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A rich locality in South Kensington: the fossil hominin collection of the Natural History Museum, London.

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ABSTRACT

The primacy of fossils in the Natural History Museum (NHM) collections goes back to the very origins of the Museum, but the first fossil hominins to come to the NHM were probably the Upper Palaeolithic remains from Bruniquel, which were accessioned in 1864. This founded a collection which has continued to expand into this century. While there have been many compilations and descriptions of the fossil hominin collection at the NHM over its long history, to our knowledge no-one has prepared a review of the collection itself. The intention of the current paper is to synthesise earlier sources with accounts of new finds, revised chronologies and rediscovered treasures in order to illustrate the breadth and continuing importance of the fossil hominins curated at the NHM. We list and discuss all the hominin material known or thought to pre-date the Holocene. These form a collection of great importance, both in terms of their research value, and in terms of the history of science. With the application of new investigative techniques such as aDNA and micro-CT, the material remains central to palaeoanthropological research in the 21st Century.

1. INTRODUCTION

The Natural History Museum (NHM) houses collections of global importance for which its stated purpose is both "to conserve, curate and enhance national collections... [and] to further research on the collections" (BM(NH), 1977, 1.). What are now the NHM collections began life as part of the collections of Hans Sloane. Sloane was one of the leading physicians of his day and served as president of both the College of Physicians and the Royal Society; he was also a passionate and prolific collector, particularly of natural history specimens (Thackeray & Press, 2009). After Sloane's death in 1753, his collection was bought for the nation by Parliament for a then enormous sum, which was raised by public lottery (Thackeray & Press, 2009). The Sloane collection formed the majority of the founding collection of the British Museum, which was established by an Act of Parliament in 1753 (Thackeray & Press, 2009). The British Museum opened first in Montagu House, near Bloomsbury Square, and then moved to the current (British Museum) site from 1827 (MacLeod, 2006).

Arriving at the British Museum in 1856, the new Superintendent of Natural History, Richard Owen, was dismayed by the conditions in which the collections were housed and he began a campaign to set up a separate museum to house the natural history specimens (Thackeray & Press, 2009). He was eventually successful and the British Museum (Natural History) [henceforth BM(NH)] became physically independent from the British Museum proper when the natural history collections were moved to the current South Kensington site. Building work in South Kensington started in 1873 and Waterhouse's new building opened in 1881; it is the oldest and most famous part of the current NHM (Thackeray & Press, 2009). The BM(NH) only became formally independent of the British Museum in 1963, when it was declared so by an Act of Parliament (BM(NH), 1977) and, having been referred to colloquially as the Natural History Museum for many years, in 1992 this name was finally made official.

Following the Second World War, a consensus was reached among many British teaching establishments that a national museum was the best place to store human skeletal remains, which would be of more use as a single collection (Kruszynski, 1978). This led to the donation to the NHM of thousands of anthropological and palaeoanthropological specimens from institutions such as the Royal College of Surgeons (RCS) and University of Oxford. By the 1960s these donations necessitated new housing for the Anthropology collections and in 1977 the new sub-Department of Anthropology (previously created under the Deputy Keeper, Kenneth Oakley) was moved to the new East Wing extension of the Museum.

The importance of fossils in the NHM collections goes right back to Sloane's founding collection (MacLeod, 2006), but the first fossil hominins to come to the NHM were probably the Upper Palaeolithic *H. sapiens* remains from Bruniquel, which were purchased on behalf of the Museum by Richard Owen in 1864 (Owen, 1869). This was to be the beginning of a collection which has continued to expand into this century. Fossil hominins in the collection have been acquired in a variety of ways. Several of the NHM's most important hominin fossils (e.g., the Tabun Neanderthal remains, Skhul 9, and Forbes' Quarry) have come to the Museum from the RCS (Wood, 1979), whilst others were donations, such as the Broken Hill material, given to the NHM by the owners of the mine where it was discovered in 1921 (Woodward, 1921).

There have been successive descriptions of the hominin fossil collections at the NHM over their long history. For example, the 'Guide to the Department of Geology and Palaeontology in the British Museum (Natural History)', published by the Museum in 1890, described the display of fossil (or subfossil) human remains, including those from Kent's Cavern and Bruniquel (Woodward, 1890). A little later the Museum published a more specific pamphlet, 'A guide to the fossil remains of Man in the Department of Geology and Palaeontology in the British Museum (Natural History)', due to increased public interest in human fossils generated by the 'discovery' of the Piltdown remains (Woodward, 1922). At that time there were few actual hominin fossils in the NHM collections, but the Museum boasted a large collection of recent H. sapiens from all over the world, some of which was displayed divided into the racial typology typical of the time and detailed in a separate guide (Lydekker, 1908). The NHM specimens have also been covered by important international works on hominin fossils; the 'Catalogue des Hommes Fossiles' by Vallois and Movius (1953) was the first comprehensive account of the fossils known at that time. In the catalogue remains are divided by country and described by experts in each region. In the early 1970s, a team from the NHM set out to up-date the 'Catalogue des Hommes Fossiles'. Oakley et al. produced the 'Catalogue of Fossil Hominids' in three parts published 1967-1977 (I: Africa, II: Europe, III: Asia and the Americas, followed by a second African edition). Following Vallois and Movius' lead, for each fossil there is a summary of its discovery, anatomical description, geological deposit and stratigraphic information, age of the fossil, archaeological context, palaeontological context, bibliography, and institution holding the fossils. Again, each geographical section was compiled by an expert, or experts, working in that region. This is still the most comprehensive and wide-ranging account of fossil hominin remains available.

Although a global up-date of the 'Catalogue of Fossil Hominids' has not yet been attempted, smaller scale overviews of different groups of fossil hominins have been published (e.g., Wood, 1979; Stringer, 1990) and more comprehensive works (e.g., Schwartz and Tattersall, 2002a & b; Wood, 2011) have included coverage of many of the specimens. The intention of the current paper is to synthesise these earlier sources with accounts of new finds, up-dated chronologies and rediscovered treasures in order to illustrate the breadth and importance of the collection of fossil hominins at the NHM. We hope this synthesis can also pay homage to our colleague Andy Currant, who did so much to progress the curation of the NHM's fossil mammal collections during the last 40 years. Many of the mammals he curated are from the same sites as the fossil hominins discussed here.

2. THE FOSSILS

2.1. Africa

2.1.a. Broken Hill 1

The beautiful cranium Broken Hill 1 (BH1) was found in quarried deposits within a hill at Broken Hill, Northern Rhodesia (now Kabwe, Zambia) in 1921 by a team of lead miners supervised by Tom Zwigelaar (Woodward, 1921; Schwartz & Tattersall, 2002b; Wood, 2011). In 1921-5, more fragmentary hominin fossils (mainly postcrania) representing at least another two individuals were found at the site by Armstrong, Whittington, and Hrdlička (Schwartz & Tattersall, 2002b). The remains of extinct fauna and Middle Stone Age artefacts were also recovered (Wood, 2011).

The remains from Broken Hill are heavily mineralised (Oakley *et al.*, 1977), which probably accounts for their excellent preservation; the cranium is complete except for the part of right side of the neurocranium and cranial base (Schwartz & Tattersall, 2002b). BH1 is a robust specimen, presumed male due to its large face and browridges (Wood, 2011). The neurocranium is fairly long and low, the frontal bone is low and sloping, and there is considerable postorbital constriction posterior to the browridges, which are some of the largest of any known hominin. These are all primitive characteristics reminiscent of *H. erectus* (Rightmire, 2001). There is also, however, endocranial expansion in comparison with *H. erectus*, and the shape of the temporal, parietal and occipital bones, and the degree of basicranial flexion, are more similar to *H. sapiens* (Rightmire, 2001).

The BH1 cranium can be associated with a left tibia and, less certainly, a femoral diaphyseal fragment, but the other hominin remains cannot be provenanced (Stringer, 1986). There is a maxilla, which is smaller than that of BH1 and might be that of a female of the same species (Schwartz & Tattersall, 2002b). It is similar in morphology, but does show a canine fossa, unlike BH1 (Stringer, 2013) and somewhat resembles the early *H. sapiens* Ngaloba maxillae (Tanzania) (Stringer, 1986). The postcranial fragments comprise a distal right humerus, right innominate, left innominate, sacrum, left tibia, proximal right femur, proximal left femur, distal left femur and left femoral diaphysis (Oakley *et al.*, 1977; Stringer, 1986). The right innominate (probably also female) is of particular interest as it shows several features that distinguish it from australopithecine and also late Pleistocene pelvic morphology, which shows the antiquity of at least some of the postcrania. The tibia shows that BH1 would have been tall, about 180 cm, but more slightly built than reconstructions of

other *H. heidelbergensis*, such as Boxgrove; it is possible that this difference represents adaptation to different climates (Stringer, 2013).

BH1's maxillary dentition is nearly complete, but is very worn, and unusual for a human of this antiquity in showing severe caries and several abscesses (Montgomery *et al.*, 1994). There are also several temporal lesions, including a large, round hole on the external squamous temporal. This lesion cannot have a traumatic cause during life, as sometimes suggested (see Stringer, 2013), as it is sited over a major meningeal artery. Had the cranium been penetrated from the outside, the individual would not have lived long enough for the wound to develop the visible signs of healing. The lesion also has outwardly-everted margins, suggesting it was caused in life by an as yet uncertain pathology from inside the braincase (Montgomery *et al.*, 1994). The other lesions are most plausibly explained as post-mortem trauma.

BH1 was dated to approximately 700-300 ka using faunal analogies, correlation with palaeomagnetic records at other sites and sedimentation rates (Klein, 1973). A more recent review concurs, based on the fauna, that > 490 ka is most plausible (Millard, 2008). However, new dating is now underway using ESR on tooth enamel, and U series dating on various bones and sediment. The reliability of the new dates is complicated by the presence of water in the mine, which interferes with the ESR signal, but archaeological records and mineral accumulation suggest that the cranium derived from above the prevailing water level (Stringer, 2013). It is also impossible to compare U ratios with background radiation, as is usual practice, because no *in-situ* sediments are left at the site; however, some preserved sediment samples do exist and these are being used to calibrate the results from the fossils. So far, the U series and ESR results suggest that the cranium dates to 200-300 ka.

BH1 was the first important human fossil found in Africa (Stringer, 2013) and was initially designated as the holotype for a new species, '*Homo rhodesiensis*' (Woodward, 1921). The coining of a new genus for the fossil ('*Cynanthropus*'), by Pycraft (1928), who mistakenly reconstructed a stooping posture from the postcrania (Schwartz & Tattersall., 2002b), was swiftly abandoned and successive authors in the first part of the last century focused on the specimen's *H. erectus*, *H. sapiens* or supposed Neanderthal affinities (Oakley *et al.*, 1977). Having subsequently long been classified as 'archaic' *H. sapiens* (Schwartz & Tattersall, 2002b; Stringer, 1986), BH1 is now often diagnosed as *H. heidelbergensis*. The specimen is an important part of the Euro-African hypodigm for this taxon, due to its similarities to other Middle Pleistocene material, particularly the Petralona cranium from Greece (e.g., Friess, 2010; Rightmire, 2013; Stringer, 2012a; Stringer & Buck, 2014; Wood, 2011).

2.1.b. Kabua

In 1959 Thomas Whitworth found fossil human remains close to Kabua water hole (Turkana, Kenya). As a geologist, he contacted the regional palaeoanthropological experts, the Leakeys, for help and the fossil remains they subsequently excavated consist of cranial fragments from three individuals (K1, 2, and 3), and a loose molar found close to K1. Some postcranial remains were also found associated with K1, but unfortunately these disintegrated in transit and were disposed of on return to England (Whitworth, 1966).

Whitworth characterised the Kabua Lake beds as probably late Pleistocene based on dates from previous researchers (Whitworth, 1965a) and corroborated by the fossil mammal

remains and mollusc shells found *in situ* (Whitworth, 1960, 1965a, 1965b, 1966). Uranium and fluorine relative dating carried out by Kenneth Oakley appear, from correspondence in the NHM archives, to have been inconclusive. Whitworth (unpublished document in archives) also records that shells from a band situated about 15 m above the base of the Kabua lake beds were radiocarbon dated in 1967 by a New Jersey company; the age determined was 7108 ± 140 years BP. The result was unexpected given previous evidence, so the dating was repeated with a fresh sample, which yielded a maximum date of 7500 BP. This could make the hominins, found further up the sequence, as young as ~5500 BP. The remains are currently undergoing ESR and U series dating in an attempt to clarify the age of the fossils, with indications that K1, at least, is definitely of Pleistocene age.

K1 consists of most of a calvaria, a right hemimandible, a fragment of maxilla and two isolated molar teeth (Whitworth, 1966). The bones are distorted by the fossilization process, but the cranium appears long and narrow, with a sloping frontal and weakly developed supraorbital tori (Whitworth, 1966). The cranial bones are quite thick; the mandible is very robust, but seems to show a chin (Whitworth, 1960). K2 consists of part of a frontal including the upper margins of the orbits. The bone is much thinner than that of K1. K3 is a small parietal fragment. Some interesting bone artefacts and various lithics were also recovered from the site, but they were surface finds, and unlikely to have been of similar age to the hominin remains (Whitworth, 1965a).

2.1.c. Kanam

The hominin remains from Kanam were discovered in 1932 by a team led by Louis Leakey (Anon, 1933; Oakley *et al.*, 1977) in an erosion gully at Kanam West, near Lake Victoria. Kanam is close to the site of Kanjera, where late Pleistocene/early Holocene hominins were also found (see below) (Oakley *et al.*, 1977). Oldowan tools have been found in the Kanam beds, but these were not clearly associated with the mandible (Wood, 2011).

The Kanam remains consist of the anterior portion of a mandible. The inferior border of the mandible is broken and most of the teeth (with the exception of the two right premolars) are broken off at the roots (Leakey, 1935). The mandible is robust and thick both mediolaterally (this may be affected by the pathology mentioned below [Montagu, 1957]), and superoinferiorly (Leakey, 1935). A possible sarcoma is present on the posterior surface of the mandibular symphysis and although Leakey pronounced the specimen to have a "very pronounced mental eminence" (Leakey, 1935, 19.), later researchers have argued that the original morphology of the anterior symphysis is unknowable due to the pathology (Montagu, 1957; Wood, 2011). The mandible was originally inferred to be late Pliocene or Early Pleistocene, based on correlations with the Kanam beds, association with fossil mammals and relative mineralisation (Leakey, 1935). However, this dating was later contested by Boswell (Boswell, 1935, see Kanjera below). Leakey designated the Kanam mandible as the type specimen of a new species, '*H. kanamensis*', which he thought was very close to *H. sapiens*, and its probable direct ancestor (Leakey, 1935).

2.1.d. Kanjera

Kanjera consists of a series of fossil-bearing sediment outcrops in the foothills of the Homa Peninsula, Lake Victoria, in western Kenya. The site is split into northern and southern exposures, with the northern exposures the most excavated (Plummer & Potts, 1995). In addition to the hominin remains, the sites have yielded Acheulean artefacts and extinct fauna

(Oakley *et al.*, 1977). The hominins were discovered by a team led by Louis Leakey 1932-3 (Kanjera 1-5) and 1935 (part of Kanjera 3) (Leakey, 1935). Further fragments were collected in 1974, 1975, 1981 and 1987 (Plummer & Potts, 1995). Fragments of Kanjera 1, 2 and 4 were all found in close proximity to one another. Kanjera 1 and 4 were surface finds, whereas Kanjera 2 was found several inches into the sediment. Kanjera 3 was discovered *in situ*, buried about 60 feet away (Plummer & Potts, 1995). The elements known for Kanjera 1-7 are listed in Table 1, below.

Individual	Cranial elements	Axial elements	Appendicular elements	Condition
Kanjera 1	Frontal			Fragment
	Parietal			
				Very
	Occipital			fragmentary
Kanjera 2	Parietal			3 pieces, very fragmentary
		Rib		Partial
Kanjera 3	Frontal			8 pieces
	Parietal			Partial
			Phalanx	
				Very
	Occipital			fragmentary
			Femur	
Kanjera 4	Frontal			2 fragments
Kanjera 5			Femur	2 fragments

Table 1: Elements found for Kanjera 'individuals' 1-5 (Oakley et al., 1977).

Kanjera 6 and 7 were found at a slightly different site (several hundred metres away) by an expedition from Yale in 1974. These latter individuals (if any of the Kanjera individuals are indeed such) consist of 15 cranial fragments and two pieces of right innominate. Several (but not all) of the Kanjera individuals have long crania and quite thick cranial bones, but the latter may indicate anaemia, rather than indicating great age or primitive morphology, as was argued by Leakey (Plummer & Potts., 1995). The fragmentary postcranial remains indicate large body mass and high robusticity. The general morphology of the collected hominin remains is consistent with burials in Holocene shell midden sites at nearby Kanam East (possibly 4-8 ka; Plummer & Potts., 1995).

Leakey claimed the Kanjera hominins were of Middle Pleistocene age, based on fauna and artefacts. The apparent association of *H. sapiens* with Acheulean tools and extinct fauna contributed to Leakey's view that modern humans had a long, separate, lineage in East Africa extending back to the Lower-Middle Pleistocene (Wood, 2011). Leakey's assertion that the Kanjera hominins were Middle Pleistocene was subsequently contested by Boswell (1935), a geologist who visited the site with Leakey and claimed that the sediments had subsided and resulted in mixed remains. However, Boswell (1935) could not be sure he was examining the exact layers from which the human remains had originated. Boswell's claims led to great controversy and to criticism over Leakey's failure to properly document the discovery sites (Behrensmeyer *et al.*, 1995; Plummer & Potts, 1995). Later excavations led by the Smithsonian Museum in the 1980s failed to find evidence of the sediment slumping described by Boswell, and so rejected this explanation of the co-occurrence of the fauna and hominins (Behrensmeyer *et al.*, 1995). The date of the remains is currently still unclear, but Kanjera 3 is likely to be an intrusive, younger burial into a bed of Early Pleistocene age (Plummer & Potts, 1995). Radiocarbon dating suggests a latest Pleistocene to early Holocene date for the sediments where the other Kanjera hominin fossils were found, although the remains may be older (Plummer & Potts, 1995).

2.1.e. Laetoli canine

The famous Laetoli site in the southern Serengeti, Tanzania, is one of the most important sites for human evolution in the world. At Laetoli the Ngaloba beds, from which the Pleistocene early *H. sapiens* cranium LH18 derives (Day *et al.*, 1980), overlie the older, Pliocene Laetolil beds (Leakey *et al.*, 1976). It is also the site of the celebrated Laetoli footprints. Volcanic tuffs bracketing the fossil-bearing Pliocene beds are dated to 4.36-3.63 Ma (Deino, 2011). In addition to the NHM hominin canine, an extensive assemblage of nonhominin mammalian fauna and many other hominin fossils have been found from these beds (Leakey *et al.*, 1976). In 1935 Louis Leakey recovered a large assemblage of fossil fauna from the Laetolil beds and sent part of this, a collection of fossil monkeys, to what was then the BM(NH). The hominin canine was rediscovered in this collection and recognised as a hominin by Delson, Andrews, Stringer, and White (White, 1981).

The canine is a worn, permanent mandibular canine with damage to the cusp, and the distal part of the root missing. The specimen has been attributed to *Australopithecus afarensis* based on its shape and wear (White, 1981). The morphology of the crown suggests the presence of a canine/P₃ diastema as for other Pliocene hominins and its shape is generally primitive (White, 1981). The overall shape and inferred masticatory mechanics of the canine confirmed the primitive nature of *A. afarensis* canines, which show similarities with Miocene apes from Eurasia and extant *Pan* (White, 1981). Although not appreciated as such at the time, the tooth also represents the first australopithecine found after Dart created the genus, and the first australopithecine to be found in East Africa (White, 1981).

2.1.d. Singa

The Singa calvaria was discovered by Bond in 1924 at the base of the seasonally exposed bed of the Blue Nile, near the administrative post of Singa, eastern Sudan (Woodward, 1938; Schwartz & Tattersall, 2002b; Spoor *et al.*, 1998). The fossil is dated to a minimum age of 131-135 ka by U/Th mass spectrometry on sediments from the inside the calvaria and ESR analyses on associated faunal remains (McDermott *et al.*, 1996).

The Singa fossil is a calvaria lacking parts of the cranial base, zygomatic arches and the lateral orbital regions (see Figure 1). The occipital region is partly reconstructed (Stringer *et al.*, 1985a). The surface of the bone is very weathered and there is a large pit of uncertain origin on the right frontal (Schwartz & Tattersall, 2002b). The bone of the vault is thin, except in the regions of the parietal bosses, which may be pathological (see below). The braincase is relatively long anteroposteriorly, moderately tall superoinferiorly, and very broad mediolaterally across the parietal eminences, yet what remains of the face is fairly narrow mediolaterally. The frontal is fairly upright and the supraorbital tori are moderate, and do not extend anteriorly beyond glabella, yet there is fairly strong postorbital constriction. (Schwartz & Tattersall, 2002b).

Singa was initially thought by Smith Woodward (Woodward, 1938) to be ancestral to the Khoi-San of southern Africa due to its pronounced parietal bossing; however, it was subsequently noted this was probably due to pathological remodelling (see below) (Wood, 2011). There have been successive interpretations of Singa's place in human evolution, ranging from relating the anterior part of the calvaria to that of 'archaic' Africans such as Broken Hill, to determining it to be a 'Neanderthaloid' hybrid, to describing the specimen as a late Pleistocene, but non-modern, H. sapiens (Stringer, 1979). In the most thorough study to date, Stringer showed Singa to be closer in size and shape to earlier hominins than to recent H. sapiens, despite its relatively late date. The calvaria is similar to H. erectus in its short, low vault and broad cranial broad base, but it is broader across the parietals, has a less angulated occipital and more derived frontal morphology. It also has a greater endocranial capacity than H. erectus, bipartite supraorbital tori and thinner cranial vault (notwithstanding the parietal bosses). Singa is differentiated from recent H. sapiens by its low, robust temporal, broad supraorbital tori and robust interorbital region. Stringer concluded that the fossil was a late 'archaic' H. sapiens, closer to Jebel Irhoud and Omo 2 than to Broken Hill (Stringer, 1979). This opinion is echoed by McDermott et al. (1996), who concluded that the mosaic of primitive and derived features seen in Singa suggest it to be part of a highly variable late Pleistocene African population close to the origin of *H. sapiens*.

The Singa calvaria exhibits possible pathology on its parietals; the vault thickness is increased in conjunction with expanded diploe almost four times the width of the cortical bone (Stringer et al., 1985a). This morphology could be caused by a blood disease such as anaemia (compare Spoor et al., 1998; Stringer et al., 1985a). CT visualisation shows that the right temporal also lacks a bony labyrinth, a pathology not so far found in any other fossil hominin. Spoor et al. suggested pathological labyrinthine ossification following an infection of the labyrinth membrane. This may have been due to a blood-borne infection (such as septicaemia) or a blood disorder such as anaemia, which fits with some explanations for the parietal pathology (Spoor et al., 1998). Labyrinthine ossification can also occur if blood supply to the region is compromised. Singa has a wider internal auditory meatus on the right side, with possible evidence of a lesion which could have cut off blood supply to the labyrinth. Ossification could have taken at least a year, showing that Singa must have survived for a considerable period after infection or with the lesion disrupting blood flow. Ossification would have resulted in deafness, vertigo, involuntary uncontrolled movement of the eyes and ataxia; therefore, it is possible that the Singa individual would have needed care to survive as long as it did with these impairments (Spoor et al., 1998).

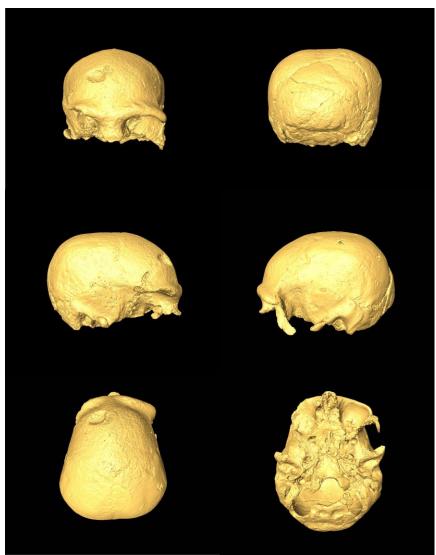


Figure 1: Singa (early *H. sapiens* from Sudan) From left to right, top to bottom, views of front, back, right, left, top, and bottom of calvaria. Image from virtual reconstruction of microCT data. Copyright: L. Buck, data: NHM.

2.2. Asia

2.2.a. Shukbah/el-Wad/Kebara/Skhul (Keith collection)

In 2001 a collection of human fossils from the Levant, which had belonged to Arthur Keith and was held at the RCS after his death, was transferred to the NHM to join other parts of the UK-based Mount Carmel collection. The collection was largely unlabelled and required thorough detective work, starting in 2011, by several researchers and curatorial staff at the NHM. This was complicated by the destruction during World War II of most of the original documentation on the Keith collection. The main provenance of the remains was established as Shukbah Cave; smaller numbers also came from el-Wad, Kebara and Skhul (De Groote *et al.*, 2014).

The Keith collection is significant because it includes individuals from the Natufian type-site as well as fragmentary Levantine Neanderthal remains. The Near Eastern Neanderthals are of particular interest due to their potential over-lap with *H. sapiens*

dispersing out of Africa; the Middle East is a key site for possible Neanderthal-*H. sapiens* interbreeding.

Shukbah

Shukbah Cave is in the valley of Wadi en-Natuf, near the village of Shukbah, near Jerusalem (Oakley *et al.*, 1975). The site was discovered by Père Mallon in 1924 and excavated by a team led by Dorothy Garrod beginning in 1928 (Garrod, 1928; Oakley *et al.*, 1975). The site is divided into strata from A to D. Level B of the site contained eleven human burials and what became known as Natufian archaeology; Shukbah is the type-site for the Epipalaeolithic Natufian culture (De Groote *et al.*, 2014). Lower down the sequence, level D contained Mousterian archaeology and human remains, some of which appeared to be intrusions from the Natufian layer, and some which appear to be coeval with the Mousterian lithics (De Groote *et al.*, 2014).

The *H. sapiens* remains from Shukbah include material from at least 45 individuals, males and females, neonates to elderly individuals (Keith, 1931). Of the numbered Natufian specimens in the NHM collections there are four partial adult skeletons, 26 adult partial crania/individuals represented by cranial fragments, nine adults represented by postcranial fragments, five adults represented by dental remains, six infant/juvenile partial skeletons, two juveniles represented by cranial fragments and four juveniles represented by postcranial fragments (De Groote *et al.*, 2014).

The remains from Shukbah level D (associated with Mousterian archaeology) consist of a molar (a right M_2), zygomatic fragment, fragment of temporal, hemi-mandible, femoral fragment, and talus, of which the latter three may be Natufian intrusions from level B. The temporal fragment, which preserves the auditory bulla, and the root of the juvenile zygomatic are probably Neanderthal (De Groote *et al.*, 2014).

El-Wad

El-Wad Cave is in the Wadi el-Mughara valley in the Mount Carmel range, near Haifa (De Groote *et al.*, 2014). The cave was first excavated by the Department of Antiquities of Palestine in 1928 and was subsequently investigated by Garrod 1929-33. The sediments at the site range from Middle Palaeolithic to Natufian. The remains now held in the NHM are listed below in Table 2.

El-Wad level	E	D	В	G
Industry	Upper Palaeolithic	Upper Palaeolithic	Natufian	Middle Palaeolithic
Skeletal elements	Isolated teeth	An atlas	Partial foot	right M ₂
	Cranial fragments	A mandibular corpus		
	Mandibular fragments	2 isolated teeth		
	Pedal fragments			
	A vertebra			
	A manual phalanx			
	A tibia			

Table 2: Skeletal elements from El-Wad in the NHM collections (De Groote et al. 2014).

Kebara

Kebara Cave is a site at the foot of Mount Carmel, just south of the Wadi el-Mughara. The site was excavated by Turville-Petre and Baynes under the auspices of Garrod, at the same time as she was excavating El-Wad (De Groote *et al.*, 2014). The sediments at Kebara range from recent (layer A) to Levalloiso-Mousterian (layer D) and encompass Bronze Age, Natufian, what Garrod called Kebaran, Upper Palaeolithic and Mousterian (De Groote *et al.*, 2014). The famous Kebara Neanderthal remains were later discovered at the same site by teams led by Stekelis, and Bar Yosef (Wood, 2011).

The Kebara (layer D) material now housed at the NHM consists of Upper Palaeolithic remains of both adults and children. There are five mandibular fragments, two distal left humeri and two proximal left ulnar fragments. One mandibular corpus represents a possible Natufian intrusion from an upper level (De Groote *et al.*, 2014). In addition to the material derived from Keith's collection, there are remains from a further individual from Kebara in the NHM collections. Kebara 10 (layer C) consists of a fragmentary adult humerus associated with Upper Palaeolithic archaeology (Oakley *et al.*, 1975).

Skhul

As discussed further below, Skhul is a site in the Wadi el-Mughara, Israel, from which the remains of at least ten individuals were excavated. Included in Keith's collection inherited by the NHM were bone fragments labelled as being associated with Skhul 7 and 9. However, it has not been possible to confirm this attribution for these fragments (De Groote *et al.*, 2014).

2.2.b. Skhul 9

Skhul 9 comes from the site of Mugharet es-Skhul (see above). The site comprises a small cave, and a larger external rock-shelter and terrace. Most of the archaeological and hominin remains come from the latter (Wood, 2011). Skhul 9 is part of a larger assemblage of human remains from the site, some of which are much more complete. The Skhul fossils were discovered by McCown in 1931-2 as part of a larger rescue dig in the Mount Carmel area directed by Garrod, which was instigated because the caves were being quarried for limestone to build the new harbour at Haifa (McCown, 1932; McCown & Keith, 1939; Wood, 1979, 2011; Schwartz & Tattersall, 2002b;).

There is evidence that some of the Skhul individuals were intentionally buried (Garrod & Bate, 1937), which explains their good preservation. Skhul 4 and 5 are the individuals best represented, with both cranial and postcranial material preserved (Schwartz & Tattersall, 2002b). Skhul 9, a purported elderly male, consists of a fragmentary calotte (see Figure 2) with some facial bones, fragments of pelvis, a femur and hand/foot bones, together with some scraps of vertebrae, ribs and a scapula (Oakley *et al.*, 1975). The supraorbital tori are continuous, rounded and merge with the preserved part of glabella. A long, shallow supratoral sulcus flows into an apparently sloping frontal. The preserved nasal margin suggests the nasal aperture was rather small (Schwartz & Tattersall, 2002b). The fossils were transported from Palestine to England, and Keith and McCown removed the Skhul (and Tabun) remains from their matrix at the RCS facilities. As with much of the rest of the material, the preparation and reconstruction of Skhul 9 may have worsened the already badly preserved detail of the morphology. The reconstructed regions have been coloured to match the original bone, which makes it difficult to distinguish between the two (Schwartz & Tattersall, 2002b). The material was divided between the Rockefeller Museum, Jerusalem,

Peabody Museum, Harvard, and the RCS. Skhul 9 later came to the NHM from the RCS (Wood, 1979).

In the first description of the Mount Carmel material, McCown and Keith recognised that Skhul had more *H. sapiens* affinities than Tabun. A possible ancestor-descendant relationship was originally hypothesised between the two, which were thought to form a single evolving population that they named '*Palaeoanthropus palestinensis*', showing features intermediate between Neanderthals and *H. sapiens* (McCown, 1933; Schwartz & Tattersall, 2002b). Skhul was at one stage believed to be only around 40 ka based on fauna and lithic similarities to Tabun (Wood, 2011). However, the Skhul material (Skhul 2, 5 and 9) is now dated to between 130 and 100 ka using ESR, U series, and thermoluminescence analyses (Grün *et al.*, 2005). It has even been argued that Skhul 9 may be older than the other two fossils, as suggested by its morphology and lower stratigraphic position (Grün *et al.*, 2005; Stringer, 1996). The new dating required a rethink in terms of Skhul's phylogenetic position, showing Neanderthals were chronologically later than some *H. sapiens* in the Levant, providing indirect support for a recent African origin for *H. sapiens*, rather than the regional evolution of *H. sapiens* from 'archaic' *Homo* including Neanderthals (Stringer & Buck, 2014).



Figure 2: Skhul 9 cranium (early *H. sapiens* from Israel). Front (left) and left (right) views. Copyright: NHM, London.

2.2.c. Tabun

The remains of Tabun C1 come from Mugharet et-Tabun Cave in the Wadi el-Mughara (Oakley *et al.*, 1975). The site is very close to Skhul in the southern part of the Mount Carmel range (Wood, 2011). Tabun was excavated from 1929-34 by the Joint Expedition of the British School of Archaeology in Jerusalem and the American School of Prehistoric Research, directed by Garrod (Garrod, 1932; Oakley *et al.*, 1975). Garrod defined several archaeological levels, with level C containing the majority of the hominin remains. In total the remains of up to 14 individuals were recovered, the most complete of which is the fragmentary skeleton, Tabun C1 (Wood, 2011), which is held at the NHM. The Tabun C1 skeleton is thought to represent a burial, largely because its elements were articulated (Schwartz & Tattersall, 2002b). Although Tabun C1 was excavated from level C, it may represent an intrusion from a subsequent layer, probably the over-lying level B (Grün & Stringer, 2000; Schwartz & Tattersall, 2002b; Wood, 2011). The latest U series and ESR

analyses support a date of ~122 ka, making it broadly contemporaneous with the remains from Skhul (Grün & Stringer, 2000). As with the Skhul material, Tabun C1 was formerly held at the RCS and was transferred to the NHM in 1955 (Oakley *et al.*, 1975).

Tabun C1 consists of a fragmentary cranium, a more complete mandible and dentition (missing the left M³), and a relatively complete post-cranial skeleton (Oakley *et al.*, 1975). The cranium lacks most of the face and the cranial vault has been extensively reconstructed from multiple fragments. When complete, the neurocranium would have been small, relatively long and low. A small suprainiac fossa is visible on the occipital and, from behind, the neurocranium has an "en bombe" shape (Schwartz & Tattersall, 2002b). The supraorbital tori are moderately large and the interorbital region is quite broad, as is the nasal aperture, from what is preserved. The mandible is lightly built and lacks a chin (Schwartz & Tattersall, 2002b). In their initial description, McCown and Keith (1939) combined the material from Skhul and Tabun as '*Palaeoanthropus palestinensis*' (see above). This species was conceived of as the last in a series of extinct hominids that "show a preponderance of Neanderthal characters." (p. 18). The Tabun remains have Neanderthal affinities not seen in the Skhul fossils and it is now generally agreed that Tabun C1 is a lightly built, adult female *H. neanderthalensis* (Schwartz & Tattersall, 2002b; Wood, 2011).

In addition to Tabun C1, seven isolated teeth from Tabun are held in the NHM collections, attributed to Tabun BC7 (Coppa *et al.*, 2005). These teeth were determined by ESR and U-series analyses of the enamel of one of the BC7 molars to derive from Tabun Layer B, and an age of ~90 ka was estimated (Coppa *et al.*, 2005). The teeth can be diagnosed as Neanderthal (Coppa *et al.*, 2005, 2007).

2.3. Europe

2.3.a. Boxgrove

The Boxgrove site is in Eartham Quarry, near Boxgrove village in southern England (Roberts *et al.*, 1994). In addition to the hominin remains, Boxgrove is famous for the discovery of large numbers of Acheulian bifaces (Stringer *et al.*, 1998). Excavations at Boxgrove began in 1982 in order to study Middle Pleistocene horizons at the site before they were destroyed by quarrying (Roberts *et al.*, 1994) and continued for more than a decade. A hominin tibia, Boxgrove 1, was found in 1993, followed by two isolated hominin incisors in 1995-6 (Hillson *et al.*, 2010). The tibia is dated to marine isotope stage (MIS) 13 (~534-478 ka) primarily by biostratigraphy (Roberts *et al.*, 1994; Wood, 2011).

Boxgrove 1 is an adult left tibia lacking both proximal and distal epiphyses. The tibial fragment is approximately 30 cm long and broken near the midshaft. Its morphology includes "a medially placed nutrient foramen, a well-marked soleal line and a particularly prominent vertical line" (Roberts *et al.* 1994, 311.). Using comparisons with Neanderthal tibiae, the Boxgrove specimen is estimated to have been longer than 355 mm when complete. The minimum cross-sectional dimensions of the bone approach the maximum for Neanderthals and body mass is estimated at well over 80 kg. This diaphyseal robusticity and the reconstructed body mass are consistent with adaptation to a cool climate (Stringer *et al.*, 1998). Boxgrove 2 is a permanent lower right central incisor and Boxgrove 3 is a permanent lower left lateral incisor (Hillson *et al.*, 2010). Both are thought to have come from the same adult, but from a different individual than Boxgrove 1. The teeth are substantially worn,

exposing secondary dentine deposition in the pulp cavity and extensive flint-induced scratches on the labial surfaces. Wear and calculus deposits on the labial side of the tooth roots shows that they were exposed through the alveolar bone in life, which may indicate damage to the gums or extreme dental loading on the anterior teeth (Hillson *et al.*, 2010).

The Boxgrove material is preliminarily attributed to *H. heidelbergensis* based on the age of the material, the pronounced robusticity of the tibia and the similarity of the tooth morphology to the Mauer specimen (Hillson *et al.*, 2010). However, the lack of comparative Middle Pleistocene postcranial fossils, apart from the slightly later Sima de los Huesos material (Carretero *et al.*, 2012), makes this somewhat tentative for the tibia (Stringer *et al.*, 1998). Despite the fragmentary nature of the specimen, the rarity of early Middle Pleistocene postcranial remains mean that this specimen makes an important contribution to the understanding of postcranial morphology in *H. heidelbergensis*. The wear on Boxgrove 2 and 3 is important for its behavioural implications in this taxon, suggesting paramasticatory behaviour (Hillson *et al.*, 2010), as also inferred for Neanderthals (e.g., Smith, 1976).

2.3.b. Bruniquel

Bruniquel les Forges is a cave high in the cliff wall of the Aveyron valley, near Montauban, France. Human remains, Magdalenian artefacts and extinct fauna were discovered under a layer of stalagmite during the 19th Century (Owen, 1869; Oakley *et al.*, 1971). The first fossils were found by Garrigou, Martin, and Trutat in 1863 (Garrigou *et al.*, 1863), and the remains of subsequent individuals were discovered by the owner of the cave, the Viscount de Lastic St. Jal, and Richard Owen in 1863-4 (de Lastic, 1867; Owen, 1869). The fragmentary human fossils are the remains of several modern *H. sapiens* individuals, and include both cranial and postcranial elements, from both adults and children (Owen, 1869; Oakley *et al.*, 1971). Some of the Bruniquel les Forges material was secured by Owen for the NHM, whilst some remain in France. A Magdalenian antler harpoon from the site has been radiocarbon dated to 11,750 \pm 300 years old (uncalibrated) (Barker *et al.*, 1969).

2.3.c. Devil's Tower (Gibraltar 2)

This Neanderthal child's partial cranium was found in Gibraltar in 1926 by a team led by Garrod (Garrod *et al.*, 1928). The Devil's Tower site is situated in a cleft in the North Face, not far east of Forbes' Quarry (see below). Also found at the site were faunal remains, late Mousterian archaeology and charcoal from ancient fires (Stringer, 2012c). The fossil was first described as a Neanderthal by Elliot Smith (Garrod *et al.*, 1928), an attribution that remains uncontested (Schwartz & Tattersall, 2002a). Unfortunately, it has not been possible to directly date the Devil's Tower fossils, but an age of *c*. 50 ka has been posited by extrapolation with similar archaeological context at the nearby Gorham's Cave (Oakley *et al.*, 1971). The NHM archives record that the Devil's Tower remains were "presented by the Trustees of the Percy Sladen Fund" in 1928 (pers. comm. R. Kruszynski, Anthropology curator). The Percy Sladen Memorial Fund is administered by the Linnean Society and this record likely refers to funds given to the Museum to purchase the fossil.

The specimen consists of parts of the upper and lower jaws (including teeth) and braincase of a Neanderthal child (Figure 4). When complete, the cranium would have been large (for the child's age), and low and oval in posterior view (Schwartz & Tattersall, 2002a); the frontal shows a very broad interorbital region and prominent glabella with the beginnings of brow ridges, which traits are characteristic of Neanderthals (Stringer *et al.*, 2000).

The remains were generally thought to be of a child of approximately five years old, but this conclusion was challenged in 1982 by Tillier, who suggested that the bones might represent two children, one aged about three years (the temporal bone) and the other about five (the rest of the bones) (Tillier, 1982). Using the then novel technique of counting perikymata on an incisor, it was possible to counter this suggestion by inferring that the Devil's Tower child was about four years old at death, and by comparing perikymata of children with known ages at death and their temporal bone morphology it was confirmed that the Devil's Tower remains belonged to a single individual (Dean *et al.*, 1986; Stringer *et al.*, 1990). A CT data-based virtual reconstruction of the cranium subsequently enabled mirroring of unilaterally missing elements and allowed the estimation of the soft tissue parameters, which supported this conclusion (Ponce de Leon & Zollikofer, 2000). There has been much debate over Neanderthal life history and the ontogeny of characteristic craniofacial traits; the accurate dental aging of the Devil's Tower child means that it is important in this discussion (Ponce de Leon & Zollikofer, 2001; Smith *et al.*, 2012).



Figure 3: The Devil's Tower (Gibraltar 2) Neanderthal child. Copyright: NHM.

2.3.d. Forbes' Quarry (Gibraltar 1)

The Neanderthal cranium from Forbes' Quarry was recovered from the North end of the rock of Gibraltar in 1848, probably by Captain Brome, the Governor of the military prison (Busk, 1864; Wood, 1979), and its discovery was first announced to the Gibraltar Scientific Society in March of that year (Busk, 1865). The fossil cranium was actually found before the type specimen from the Neander Valley (Feldhofer) in Germany (there was an even earlier Neanderthal discovery from Engis, but its distinctive characteristics were less pronounced due to its young age, and it was not appreciated for what it was until over a hundred years later). It is, therefore, only due to an accident of history that the species is called *Homo neanderthalensis* and not '*H. calpicus*', as suggested in a letter by Falconer in reference to the classical name for Gibraltar (Anon, 1937a; Stringer, 2012c). In 1862 Brome's fossil

collection from another Gibraltar cave came to England and this material led Busk and Falconer to travel to Gibraltar, where they saw the Neanderthal cranium and brought it back to Britain (Busk, 1864, 1865; Wood, 1979).

The cranium is well-preserved except for the left side of the neurocranium and the basicranium. Neanderthal features include the long, low cranial vault, occipital bun, suprainiac fossa, the rounded shape of the braincase when seen from behind, the high degree of mid-facial prognathism, lack of canine fossa, double-arched supraorbital tori and sloping frontal (Wood, 1979). Due to its size and relative gracility, Forbes' Quarry is usually judged to be female (Stringer, 2012c).

Unfortunately, the removal of the Pleistocene sediments at Forbes' Quarry has prevented the fossil from being accurately dated, but Middle Palaeolithic remains from more recent excavations at Vanguard's and Gorham's Caves on Gibraltar have been dated to >42 and >30 ka respectively (Bronk Ramsey *et al.*, 2002; Finlayson *et al.*, 2006; Stringer *et al.*, 2008). Unpublished luminescence studies from sediment attached to the cranium suggest the Forbes' Quarry specimen may date to about 50 ka.

The importance of the fossil was not appreciated at the time of its discovery, despite Busk (1864) pointing out its similarity to the Feldhofer specimen in 1864 (Wood, 1979; Stringer, 2012c). Busk also pointed out the value of the Gibraltar cranium in showing that the Feldhofer fossil could not be a single, pathological, anomaly, despite the opinions of many at the time (Stringer *et al.*, 2000). However, the specimen was not properly studied further until 1911, when it was described by Sir Arthur Keith (Keith, 1911). Forbes' Quarry was originally part of Flowers' collection at the RCS (Wood, 1979) and was transferred in the 1950s to the NHM (Kruszynski, 1978).

2.3.e. Genista Cave

Genista 1 is a single, deciduous, *H. sapiens*, unerupted molar (probably a left second lower molar) (Tim Compton, pers. comm, but see Oakley *et al.*, 1971). Genista cave is a large fissure in a cliff about 17 m above sea-level at the South end of Gibraltar. The tooth was discovered by prisoners working under the direction of Captain Brome (see above) in 1865 (Anon, 1937a; Oakley *et al.*, 1971). The cave is named after Captain Brome, Genista being the Latin for the brome plant (Duckworth, 1911; Anon, 1937b). A large collection of fossil fauna was also excavated from the fissure by Brome's team (Busk & Falconer, 1865).

2.3.f. Gough's Cave

Gough's Cave is a limestone cavern on the east side of Cheddar Gorge, in the Mendip Hills, Somerset (Davies, 1904). The cave has been developed as a tourist attraction (initially to showcase its impressive stalactites) since the late 1800s, leading to many ad-hoc finds, and in 1986-92 a more thorough excavation of one small region the cave was carried out by the University of Lancaster/NHM (Stringer, 2000). Also known as 'Cheddar Man', the famous Gough's Cave 1 was discovered by workmen working for Mr Gough, the owner of the cave, in 1903 (Davies, 1904; Seligman & Parsons, 1914). In addition to the various human remains, a great quantity of faunal remains and artefacts has been recovered from the site over the course of the excavations and "improvement works" (Stringer, 2000). Pleistocene occupation at Gough's Cave seems to span a relatively short period, up to about 200 years, beginning after ~14,700 cal BP. Gough's is one of the first sites to show human re-colonisation of South-west Britain after the Last Glacial Maximum (LGM) (Jacobi & Higham, 2009). The remains of at least nine individuals are present in three chronological groups. One child and two adolescents are later Holocene, one adult (GC1) is Mesolithic, and one child, two adolescents, and two adults are Magdalenian (Humphrey & Stringer, 2002). Originally housed in the Cheddar Cave Museum, most of the human material has since been transferred to the care of the NHM through the generosity of the Longleat Estate.

Gough's Cave 1

The GC1 skeleton, dated to 9230-8930 BP radiocarbon years (Stringer, 2000), is still the most complete ancient human skeleton from Britain. The cranium (Figure 5) is fairly complete, but has fragments of the basicranium, right cranial and orbital wall, left frontal/parietal, and left parietal/temporal missing (Humphrey & Stringer, 2002). The muscle attachments on the cranium are robust and the individual is thought to be male, yet other facial features such as the supraorbital region are comparatively gracile (Humphrey & Stringer, 2002), as is the postcranial skeleton. There is a lesion on the right supraorbital margin, which suggests a nonspecific infection resulting in osteomyelitis (Humphrey & Stringer, 2002). Six maxillary molars are present and these are worn, but the other maxillary dentition is missing; the mandible preserves all the teeth except the right premolars (Humphrey & Stringer, 2002). The GC1 skeleton also preserves a mandible, vertebrae, sacrum, ribs, clavicles, humeri, radii, ulnae, metacarpals, phalanges, femora, tibia, a talus, and a calcaneus all in a variable state of preservation (Oakley *et al.*, 1971; Churchill, 2001a; Trinkaus, 2001; Churchill & Holliday, 2002; Trinkaus, 2003).



Figure 4: Gough's Cave 1 skull (Mesolithic H. sapiens). Copyright: NHM.

Other Gough's Cave remains

GC2 is a late Pleistocene adult (possibly adolescent) calotte discovered in 1927-8 (Keith & Cooper, 1929). GC3 is the late Pleistocene calvaria of a child of approximately three years of age, which exhibits signs of both cribra orbitalia and cannibalism (Humphrey & Stringer, 2002). GC4 comprises four late Holocene unassociated cranial fragments, found in 1927-8, tentatively assigned to the same individual based on stratigraphic position and an inferred age-at-death of approximately 12-14 (Humphrey & Stringer, 2002). GC5 is a late Holocene mandibular fragment, GC6 is a late Pleistocene mandible found in 1928-9, and GC7 is a late Pleistocene fragment of an adult left parietal found by workmen in 1950 (Humphrey & Stringer, 2002). Many further fragments of human remains, both of the same and additional individuals, most dated to the late Pleistocene, were discovered in 1986-1992 (Currant *et al.*, 1989; Churchill, 2000, 2001b; Stringer, 2000; Trinkaus, 2000; Humphrey & Stringer, 2002; Hawkey, 2003).

The late Pleistocene (~14,700 cal BP) human remains from Gough's Cave are remarkable because they show extensive evidence of apparent cannibalism, including abundant cut-marks, percussion marks and peeling. Human postcranial fragments show the same butchery signature as fauna from the site and the two are often mixed together. This has led to the interpretation of nutritional cannibalism (Andrews & Fernández-Jalvo, 2003). In contrast to the treatment of the postcranial remains, Gough's Cave is also the site of the earliest known directly-dated human skull-cups (Bello *et al.*, 2011). The practice of creating vessels from human crania has been historically widespread according to ethnographic records, although archaeological examples are very rare. Analyses of cut and percussion marks show that the crania were painstakingly cleaned and skilfully shaped into vessels. This careful preparation of the crania is indicative of ritual, rather than nutritional cannibalism (Bello *et al.*, 2011).

2.3.g. Neschers

The NHM holds a left adult *H. sapiens* calcaneus from the site of Neschers in the Auvergne region, eastern France. Neschers is a Magdalenian site, dated to approximately 12.5 ka (Miallier *et al.*, 1994). The calcaneus was probably discovered by the Abbé Croizet (Oakley *et al.*, 1971), who excavated the cave between 1835 and 1842 (Bello *et al.*, 2013a), and it would have come to the BM(NH) in 1848 when the Abbé's collection was purchased (Bello *et al.*, 2013b).

2.3.h. Swanscombe 1

The partial calvaria from Swanscombe was discovered in Barnfield Pit, a gravel pit in the village of Swanscombe, Kent, UK (Marston, 1936, 1937; Ovey, 1964). The gravels are dated to about 400 ka (Stringer *et al.*, 1999; Schwartz & Tattersall, 2002a). Barnfield Pit was already known for its numerous Acheulian lithic finds (Conway *et al.*, 1996; Stringer & Hublin, 1999). Swanscombe 1 consists of three cranial bones (Figure 6); the occipital and left parietal fragments were found by Marston in 1935 and 1936, respectively, and the right parietal was found by B. and J. Wymer and Gibson in 1955 (Wymer, 1964). *Contra* Oakley *et al.* (1971), the calvaria is now thought to be that of a female, based mainly on its moderate muscle markings (Stringer, 1985b; Schwartz & Tattersall, 2002a), and a fairly young adult due to the patency of the sutures (Stringer, 1985b).

The parietal bones are short, flat and relatively thick (Weiner & Campbell, 1964; Stringer, 1974). A broad, shallow suprainiac fossa is visible on the occipital and the foramen magnum is oval in shape (Schwartz & Tattersall, 2002a). It is inferred that, when complete, the neurocranium was low and relatively broad across the base (Stringer, 1974). The internal surface of the bones is less weathered than the external. Because of this better preservation, the blood vessels and imprint of the brain are clearly visible; no obvious differences to *H. sapiens* brain organisation can be determined (Stringer, 2006).

The Swanscombe fossil's affinities with H. sapiens, such as its estimated large brain size, were emphasised when it was first described and it was placed in various positions as a H. sapiens ancestor by different authors (Schwartz & Tattersall, 2002a). These H. sapiens-like characteristics are now thought to be largely primitive retentions from a shared ancestor (Stringer & Hublin, 1999). Over time, attention has instead turned to the Neanderthal characteristics of the fossil, particularly in its occipital morphology. The occipital bone shows a suprainiac fossa, a possible Neanderthal apomorphy (Stringer et al., 1984), and what remains of the basicranial morphology is Neanderthal-like (Stringer & Hublin, 1999) while the parietal bones are rather primitive (Stringer & Hublin, 1999). In its combination of Neanderthal and more primitive features, Swanscombe resembles several other European fossils. Its similarity to the Steinheim cranium (Germany) has long been noted (Wolpoff, 1980; Stringer, 1985b; Schwartz & Tattersall., 2002a; Wood, 2011), and it is also analogous in some regards to the cranial material from Sima de los Huesos, Atapuerca (Spain) (Stringer, 2012a), Reilingen (Germany) (Dean et al., 1998), and Saccopastore 1 (Italy) (Stringer, 1974). Both Steinheim and Sima de los Huesos fossils have been attributed H. heidelbergensis (e.g., Bermudez de Castro et al., 2004; Friess, 2010; Harvati et al., 2010) or described as an early H. neanderthalensis (Rightmire, 1998; Tattersall, 2007; Stringer, 2012a). Saccopastore and Reilingen are generally agreed to be early Neanderthals (Dean et al., 1998; Bruner & Manzi, 2006). In combination with similar fossils such as those mentioned above, Swanscombe may support the concept of a slow, non-linear, accretion of Neanderthal characteristics over time and space (Stringer, 1985a; Stringer & Hublin, 1999; Hublin, 2007).



Figure 5: Swanscombe 1 early *H. neanderthalensis* partial calvaria. From left to right: back, right and top views. Copyright: NHM.

3. CONCLUSION

The hominin fossils at the NHM form a collection of great importance, both in terms of their research value and for the history of science. Several specimens are associated with individuals who played key roles in the development of palaeoanthropology over the last two centuries. Some, such as Arthur Smith Woodward (former keeper of Geology), fossil fish

expert, Piltdown fraud suspect, and first person to describe Broken Hill and Singa (Woodward, 1921, 1938;), and Kenneth Oakley (former Head of the sub-Department of Anthropology), who is known for his innovative dating methods (now largely superseded) and work in helping to expose the Piltdown fraud, were employed at the NHM. Others, such as Dorothy Garrod, the celebrated archaeologist who discovered many iconic hominin fossils from the Near East (Bar-Yosef & Callander, 2006) and Arthur Keith, expert anatomist, Conservator at the Hunterian Museum and President of the Royal Anthropological Institute, collected and/or described key fossils in the collections, but all contributed significantly to the way in which we think about human evolution today.

The display of hominin fossil material at the NHM has also changed over the years, reflecting shifting priorities. Not only do texts explaining the material and the reconstructions of specimens/species change with improvements in understanding and shifting opinion in the field, but in recent years there has been a new emphasis on showing original fossils to the public and a move away from the use of casts in galleries. Currently, Forbes' Quarry and BH1 rotate on display in the 'Treasures' gallery. This reflects the increased importance placed by the Museum, as a partially publicly-funded institution, on being public visitor-orientated.

Parallel to its new role in the public galleries, the material housed at the NHM is still under regular study by both internal and external researchers. The Broken Hill and Kabua material, for example, is currently being re-dated using U series and ESR methods. The continuous study by generations of researchers has, in some cases, changed our thinking on individual specimens over the years. The Langwith Bassett (Oakley, *et al.*, 1971) and Tornewton (Stringer & Powers, 1978) material, once thought to be Pleistocene *H. sapiens*, are now known to be Iron Age (Hedges *et al.*, 1991) and Neolithic (Hedges *et al.*, 1997), respectively. The infamous Piltdown fraud (Weiner & Stringer, 2003; Stringer, 2012b) was also eventually exposed publicly as a fake in 1953 after the material was studied by researchers at the NHM and University of Oxford. This latter material is currently being reanalysed using the latest technology and methods, including ancient DNA retrieval techniques, geometric morphometric analyses, microCT scanning, rare earth analysis, isotope analysis and XRF, in an attempt to finally discover who committed the deception and why.

The NHM hominin fossil collection continues to be important in the broader scope of palaeoanthropological research, which uses the latest methods to address some of the most debated topics in the field. For example, several specimens, including the Gough's Cave material, are currently undergoing ancient DNA testing. It is hoped this will add to our understanding of how the first people to repopulate Britain after the LGM relate to current populations. New technologies at the Museum also enable further light to be shed on long-standing puzzles. For example, the Museum's microCT scanner has enabled the virtual segmentation and 3D shape analysis of fossils to study the controversial relationship between pneumatisation, morphology and ecology in different taxa (Buck *et al.*, 2012), and analyses of the enamel dentine junction morphology as part of the continuing work on the Piltdown dental remains has been informative in determining the species used to make up the fake (Stringer *et al.*, research in progress). These studies and many others, in combination with recent new housing for the fossil material and improvements in documentation, continue to fulfil the NHM's mission statement (BM(NH), 1977).

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