Review Article

A Brief Overview of the Last 10 Years of Major Late Pleistocene Discoveries in the Old World: *Homo floresiensis*, Neanderthal, and Denisovan

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In the last ten years, new fossil, archaeological, and genetic data have significantly altered our understanding of the peopling of the Old World in the Late Pleistocene. Scholars have long been challenged to define humanity's place in evolution and to trace our phylogeny. Differences in the skeletal morphology of hominin fossils have often led to the naming of distinct new species, but recent genetic findings have challenged the traditional perspective by demonstrating that modern human DNA contains genes inherited from Neanderthals and Denisovans, thus questioning their status as separate species. The recent discovery of *Homo floresiensis* from Flores Island has also raised interesting queries about how much genetic and morphological diversity was present during the Late Pleistocene. This paper discusses the nature and implications of the evidence with respect to *Homo floresiensis*, Neanderthals, and Denisovans and briefly reviews major Late Pleistocene discoveries from the last ten years of research in the Old World and their significance to the study of human evolution.

1. Introduction

In the literature of human evolution, recent years have been marked by new questions of what it means to be human. Scholars have long been challenged to define humans' place in evolution and to trace our phylogeny. Differences in the skeletal morphology of hominin fossils have often led to the naming of distinct new species. *Species* are traditionally and most often defined as a population or group of populations capable of interbreeding and producing fertile offspring [1], although Mayden [2] more recently have identified at least 24 alternative species conceptualizations (see also de Queiroz [3] for a discussion of modern versus traditional species definitions).

Recent genetic findings have challenged the traditional biological perspective by demonstrating that modern human DNA contains genes inherited from Neanderthals and Denisovans [4–6]. Not only do modern humans partially share their lineage but genetic evidences also indicate that these different hominins were capable of interbreeding and producing viable offspring, thus questioning their status

as separate species. Genetic data to date indicate that at least Neanderthals, anatomically modern humans (AMH, i.e., humans with skeletons similar to those of present-day humans), and Denisovans were variants of a single breeding population of *Homo*, even though they present vast spatiotemporal differences in their skeletal morphology and artifactual productions. Despite these findings, however, in general the human family tree has continued its trend toward expanding "bushes" and taxonomic diversity, including the announcement of the new species *Australopithecus sediba* by Berger and collaborators [7]. The genetic evidence for interbreeding along with the traditional concept of species proposed by Mayr [1] might lead to these Late Pleistocene populations being integrated into a single species; however, it is also clear that a host of phylogenetic and taxonomic problems remains unresolved after subsuming the reproductively viable groups into one species. In addition, since the discovery in September 2003 of *Homo floresiensis* from Flores Island, different interpretations have raised interesting queries about how much genetic and morphological diversity was present during the Late Pleistocene [8, 9].
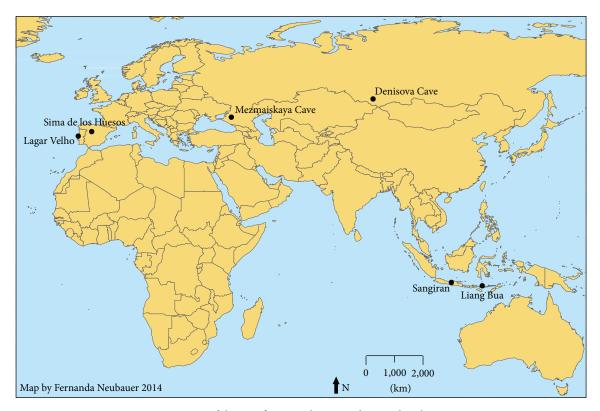
FIGURE 1: Map of the significant site locations discussed in this paper.

In the last ten years, new fossil, archaeological, and genetic data have significantly altered our understanding of the peopling of the Old World in the Late Pleistocene. This paper aims to discuss the nature and implications of the evidence with respect to *Homo floresiensis*, Neanderthals, and Denisovans. This paper briefly reviews these major Late Pleistocene discoveries in the Old World and their significance to the study of human evolution. It is not my intention to settle any debates, new or old, but instead to discuss briefly how several recent discoveries bring new complexities and considerations to the field of Old World Late Pleistocene research related to *Homo floresiensis*, Neanderthals, and Denisovans.

2. *Homo floresiensis*

In 2004 Brown, Morwood and collaborators published the findings of skeletal remains of small-bodied hominins from their excavations in Liang Bua (Figure 1), a large limestone cave on the island of Flores in eastern Indonesia, and suggested that they represented a new species that they named *Homo floresiensis* [8, 9]. According to the original reports, the hominins on Flores were 1 m tall and had an endocranial volume of approximately 380 cm^3, equivalent to the smallest-known australopithecines. The most complete specimen named LB1 was identified as a female due to its pelvic anatomy, and as an adult because of the teeth eruption and wear and epiphyseal unions. LB1 skeletal bones, some of which were still articulated, included a fairly complete cranium and mandible. The bones were recovered from a

small area dated with calibrated accelerator mass spectrometry (AMS) to c. 18 ka by two samples (ANUA-27116 and ANUA-27117). Associated deposits contained 32 stone tools and faunal remains, including Komodo dragon and dwarfed species of *Stegodon* (MNI 26). But another level that also contains *H. floresiensis* remains had up to 5,500 artifacts per cubic meter, including points, blades, and perforators. LB2, the left mandibular third premolar of another specimen, yielded an age of 37.7 ± 0.2 ka (sample LB-JR-6A/13-23) by thermal ionization mass spectrometry (TIMS). Based on these dates, the researchers originally suggested that the *H. floresiensis* existed from before 38 ka until at least 18 ka. In the following year, after more evidence was analyzed from the site, Morwood et al. [10] inferred new dates of 95-74 to 12 ka for the presence of *H. floresiensis* in Liang Bua. The new discoveries included the butchered Stegodon bones, evidence of the use of fire, and hominin remains of a second adult mandible and postcranial material from other individuals.

As the discoveries received global attention, scholars soon questioned where to place *H. floresiensis* in the hominin phylogenetic tree, and within broader cladistic analysis (e.g., [11–13]). Some scholars hypothesized that *H. floresiensis* evolved from early Javanese *Homo erectus* with dramatic island dwarfism due to long-term isolation (e.g., [14]). This idea was first proposed by the discoverers [8, 9], who soon after reviewed their assessment and concluded that the genealogy of the new hominin species was uncertain due to some of their similarities with *Australopithecus*, and were not likely descendants of *H. erectus* nor *H. sapiens*

[10]. Others suggested that *H. floresiensis* were not insular dwarfed descendants of *H. erectus*, but of a lineage of Ling Bua hominins that left Africa before 1.8 Ma, likely before the evolution of the genus *Homo*, and arrived on Flores in the Middle Pleistocene (e.g., [15]). Contrary to both of these perspectives, there are scholars who have refuted the idea that *H. floresiensis* represent a new species, arguing that the specimens represent a microcephalic *Homo sapiens*, which is a pathological anomaly (e.g., [16, 17]). However, a growing number of researches have supported the idea that they represent a new and puzzling species (e.g., [8–15, 18–25]). They have critiqued the pathological view due to its inability to explain how a diseased population could persist for over 50,000 years and encompass the full range of phenotypes observed in *H. floresiensis*. In addition, the Roberts et al. [26] study did not support the claims that the variety of specimens with consistent skeletal morphological features in different levels was explained by taphonomic or disturbance events as described by proponents of the pathological disorder theory. They collected an extensive series of 85 samples that were dated using 7 numerical-age methods (radiocarbon, thermoluminescence, optically stimulated luminescence, infrared-stimulated luminescence, uranium-series, electron spin resonance, and electron spin resonance/uranium-series) to establish the geochronological information for Liang Bua and its immediate environments. This produced a robust chronological framework for the archaeological, faunal, and sedimentary sequences at Liang Bua. The results obtained indicated good stratigraphic coherence, and the age estimates provide a series of self-consistent chronologies for the hominin and artifact-bearing deposits spanning the last c. 100 ka. There is evidence that hominins were present in Flores as early as 1 Ma by the discovery of 45 stone tools *in situ*, but no animal or hominin remains were found in that context [27]. There is also evidence of *H. erectus* recovered at Sangiran (Central Java, Indonesia) (Figure 1) dating to nearly 1.6 Ma and of more than 80 specimens from ages ranging from 1.51 to 0.9 Ma [28].

Due to the lack of evidence, however, it is unclear whether *H. floresiensis* descended from these first inhabitants of Flores Island and went through an insular dwarfing process, as well as if they were a completely different species or variants of the same species of *Homo*. Furthermore, there is still no agreement on whether they belong to the genus *Homo* or *Australopithecus*. Only future genetic studies will disclose whether *H. floresiensis* were able to interbreed with other hominins, or if modern humans share a percentage of their DNA as in the case of Neanderthals and Denisovans.

3. Neanderthals

The first Neanderthal skeleton recovered was a child's skull excavated in late 1829 or early 1830, estimated to be four to six years old at the age of death, although the discovery was only recognized about a century later. The specimen was recovered at Engis cave in Belgium by the physician Schmerling [29, page 379] and [30, page 17]. However, the first skeletal remains to be recorded as a Neanderthal were a male found in the Kleine Feldhofer Grotte near Dusseldorf, Germany, in 1856. King [31] soon created a new taxonomic category, *Homo neanderthalensis*. Today however many scholars attribute Neanderthals to the taxonomic category *Homo sapiens neanderthalensis* to emphasize that they were more similar to modern *Homo sapiens* than being different (e.g., [32]). Indeed, after the recent discovery in 2010 by Green et al. [4] in which modern humans share a percentage of the Neanderthal genomic DNA sequence and therefore interbred with AMH, some scholars now accept that they were not two different species but instead represent variants of the same. Their studies indicate that non-African individuals retain an average of 1 to 4% of Neanderthal DNA. Janković [29, page 395], before the announcements of these genetic findings, had already defended this hypothesis and argued that "Neanderthals are seen as an extinct group of populations, not an extinct or separated species, and are expected to have contributed to some extent to the early modern human gene pool in Europe." In addition, Zilhão and collaborators [33–35] had also argued that Neanderthals interbreed with AMH much earlier than the genetic findings. The authors argued that the fossil remains of a child recovered from the Lagar Velho rock shelter in Portugal (Figure 1) combined skeletal features of Neanderthal (e.g., short, thick limb bones) and modern humans (e.g., modern teeth and chin), representing to them direct evidence that both interbred and contributed to our gene pool. The authors suggested that Neanderthals disappeared by being absorbed into the early modern human population. Radiocarbon results from the charcoal lens under the child's legs and from animal bones associated with the burial yielded a date of 24.5 ka, about 3,000 years after Neanderthals presumably disappeared from western Iberia.

To date, the skeletal remains of more than 500 Neanderthal individuals are known, and surprisingly about half of these are children [30, page 17]. This represents a high number of child specimens if we consider that hominin remains are rare because the fossilization and survival of a skeletal over a large time span is an unusual and lucky event. Due to their smaller size and fragility, the finding of subadult skeletal remains is even rarer. This factor led Stapert [30, page 17] to suggest that Neanderthal child mortality must have been higher than 50% and they often died quite young. The author also argues that there may have been many reasons for the high mortality among Neanderthals such as food shortage, unbalanced diet, and violence. However, Estabrook [36] analyzed many Neanderthal skeletal remains to verify if the occurrences of trauma present in them are high. The author [page 346] "found no evidence that Neanderthals experienced trauma more frequently or with a different distribution throughout the body beyond what is commonly experienced by modern humans in the context of hunter-gatherers, nomads, semisedentary foragers, and medieval small landowners." Furthermore, Estabrook' data did not support the assertion that trauma played a more influential role in the lives of Neanderthals than any of the groups mentioned above.

Researchers have also focused on understanding Neanderthal's cognitive capabilities and how their behaviors were

compared to modern humans. Some scholars have argued that Neanderthals had a shorter childhood compared to AMH (e.g., [37, 38]), while others argued that both had similar growth rates (e.g., [39]). Based on their data of enamel and dental growth studies, Rozzi and de Castro [38] suggest that Neanderthal dental crown formed 15% quicker than modern humans. If all aspects of dental development were foreshortened to the same degree, it would have taken about 15 years for Neanderthals to reach adulthood. Furthermore they conclude that, despite having a large brain (with cranial capacities of 1,200 to 1,626 cm^3), Neanderthals were characterized by having a short period of development even compared to their ancestor *Homo heidelbergensis*. De León et al. [39], however, based on their analysis of Neanderthal neonate brain sizes, argue that the duration of pregnancy of Neanderthals and modern *Homo sapiens* were similar, suggesting relatively equivalent fetal growth rates. The authors also suggest that Neanderthal brains expanded at a higher rate and attained larger adult volumes than modern *Homo sapiens*, but they reached adult sizes within the same time period and along equivalent trajectories. Meanwhile, Kondo et al. [40] studied the growth patterns of neurocranium, faces, and mandibles from Neanderthals and modern humans. Their results were interpreted as showing that neurocranial and facial growth were similar in Neanderthals and modern humans but in contrast, the growth of Neanderthal mandibles was more accelerated—at least during the postnatal-to-preadolescent period between ages two and ten years—than that of modern humans. However, the authors conclude that their results are premature and that it is unclear if Neanderthal growth was more accelerated than modern humans or if they represent the same pattern of widely differing growth profiles as modern populations. The studies conducted by Rozzi and de Castro [38], de León et al. [39], and Kondo et al. [40] demonstrate that the question of the length of Neanderthal childhood is a discussion that is still unresolved among scientists.

Although some researchers suggested that Neanderthals did not intentionally bury their dead (e.g., [41]), examining the literature, Pettitt [42, page 3] suggests that there are 32 to 36 convincing indicators of Neanderthal burial practices. Mezmaiskaya Cave (Figure 1), located in northern Caucasus, is an interesting site due to the finding of two intentional burials of Neanderthal infant skeletons that were recovered from layers associated with animal remains and Mousterian artifacts. According to Golovanova et al. [43], the excavations at the site were well executed to the extent that Neanderthal subsistence strategies could be established. The stratigraphic layers containing the burials were radiocarbon dated to 32 ka (LE-4735) and to >45 ka (LE-3841). The region where the cave site is located is characterized by a rich diversity of fauna and flora. Many thousands of faunal remains were recovered from the Neanderthal Mousterian occupation layers at the site. Medium to large sized mammals were common, with a predominance of steppe bison (*Bison priscus*), Caucasian goat (*Capra caucasica*), and Asiatic mouflon (*Ovis orientalis*). The analysis of a sample of 479 large mammal bones indicated that many exhibit traces of carnivore damage and lithic tool

cut marks. Stone tool cut marks were present on 7% of the bison bones and 5% of the goat, sheep, and red deer bones, representing different stages of the butchering process, including dismemberment and filleting. The dental crown of the lower third molars was measured to provide the age of mortality of bison (N. 19) and goats and sheep (N. 22), which represent a preference for prime-age adults. This finding led Golovanova et al. [43, page 85] to conclude that "such a profile is not consistent with the pattern of scavenged remains, and these data, in conjunction with the tool cut marks, indicate that most of bison, goat, and sheep remains represent animals hunted by the inhabitants of Mezmaiskaya Cave." Of course the type of meat and edible plants that were part of Neanderthals' diet varied widely from each region depending upon the surrounding fauna and flora available, but the case study from Mezmaiskaya cave shows strong evidence that Neanderthals were efficient hunters. A number of studies have focused on Neanderthal subsistence behavior, most of which portray it as synonymous with hunting and fishing specialization (e.g., [43–45]).

Further, the Paixão-Côrtes et al. [46] study of 162 cognitive genes among Denisovans, *H. sapiens*, and Neanderthals revealed that, due to the great similarity in some of the cognitive genes, they might have shared more behavioral traits with modern humans than previously thought. Abi-Rached et al. [47] suggest that on migrating out of Africa, AMH encountered archaic hominins, residents of Eurasia for more than 200,000 years, who had immune systems that were better adapted to local pathogens, and their interactions significantly shaped AMH immune systems through adaptive introgression of the archaic alleles.

4. Denisovans

In 2010, Krause and collaborators [48] reported the discovery of a distal phalanx bone of a young female from the Denisova Cave in Siberia (Figure 1), which was dated by poorly associated fauna to 30 to 50 ka. They extracted DNA from the bone and concluded that it belonged to a previously unknown type of archaic hominin. They were cautious to avoid defining the hominins as a new species and instead called them Denisovans. In contrast to every other hominin population (e.g., Neanderthals, *H. floresiensis*), who have been recognized based on their skeletal morphology, the Denisovans were the first hominin groups identified through genetic evidence. Denisovans were a sister group of Neanderthals that diverged before Neanderthals interbred with AMH. Later there was admixture between Denisovans and the ancestors of Melanesians, involving primarily Denisovan males [49, page 224].

Reich et al. [5, 6] estimated that modern Melanesians have the highest percent of Denisovan DNA, ranging from 4 to 6%. Their genetic studies also indicated that mainland Eurasian populations did not have significant percentages of Denisovan DNA. The ancestors of present-day East Asians were not in Southeast Asia when the Denisova gene flow occurred into the common ancestors of Melanesians. Scholars have invested efforts to understand how they reached Australia and crossed

the Wallace's Line, one of the world's greatest biogeographic barriers, an achievement previously accomplished by *H. floresiensis* [50]. Genetic studies by Rasmussen et al. [51] indicate a two wave settlement of Asia, which reinforces the hypothesis suggested by Petraglia et al. [52] about an Asian origin of the Denisovans. Native Australians are descendants of an early human dispersal into eastern Asia that occurred probably 62 to 75 ka. The findings of stone tools dated to c. 74 ka in Jwalapuram in Southern India strengthen this hypothesis [53]. The second dispersal gave rise to modern Asians 25 to 38 ka.

Adding to this puzzle is the fact that Denisovan DNA was identified in hominins recovered from *Sima de los Huesos* in Spain (Figure 1) [54], a site that has provided long-term record of ancient DNA, including DNA from the remains of a Middle Pleistocene cave bear [55]. The *Sima de los Huesos* skeletal remains show Neanderthal-derived features (e.g., dental, mandibular, midfacial, supraorbital, and occipital morphology), but their mtDNA shares a common ancestor with Denisovans rather than Neanderthals [54]. Prüfer et al. [56] based on their genomic studies suggest that several gene flow events occurred among Neanderthals, Denisovans, and AMH, possibly including gene flow into Denisovans from an unknown archaic group (perhaps *H. erectus*). Their analysis indicates that interbreeding occurred among many hominin populations in the Late Pleistocene, but the extent of gene flow between them was generally low.

5. Discussion

Three major theories have been hypothesized to explain the human evolutionary trajectories observed during the Late Pleistocene, and these models are popularly titled: Out of Africa, Multiregional, and Assimilation. In the Out of Africa or Recent African Origin model, *H. sapiens* evolved in Africa and migrated to Eurasia and Australia after 50 ka and rapidly replaced the other *Homo* species, such as Neanderthals [57–59]. Neanderthals are seen as a different species than AMH, and the two did not interbreed. Utilizing a branching/replacement model for human evolution, in this model *H. erectus* is placed as the ancestor to modern *H. sapiens*. The Out of Africa model, however, is too rigid to keep up with the new evidences from archaeological data and genetics. Adding to this complexity, researchers must now consider how new data informs on scenarios of previous hominin dispersions (e.g., [60]).

Under the multiregional hypothesis, human populations living in Africa and Eurasia have been genetically connected since the time of *H. erectus*. Because of this gene flow, they have evolved together as a single evolutionary lineage. The concept of multiregional does not mean independent multiple origins, but rather a dependence on genetic exchanges to explain how differentiation, geographic variation, and evolutionary changes within the human species took place [61, page 134]. A middle road approach attempts to merge parts of both of these theories, known as the Assimilation model. In this model, early AMH after migrating from Africa interbred with the initial populations that they encountered

in Eurasia, which were still archaic. In this way, archaic genes entered the pool and passed their traits back to AMH, which quickly completely replaced them [62]. The key strengths of both the Multiregional and Assimilation models are in their ability to account for recent genetic and archaeological evidences and are both plausible to explain human evolution during the Late Pleistocene.

To conclude, in the last ten years scholars have introduced a variety of new hominin species, along with variants of a singular species. Many are potential candidates for the ancestor of our genus, but only time will disclose whether they will continue to be recognized as unique variants [63, page 215]. It is now acknowledged that Neanderthals and Denisovans probably did not go extinct in the classical sense but instead were merged with other populations, and some of their genetic heritage is still retained in the present-day human populations [61, page 132]. While a Neanderthal genetic contribution to the present-day gene pool is evidenced in all human populations outside Africa, a contribution from Denisovans is found exclusively in island Southeast Asia and Oceania [4–6, 54]. With all of the evidence for interbreeding, it is most likely that the hominin phylogeny represents expansive networks instead of the traditional phylogenetic trees and bushes. Furthermore, as suggested by de Castro and Martinón-Torres [60, page 108], "[t]rying to classify the hominid populations into a 'species' scheme too rigidly, and the understanding of dispersals events as directional and lineal migrations instead of expansion/contraction hominid pulses, undoubtedly interfere in the understanding of the evolutionary scenario of the genus Homo during the Pleistocene." In future studies, it will be necessary to integrate several lines of evidence—genetic, archaeological, and fossil—in order to unravel the story of our own species.

Conflict of Interests

The author declares that there is no conflict of interests regarding the publication of this paper.

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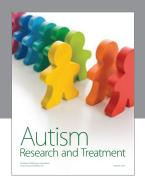
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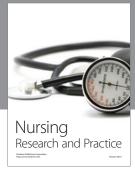
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[63] L. Cowgill, "One year in biological anthropology: species, integration, and boundaries in 2010," *American Anthropol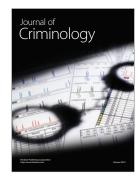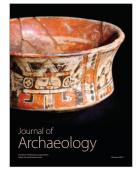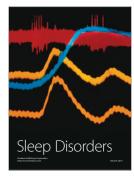ogist*, vol. 113, no. 2, pp. 213–221, 2011.