the site in 2012, and differs significantly from the three other dates obtained during the 2014 excavations (PRI-14-041-1, PRI-14-041-2 and PRI-14-041-3 clustering *ca.* 13–13.5 ka BP or 15.5–17 ka cal BP). This may indicate two distinct periods of occupation at the site, or that the first date may be too recent.

Similarly, site 8,905 is associated with the top of the Sahaba Formation (Wendorf, 1968), which suggests a probable end-of-MIS 2 age (see **Figure 2**), and therefore that the date obtained from WSU-415b is too young, particularly when considering the other date available for the site, WSU-315 (14,500 ± 490 BP) which has a calibrated range between 16.3 and 18.7 ka cal BP (**Figure 5**; **Supplementary Information 1c**). The stratigraphic position of site 1024A is uncertain, but may relate to the end of the Sahaba Formation or the beginning of the Birbet Formation (Marks, 1968, 488 and see **Figure 2**). Similarly, E71P5, near Edfu, is associated with the incision (Birbet) immediately following the deposit of the Sahaba Formation (Wendorf and Schild, 1976; Wendorf et al., 1979 and see **Figure 2**). The site of Dibeira West 1 (DIW 1), near Wadi Halfa, is associated with the Arkin Formation, a short aggradational event following the Birbet Incision (Schild et al., 1968 and see **Figure 2**). Only these three sites (E71P5, 1020 A and DIW 1) have dates than can be linked with some certainty to the interval after 14 ka cal BP. This seems very few but all three sites are associated with rich lithic material, and in the case of DIW 1, it shows evidence for repeated occupation episodes (Schild et al., 1968). This suggests that human occupation may have occurred during early MIS 1 in the main Nile Valley in southern Egypt and Nubia.

Previous studies (Vermeersch and Van Neer, 2015; Vermeersch, 2020) have suggested that the lack of evidence for human occupation in the Egyptian Nile Valley after 14 ka cal BP may be related to profound environmental changes at that time. In the context of the lake model, these include high floods occurring at the beginning of MIS 1, leading to high lake levels and subsequent breaching of the sand dune dams that were responsible for the presence of the lakes. Here, the small

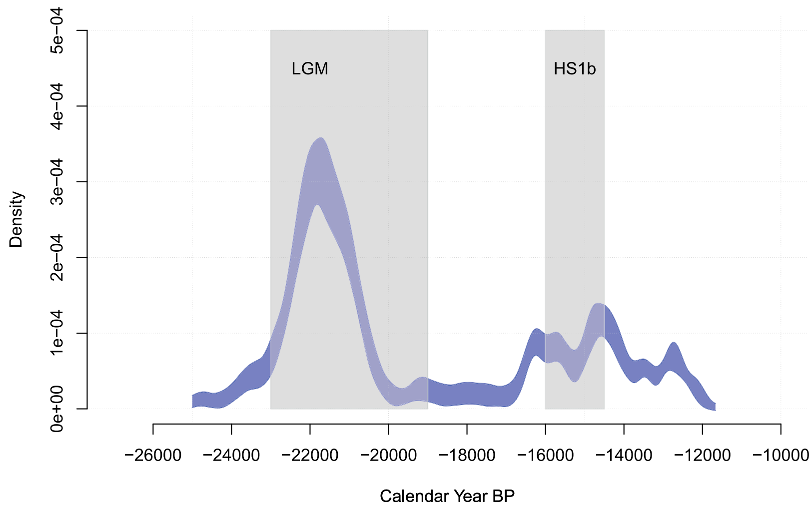

FIGURE 4 | Kernel Density Estimates for all available radiocarbon dates associates with human occupation attributed to the Late Palaeolithic (see **Supplementary Information c**). Created using the Rowcal package in R (McLaughlin, 2019).

number of dates falling in the range of 14-11 ka cal BP can be explained by the inclusion of additional dates from Nubian sites compared to the above-mentioned studies, as well as differences in the method used to calibrate and summarize the radiocarbon dataset. The presence of these dates may suggest 1), a geographical (i.e., north of southern Egypt vs. Nubia), pattern in the distribution of radiocarbon dates, or 2), that currently identified gaps in human occupation, such as the one after 14 ka cal BP in Upper Egypt, are the product of available radiocarbon dates that are biased toward some industries and, perhaps, toward certain periods of time. In the first scenario, the hypothesis of human groups moving toward the south at the beginning of MIS 1, during a period of profound environmental changes seems particularly appealing. This is especially the case in light of the evidence for high levels of inter-personal violence in the Nubian cemeteries, for which available dates indicate use at the end of MIS 2 or beginning of MIS 1. However, the biases identified in the dataset and the fact that it includes only ten dates (N = 10/91) for Sudanese Nubia, force us to also consider the second scenario.

As previous studies have already shown (Vermeersch and Van Neer, 2015; Vermeersch, 2020), the available dated archaeological material presented here shows strong evidence for human occupation during MIS 2 in the Lower Egyptian Nile Valley, and in particular during the periods documented regionally as the driest of the end of the Pleistocene (i.e., the LGM and H1, Castañeda et al., 2016). This stands in agreement with the hypothesis of the Nile Valley as an environmental refugium during MIS 2. However, the present study also shows that the available dated archaeological evidence presents major geographical (concentration of sites within southern Egypt and Nubia) and chronological (only some industries are well dated) biases. While the available data may indicate different clusters of human occupation in time and space, consistent with the hypothesis of the existence of several discontinuous refugia areas along the Nile Valley during MIS 2, this remains to be tested on a larger and more representative set of radiocarbon dates. The implementation of systematic dating programmes of Late Palaeolithic materials stored in museums using recent dating method protocols that target materials other than charcoal or bone collagen (such as apatite, e.g., Zazzo, 2014; ostrich eggshell, e.g., Tryon et al., 2018; terrestrial shells, e.g., Douka, 2017) may be a suitable research avenue to further enlarge the dataset.

Variability in the Late Palaeolithic in the Main Nile Valley: Evidence for Local Developments or External Influences?

Inferring past human population interactions from the lithic record relies on the assumption that lithic assemblages include information on past socio-cultural groups. Under this assumption, discussing human dispersals based on the lithic record amounts to identify cultural transmission across space (e.g., Tostevin, 2012, 80). However, dispersals in the genetic sense, i.e., with gene flow, may have occurred without cultural transmission. Conversely, cultural transmission across space may occur without gene flow. Once similarities in the lithic record have been identified across space, an additional challenge is to be able to distinguish between cultural diffusion (with or without gene flow) and convergence, i.e., similar forms of material culture independently produced (e.g., Groucutt et al., 2015). Determining the conditions for similarities between lithic assemblages to be interpreted as indicators for cultural transmission across space, which would be consistent with dispersal hypotheses, thus requires a well-defined theoretical framework, high-resolution archaeological and palaeoenvironmental record, as well as robust cultural taxonomies (For recent reviews on this topic, see for example Tostevin, 2012; Groucutt et al., 2015; Riede et al., 2019).

While a commonly-accepted view considers the main Nile Valley as being mostly isolated during MIS 2, several external

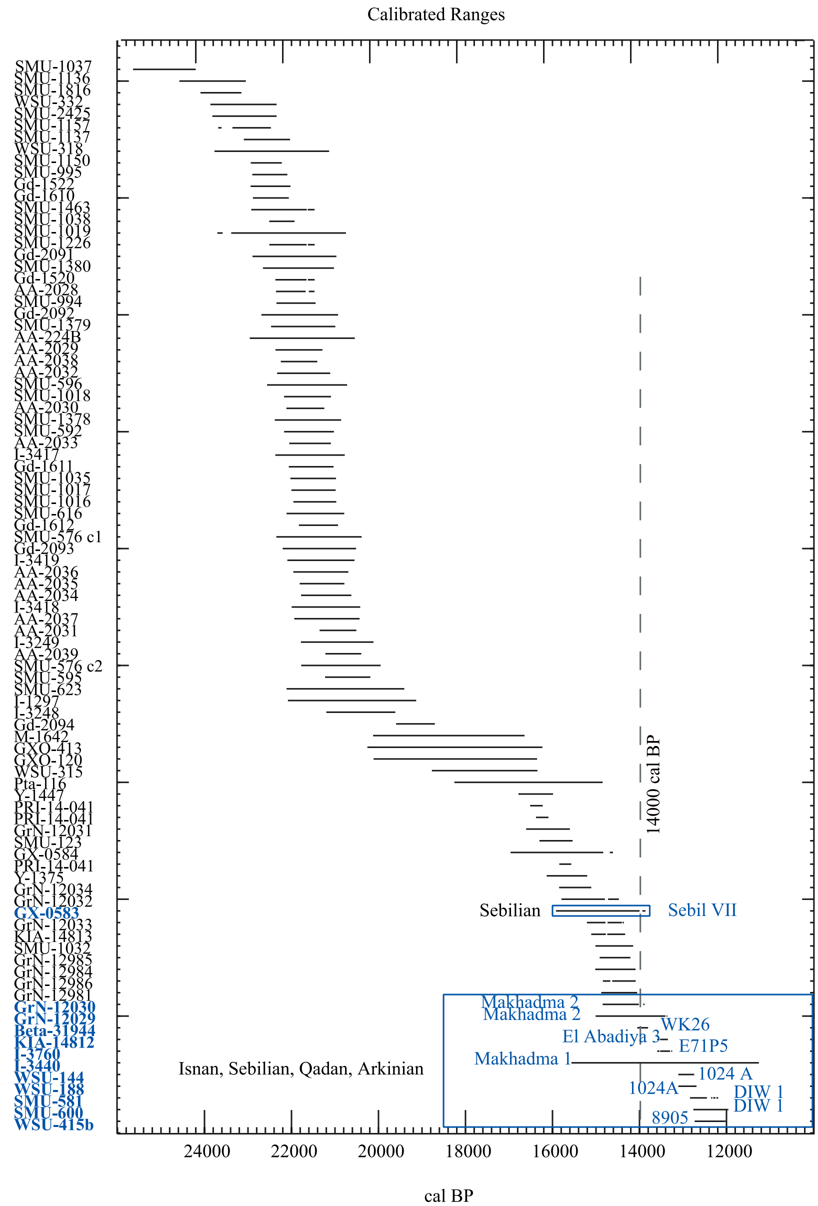

FIGURE 5 | Barplots of all two-sigma calibrated ranges of radiocarbon dates considered in the paper (N = 91). Created using Intcal20 (Reimer et al., 2020) and Calib 8.1 (Stuiver and Reimer, 1993).

influences have also been suggested (e.g., Schild and Wendorf, 2010, 116). Links with the south, toward eastern Africa, have been suggested for earlier periods, in the Middle Stone Age (e.g., Goder-Goldberger, 2013), but there is currently no supporting evidence for such contacts during MIS 2 (e.g., see discussion in Leplongeon et al., 2020). Several authors have also proposed connections between the Nile Valley and north-western Africa or the Levant during MIS 2 based on similarities in the lithic record.

Evidence for lithic similarities that have been argued to indicate contacts between the Nile Valley and the Levant at the end of the Pleistocene is mainly based on the sparse data from the Nile Delta. The unsystematic collections of microlithic artefacts by F. Debono near Helwan (see above, Debono, 1948; Schmidt, 1996; Tassie, 2014) includes tool types that are more similar to Epipalaeolithic industries from the southern Levant (e.g., Mushabian, Ramonian, dated to *ca.* 18-15 ka cal BP, Goring-Morris, 2017), than from known industries in the Nile Valley (Schmidt, 1996; **Figures 3**, **4**). Given their geographical location, they might correspond to a westward expansion of the 'territory' of the Mushabian and Ramonian, that are well attested to in the Sinai (Bar-Yosef and Phillips, 1977) rather than contacts between two different populations. However, in the absence of numbers and context, it is not possible to further interpret these similarities. In addition, a detailed comparative analysis between the Afian and Ballanan-Silsilian from sites in Upper Egypt, and Epipalaeolithic assemblages of the Negev desert in Israel failed to highlight any similarities important enough to be interpreted as indicating contacts between these two regions (Leplongeon, 2017; Leplongeon and Goring-Morris, 2018). Detailed investigation and dating of the recently found material in the Delta region (Rowland and Tassie, 2014), will be critical to discussing the place of the Nile Delta in interregional population interactions at the end of the Pleistocene.

Links between some Nile Valley Late Palaeolithic industries and the North African LSA/Iberomaurusian were suggested based on typological similarities referring to attributes such as the type (e.g., Ouchtata) or side of the retouch for backed bladelets (Schild et al., 1968; Phillips, 1972; Phillips, 1973; Close, 1978; Close, 2002). If typological similarities are evident between some Nile Valley industries and the North African LSA, their interpretation is challenging. Interpreting these typological similarities in terms of socio-cultural relationships would be an over-simplification (e.g., Close, 1978, 235). Furthermore, there is no strict contemporaneity between the Late Palaeolithic in the Nile Valley and the Iberomaurusian in North Africa. As shown above, the Late Palaeolithic in the Nile Valley broadly corresponds to MIS 2, with several sites dated to the LGM, whereas if the earliest dates for the Iberomaurusian are *ca.* 25-23 ka cal BP, the evidence remains limited for its initial phase and most of the sites are dated from *ca.* 16-15 ka cal BP (Potì and Weniger, 2019). Systematic comparisons including technological and typological aspects of the assemblages as well as an evaluation of their chronometric dating would be critical in confirming or rejecting hypotheses of contacts between the Nile Valley and north-western Africa at the end of the Pleistocene.

From a non-lithic point of view, similarities have been noted in rock art between Late Pleistocene depictions of human figures ('headless women') from Qurta and el Hosh with depictions found in a rock shelter in the Sinai Desert (Zboray, 2012; Huyge, 2018). The rock art in Sinai remains undated, and the fauna associated with the human figures there is different from what is found in the Nile Valley (e.g., equines and (non-domesticated?) camel figures are dominant). However, similarities in human figures are striking. The presence of similar headless figures in European Magdalenian art also led Huyge (2018) to suggest that it may represent potential out of or back into Africa dispersals. However, as unsettling as these similarities may seem, further dated evidence is needed to consider such a (bold) scenario.

Nonetheless, *ca.* 25 ka cal BP in North Africa, the Nile Valley and the Levant, blade/let industries with a toolkit dominated by backed pieces are documented. The significance of the presence of these broad lithic characteristics in all three regions at the same time is unclear. The emergence of these industries may reflect earlier connections between the regions (see also discussion in Vermeersch, 2020). However, beyond these similar traits, each region seems to be characterized by its own development of industries with different technological and typological characteristics. The rare systematic comparative analyses between these regions focusing on both technological and typological traits, in addition to the difficulties of interpreting lithic data in terms of socio-cultural relationships, make it currently impossible to highlight some kind of 'information sharing' between these regions during MIS 2. Currently available archaeological data therefore do not support any intensive contact between human groups in North Africa, the Levant and the Nile Valley, although this does not exclude the possibility of movement of people without cultural transmission.

HUMAN FOSSIL AND GENETIC DATA: EVIDENCE FOR A RETURN TO AFRICA DURING MIS 2?

Some General Considerations

The evolutionary history of modern humans was a complex process involving alternations between phases of expansion and contraction of populations. Mirazón Lahr (2016) identifies the period corresponding to the end of MIS 3 and MIS 2 as a period of structuring of human diversity. The environmental changes occurring during this period led to the fragmentation, or even extinction, of some populations, and thus to a loss of inter-group diversity, whereas the expansion of some groups during the Holocene led to a subsequent increase of overall diversity (Mirazón Lahr, 2016, 9). The MIS 2 African fossil record is relatively limited but recent paleoanthropological research indicates that past biological variation was greater than in extant human populations (e.g., Tryon et al., 2015; Crevecoeur et al., 2016) and that past human populations were highly structured (e.g., Scerri et al., 2018).

To test whether the Nile Valley acted as a dispersal corridor or an environmental refugium based on the human fossil record, a simple model of isolation *vs.* connection with other regions may be proposed (see **Table 1**). For isolated populations, we would expect a record showing distinct characteristics compared to the record of other regions (e.g., North African and the Levant), whereas if population interactions were maintained, we would expect to find shared variability between human groups from different regions. This model would only be valid if populations were isolated for enough time to develop distinct biological characteristics; however, how much time is necessary for the latter is difficult to evaluate.

Since the fossil record is generally limited, such hypotheses are often formulated through genetic studies, where we would expect to find evidence for population bottlenecks in the isolation hypothesis, or evidence for admixture in the contact hypothesis. Genetic studies relying on modern DNA cannot answer questions related to the precise provenance of past human populations, and distinguishing recent vs. ancient gene flow, as well as estimating the age of new gene flow, is often complex. However, ancient DNA studies can help to mitigate these problems and several recently published results show their potential to better understand human interactions in Africa in the past (e.g., Gallego-Llorente et al., 2015; Skoglund et al., 2017; Fregel et al., 2018; Van de Loosdrecht et al., 2018; Prendergast et al., 2019; Wang et al., 2020).

Here, the contribution of the currently available human fossil and genetic data to the discussion of whether the Nile Valley

TABLE 4 | List of human fossils dated to MIS 2 from the Nile Valley.

Site name and location	Geological settings	Date	Chrono-cultural attribution	Number of individuals identified	References
Site E71K1, Deir el Fakhuri, Esna	Eroding out on the surface of Ballana Dune	MIS 2?	Fakhurian	2 (burials)	Butler (1974); Lubell (1974)
Site 8905, Tushka	Top of Sahaba formation	MIS 2?	Qadan	19 (cemetery)	Schild et al. (1968)
Site GS-2B-I[a], Kom-Ombo	Within level characterized by silty coarse sand and concretionary pebbles (interpreted as a channel), probably derived from older site upstream	MIS 2	Late Palaeolithic	1 (scattered fragments of one or more human calvaria, plus a large fragment of frontal bone)	Reed (1965); Butzer and Hansen (1968)
Site E-82-6, Wadi Kubbaniya	Surface find	MIS 2?	Late Palaeolithic	1 (skeleton)	Wendorf and Schild (1986)
Site 6B28, Wadi Halfa	Surface find	MIS 2?	Halfan?	1 (fossilized mandible)	Armelagos (1964); Irwin et al. (1968)
Site 6B36, Wadi Halfa	Surface	MIS 2?	Qadan	38 (cemetery)	Hewes et al. (1964); Greene and Armelagos (1972)
Site ANE-1, Wadi Halfa	Surface, eroded sandstone bedrock	MIS 2?	Qadan?	2 (skull fragments)	Shiner (1968)
Site 117, Jebel Sahaba	Base of a Nubian sandstone inselberg, with an elevation of 160 m above sea level (asl), which is above the Sahaba silts (140 m asl) in the area	MIS 2?b	Qadan?	62 (cemetery)	Anderson (1968); Wendorf (1968)

[a]*Reed (1965) reports (I believe incorrectly) the frontal bone as coming from the site GS-2A but the preliminary report (Reed et al., 1967) as well as the detailed account by Butzer and Hansen (1968, 168) clearly places the human bone as coming from level 1 of site GS-2B-I. Contrary to what Reed (1965) states, there is no date directly associated with the level where the human bone was found.*

[b]*Nine minimum ages (radiocarbon dates on human bone apatite (Zazzo, 2014) from 8,000 to 13,600 cal BP and one radiocarbon date 13,750 ± 600 BP (from 15,000 to 18,350 cal BP; Pta-116).*

could have acted as an environmental refugium or a dispersal corridor during MIS 2 is summarised.

Human Fossil Data

Table 4 lists sites where human fossils attributed to MIS 2 have been recovered in the Lower Nile Valley. The record is divided into two categories of sites with human remains: isolated finds and cemeteries. Isolated finds are often from the surface or reworked levels, the chronological attribution of which relies on their geological context and an (often uncertain) association with archaeological sites in the immediate vicinity. In all cemeteries, as well as in some of the isolated finds, there is evidence for ‘aggressive-defensive trauma’ including parry fractures and instances of stone artefacts embedded in bones. Unfortunately, very few sites are well-dated, and for the sites that do have absolute dates, their calibrated chronology places them between the end of MIS 2 and early MIS 1. Only the cemetery of site 117 (Jebel Sahaba) possesses several direct dates on human bones, but most are radiocarbon dates on apatite and they likely represent minimum ages (Zazzo, 2014). Five dates are available for site 8,905 (Schild et al., 1968), of which three can be considered unreliable. WSU-415a was rejected as too young and a second count from the same sample (WSU-415b) gave an older age (Wendorf, 1968). WSU-417-442 was not taken into consideration here as it is a date on a combined charcoal sample from two different localities at the site. Finally, WSU-444 is also considered unreliable as it is on carbonate sample (see Dal Sasso et al., 2018 for a discussion on radiocarbon dating carbonate). The two remaining dates, from the same locality, place the site between 12,030 and 18,760 cal BP, indicating either two distinct periods of occupation or contamination problems (**see Supplementary Information 1c, d**). The attribution of these human remains to MIS 2 is therefore in most cases tentative and relies on their association with Late Palaeolithic industries, some of which are also poorly dated (see *Archaeological evidence for human occupation of the Nile Valley during MIS 2* section). Nonetheless, the geological location of some of the human remains is consistent with a chronological attribution to the end of MIS 2 or early MIS 1 (see **Table 4**).

All human remains listed in **Table 4** are characterized by a robust morphology and fall within the same range of variation, which has been interpreted as evidence that they represent closely related populations (e.g., Armelagos, 1964; Hewes et al., 1964; Anderson, 1968; Wendorf, 1968; Greene and Armelagos, 1972; Butler, 1974; Wendorf and Schild, 1986), despite differences in the ways the bodies were buried (Wendorf, 1968).

Pre-MIS 2 modern human remains in the Nile Valley consist of few individuals, namely the child of Taramsa 1 and the two skeletons of Nazlet Khater 2. These three individuals were found in contexts interpreted as burials within or in close proximity to raw material extraction sites.

Several OSL dates are available for the child burial of Taramsa 1 (Van Peer et al., 2010). Sand deposits from three extraction pits, including the one where the burial was dug, gave OSL ages consistent with other dates available for human occupation at the extraction site (ranging from 60 to 110 ka, Van Peer et al., 2010, table 10.2 p. 223). OSL dating from sand samples from within the skull gave an average of about 24 ka BP, but the excavators favor an earlier date for the burial (in particular, OSL date TAR-3, 68.6 ± 8 ka BP of sand deposits located above the burial). Recent reviews have questioned this chronological attribution, arguing that the sediment within the skull would give the most likely age for the burial (e.g., Grine, 2016, 354; Groucutt, 2020, 67). Based on the OSL dates, only a broad chronological range from MIS 4-2 can be proposed for the human burial of Taramsa 1. However, Van Peer et al. (2010, 223) associate the young MIS 2 dates with the fill of desiccation cracks, one of which was observed in stratigraphy just above the skull. They propose that these desiccation cracks formed during the arid conditions of MIS 2 and that a large amount of aeolian sand filled the cracks as well as the skull at that time. In addition, the burial was sealed by an undisturbed layer of extracted cobbles, which stratigraphically is covered by dump deposits of other Middle Palaeolithic extraction pits (Vermeersch et al., 1998). The archaeological evidence associated with the deposits surrounding the burial are attributed to the Late Middle Palaeolithic and have absolute dates corresponding to the first half of the Upper Pleistocene. Accepting a MIS 2 chronology for the burial would require explaining why older dates were obtained from deposits surrounding the burial. Finally, despite the poor preservation of the remains, and although these results must be taken cautiously as the analysis was carried out on photographs, the apparent absolute dimensions of the teeth would set the Taramsa child apart from the 'small-toothed' modern humans of the end of the Pleistocene in northern Africa (Vermeersch et al., 1998, 481). Unfortunately, the poor preservation of the human remains, the fact that a detailed morphological description was not possible, and the young age of the individual, prevent its inclusion in detailed comparisons with MIS 2 human remains.

The two burials discovered at Nazlet Khater 2 (NK2) are dated to 37,570 +350 -310 BP (39,400 cal BP, GrA-20145, Vermeersch, 2020; Vermeersch, 2002a) and have been extensively studied (Pinhasi and Semal, 2000; Vermeersch, et al., 2002b; Crevecoeur, 2008; Crevecoeur, 2012). Only the remains from one male individual were well-preserved and could be analyzed in detail. They are associated with the contemporaneous Upper Palaeolithic raw material extraction site of Nazlet Khater 4 (NK4), dated to ca. 38-34,000 cal BP (Vermeersch, 2002a). The presence of pathologies, particularly in the cervical vertebrae and the hands, are consistent with raw material extraction activities, such as heavy load-carrying with forehead straps or repeated impact on the hand while using extraction tools (Crevecoeur, 2012, 216). In addition, the NK2 individual was buried with a bifacial axe of a similar type to those found at NK4 and interpreted as extraction tools (Vermeersch, et al., 2002b). A detailed descriptive and comparative analysis of these remains shows that the NK2 individual presents a unique mosaic of features, which places him at the edge of extant variation and distinguishes him from any other known past or recent modern humans (Pinhasi and Semal, 2000; Crevecoeur, 2008; Crevecoeur, 2012). This is consistent with a growing body of evidence suggesting that Late Pleistocene human variation in Africa was much greater than current variation (e.g., Tryon et al., 2015; Crevecoeur et al., 2016; Pearson et al., 2020). Furthermore, the characteristics of the inner ear structure place the NK2 individual closer to early modern humans and European Upper Palaeolithic individuals than to recent humans. It does not present obvious similarities with MIS 2 modern humans, other than a general robust morphology.

Post-MIS 2 human remains, particularly from the Early and Middle Holocene, are known from Nubia in the context of Mesolithic or Neolithic burials (e.g., Usai, 2016; Honegger, 2019). While the hypothesis of population continuity has previously been proposed for Nubian populations from MIS 2 until the Middle Holocene (e.g., Greene, 1982), several recent studies have refuted this hypothesis (Crevecoeur et al., 2012; Galland et al., 2016; Benoiston et al., 2018). In Sudan, two cemeteries were found at El Barga (Honegger 2019), one attributed to the Mesolithic (7,800-6,900 BC) and the other to the Early Neolithic (6,000-5,500 BC). Preliminary analysis of the human remains associated with these two cemeteries show important differences between the two populations, both in terms of funerary practices and biological characteristics; the early Holocene Mesolithic individuals are extremely robust, while the Neolithic sample is more gracile (Crevecoeur et al., 2012). The Mesolithic individuals from El Barga show close affinities in their mandibular attributes and dental remains with MIS 2 Nubian populations, and are clearly separated from the Neolithic individuals (Crevecoeur et al., 2012, 27–28; Benoiston et al., 2018). Similar results were obtained when comparing dental features (Irish, 2005) and cranial and mandibular morphology (Galland et al., 2016) in a comparative analysis of human remains from Nubia, from the Late Palaeolithic to the Christian era. These results show a drastic shift in cranial, mandibular and dental morphologies and suggest a major population replacement in Nubia during the Holocene some time before the final Neolithic.

Comparisons between MIS 2 human remains from the Nile Valley and from northern Africa (Iberomaurusian) and the Levant (Epipalaeolithic / Natufian) suggest some similarities, such as in their robust morphologies and cranial features (e.g., Anderson, 1968; Greene and Armelagos, 1972; Butler, 1974) whereas other studies highlight several differences (see review in Irish (2000)). Extreme divergence in dental traits between Iberomaurusians and Late Palaeolithic Nubians were highlighted by Irish (2000), which would suggest that these populations are not closely related. In a study about regional variation in the postcranial robusticity of Late Upper Palaeolithic humans, Shackelford (2007) mentions that because of significant differences in body size, body proportion and robusticity, the Nile Valley (Nubian) and Mediterranean (North Africa and Levant) samples were treated as two different groups. In a study of the Jebel Sahaba (site 117) human remains, Holliday (2015) also highlights differences in body shape between the Jebel Sahaba individuals and contemporary North African and Levantine human remains. Nonetheless, in the comparative analysis of mandibular morphology between samples from the Mesolithic and Neolithic (Holocene) from El Barga, from Jebel Sahaba, Wadi Halfa, Taforalt (Iberomaurusian) and from the Levant (Natufian), only the Neolithic sample stands apart, while the Late Pleistocene and early Holocene populations show close results (Crevecoeur et al., 2012, figure 19).

In sum, the available data suggest the following:

- All Late Pleistocene (MIS 2/early MIS 1) human remains from the Lower Nile Valley present similarities, which is consistent with the hypothesis that they belong to the same or closely-related population(s).
- From a socio-cultural point of view, there is evidence for high levels of interpersonal violence during MIS 2 in the Lower Nile Valley and high diversity of burial practices.
- Pre-MIS 2 data from the Lower Nile Valley are too sparse to indicate (dis)continuity of human populations.
- Comparisons between Late Palaeolithic and Early Holocene human remains show similarities, but their interpretation in terms of population continuity throughout MIS 2 and 1 is hampered by the poor chronological resolution of human remains attributed to MIS 2 (see **Table 4**).
- Post-MIS 2 data from Nubia indicate a strong population discontinuity (replacement of the population?) occurring after the early Holocene and before the middle Holocene.
- If MIS 2 human remains from the Nile Valley share some general characteristic with contemporaneous human remains from other regions, and particularly from North Africa and the Levant, there is also evidence that they represent distinct human populations/groups.

Distinguishing between refugial and dispersal corridor models based on human fossil data alone is challenging (see **Table 1**). Assessing how much time is necessary for isolated populations to be characterized by distinct physical characteristics and how different two contemporaneous human groups from adjacent regions should be to demonstrate isolation is extremely complex. The limited number of human remains from the Nile Valley and their coarse chronological resolution therefore results in a human fossil record that may appear consistent with both models. This depends on whether the emphasis is put on the fact that there is some evidence for the presence of distinct human groups in the Nile Valley and adjacent regions (refugial model), or that there also is some evidence for the presence of shared characteristics (dispersal corridor model).

Genetic Data

Recent developments in genetic studies using modern or ancient DNA have been crucial in testing and proposing new hypotheses of population interactions and dispersals in prehistory. Because of their location, north-eastern Africa and the Nile Valley in particular hold a special place in the debates surrounding modern human dispersals out of and back into Africa. One particular debate concerns the occurrence of major dispersals back into Africa during the Pleistocene and potentially via the Nile Valley (e.g., Hodgson et al., 2014 and references therein). In north-eastern Africa, Eurasian admixture during a recent (*ca.* 700 BP) major back-into Africa expansion has been documented, but its impact is different in the north and south of the region (e.g., Hollfelder et al., 2017). When working with modern DNA, such recent events may contribute to hiding the signatures of more ancient (particularly Pleistocene) back-flows from Eurasia into Africa. Ancient DNA studies can contribute to overcoming this issue. For example, ancient DNA from ancient Egyptian mummies dated to between 3,000 and 1,600 cal BP showed that ancient Egyptians before the major admixture event identified above already had a strong near-eastern component, found in Levantine Neolithic individuals, suggesting an earlier influx of near-eastern ancestry (Schuenemann et al., 2017). However, all the samples analyzed in this study come from a single site, Abusir-el Melek in Middle Egypt, and results may be related more to the location of the site and the local history, rather than reflecting general trends that can be applied to all of Ancient Egypt (Schuenemann et al., 2017, 8).

Outside north-eastern Africa, in Morocco, analyses of ancient DNA from human remains dated to *ca.* 15 ka (Iberomaurusian) at Taforalt (Van de Loosdrecht et al., 2018), *ca.* 7 ka (Early Neolithic) at Ifri n'Amr and *ca.* 5 ka (Late Neolithic) at Kelif el Boroud (Fregel et al., 2018) highlight complex population dynamics in North Africa at the end of the Pleistocene and Holocene. Later Stone Age and Early Neolithic individuals appear similar from a genetic point of view, and both groups are distantly related to Levantine Natufian hunter-gatherers, indicating both a Levantine intrusion into North Africa during the Late Pleistocene and a certain degree of population continuity in northern Africa between the Late Pleistocene and Holocene. Data from Kelif el Boroud suggest that its population (Late Neolithic) results from admixture between populations related to Early Neolithic populations and European Neolithic groups from across the Mediterranean. Available data therefore point to population interactions, at least along the Mediterranean coast of Africa, in the Pleistocene before 15 ka.

Pagani and Crevecoeur (2019) discuss the potential implications of these recent genetic data on the African genetic diversity in the form of two 'entirely speculative' (their words) scenarios. Because the second of these scenarios is particularly relevant for our topic, it is briefly summarized here. It hypothesizes a fragmentation of populations during the arid Late Glacial period (MIS 4-2) in north-eastern Africa. Small subgroups of these fragmented populations would have expanded west along the North African coast and east toward Eurasia. Under this hypothetical scenario, which considers the Nile Valley as the main route out of Africa (e.g., Pagani et al., 2015), the genetic bottleneck characterizing all non-African groups, and generally linked to an out of Africa expansion of a small group during favourable environmental conditions would instead be related to the closing of the 'Nile corridor'. The fragmentation of populations would have lasted until the reopening of the Nile Valley during the Holocene, where admixture between the isolated local groups and Levantine or north-western groups would have occurred. This would be consistent with the available fossil evidence (e.g., see *Geographical and chronological patterns of human occupation in the Lower Nile Valley 447 during the Late Palaeolithic* section and Pagani and Crevecoeur, 2019), in particular the uniqueness of the human fossil from NK2, and the persistence of robust phenotypes in Nubia until the emergence of more gracile morphologies, possibly related to a population replacement when the Nile Valley reopens, after 8 ka).

Currently available genetic data, including Late Pleistocene and early Holocene ancient DNA, highlight a particularly complex history of human interactions in North Africa during the end of the Pleistocene. Although further evidence is needed to support it, the scenario proposed by Pagani and Crevecoeur (2019) seems consistent with the human fossil data from the Nile Valley and Nubia in particular, and would imply that during MIS 2 and until after 8 ka, the Nile Valley was not a dispersal corridor. Ancient DNA studies applied to the Late Palaeolithic or Mesolithic/Neolithic Nubian human remains–if DNA extraction were possible–would be critical to confirm or deny such a hypothesis.

SUMMARY AND RESEARCH PERSPECTIVES

Available palaeoenvironmental, human fossil, genetic and archaeological data all present their own limitations and offer contrasting views when considering the question of whether the Nile Valley acted as a corridor for dispersal or environmental refugium during MIS 2. Improved chronological and geographical resolution is needed in order to bring definitive support to one or the other hypothesis (or both). Nonetheless, the available evidence seems to suggest that the Nile Valley acted primarily as an environmental refugium during MIS 2. Indirect evidence from palaeoenvironmental data show that several locations at least in the Nile Valley were suitable for human occupation during MIS 2. This is supported by archaeological evidence showing human occupation during the driest episodes of MIS 2. Human occupation might also have been possible in some areas of the adjacent deserts, at least in an intermittent manner. Similarly, human fossil data suggest that human groups from the Nile Valley are different from adjacent regions, which is consistent with a scenario involving the isolation of human groups into environmental refugia (e.g., Pagani and Crevecoeur, 2019).

The hypothesis of the Nile Valley as a dispersal corridor during MIS 2 receives little support. Palaeoenvironmental data suggest that the deserts adjacent to the Nile Valley were hyper-arid over most of the period, and connectivity between the different areas identified as potential environmental refugia remains to be demonstrated. In particular, acquiring further archaeological data from the Nile Delta is critical to elucidate whether the area was inhabitable for none, part or all of MIS 2. Human fossil and archaeological records show little-to-no evidence for contacts between human groups, other than very broad similarities at the macro-regional scale. Genetic studies based on ancient DNA suggest gene flow between human groups located in the Levant and North Africa before 15 ka, but this may indicate interactions along the Mediterranean coast, without involving the Nile Valley. Other genetic studies, based on both ancient and modern DNA, suggest gene flow from Eurasia to eastern Africa, but this may have occurred before or after MIS 2. Ancient DNA studies involving samples from MIS 2 human remains from the Nile Valley would be extremely important to help elucidate the population dynamics of this region during MIS 2.

Most of the known Late Palaeolithic sites of the main Nile Valley are now destroyed. Their location, close to the Nile, makes them particularly vulnerable to the building of dams, expansion of irrigation systems and urbanization in Egypt and Sudan. Despite major Palaeolithic work in the region in the second half of the 20th century, very few fieldwork projects focusing on the end of the Palaeolithic are currently on-going in the main Nile Valley. Both renewed archaeological and geological fieldwork in areas where Late Pleistocene deposits are preserved, and reinvestigation of archival and artefact collections in museums, many of which remain only partly published, will allow us to shed further light on human-environment interactions in the Nile Valley and neighboring regions at the end of the Pleistocene.

AUTHOR CONTRIBUTIONS

AL conceived and designed the study, collected the data, performed the analysis and wrote the paper.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2020.607183/full#supplementary-material.

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