Skull and long bones – Forensic DNA techniques for historic shipwreck human remains

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Human remains in marine environments are subject to unique decomposition processes, faunal predation and other impacts on DNA. Over time, the structure of bone and its DNA is further impacted in submerged remains. Advances in technology and in the field of forensic biology have increased the options for genotyping compromised human skeletal samples. Specialist forensic DNA techniques, often adapted from ancient and archaeological DNA methods, are designed to maximise DNA recovery. A vast array of new genetic markers can now be targeted for interrogation to reveal externally visible characteristics, biogeographical ancestry or extended genetic relatives of victims. These DNA profiling techniques offer new tools in addition to traditional comparison with ante mortem samples, or close relatives. This paper reviews the current and emerging tools available for recovering and revealing genetic information from historic shipwreck remains.

Keywords: Skeletal remains, unidentified human remains, compromised samples, emerging DNA technologies, maritime archaeology

Introduction

Historically, shipwreck has occurred as a result of battle or severe storms, often resulting in the death of significant numbers of crew. Human remains are often found at these shipwreck sites (see Guareschi et al. [1] for a review) and DNA testing has been carried out on these remains with infamous examples including Henry VIII's Tudor Warship, *Mary Rose* [2]; the Dutch East India Company's flagship, the *Batavia*, associated with mutiny and mass murder [3]; the Unknown Sailor from *HMAS Sydney II* [4]; pirate Sam Bellamy's ship, the *Whydah Gally* [5]; the ancient Greek ship, *Antikythera* [6] and the *HMS Erebus* and *HMS Terror*, abandoned during the Franklin Northwest Passage expedition [7, 8]. The challenges associated with the collection, testing and DNA analysis of remains recovered from historic shipwrecks include age, environmental

insult, immersion and marine animal predation. Additional considerations around access to museum specimens also exist.

The UNESCO Convention on Underwater Cultural Heritage (2001) provides rules and governing criteria for the protection of Underwater Cultural Heritage (UCH), prioritising *in situ* preservation. World War (WW) I and WWII wrecks (including aircraft) are considered war graves by most participant countries. Where access is required, the prior removal and burial of human remains is necessary [9]. The first legislation in the world to protect UCH was written in 1964 in an amendment to the *Australian Museum Act 1959* (and then 1969). The *Maritime Archaeology Act 1973* later guaranteed the automatic protection of sites in Western Australia once they became 75 years old. The *Underwater Cultural Heritage Act 2018* extended protection to human remains in Australia.

Archaeological testing methods including radiocarbon dating [10] and organic residue analysis [11] have been applied to artefacts recovered from shipwrecks. A number of forensic techniques have also been used including craniofacial reconstruction, species identity testing and DNA profiling. For example, craniofacial reconstruction has been applied to victims of the *Vasa* [12], and HMS *Erebus* and *HMS Terror* [7, 8], and faunal remains recovered from *Mary Rose* were subject to species identity testing [2, 13-15]. While DNA has been recovered from remains associated with numerous shipwrecks (see Table 1), successful DNA-based identifications have also been reported in the case of the *HMAS Sydney II* [4] and Franklin Northwest Passage expedition vessels [7].

The age of historic shipwreck remains has usually meant that comparison to distant relatives is the only viable avenue for a DNA-based identification [4, 5]. However, the advent of massively parallel sequencing (MPS) technology has enabled emerging forensic DNA techniques such as biogeographical ancestry (BGA), externally visible

Table 1. Forensic DNA techniques applied to various historic shipwreck remains

Wreck	Date	Location	Recovery	Remains recovered	Forensic DNA analyses					References
					Species	STR	Y-DNA	mtDNA	FDP	
Antikythera	2000 BC	Antikythera, Greece	2016	Complete skeleton	Ongoing					Marchant, 2016[6]
Mary Rose	1545	Portsmouth, English Channel	1970s	Numerous skeletons (179 below deck alone)	✓					Hagelberg et al., 1989[13]; Hagelberg & Clegg, 1991[2]; Zouganelis et al., 2014[14]; Hutchinson et al., 2015[15]
Vasa	1628	Outside Stockholm Harbour, Baltic Sea	1961	Skeletons of crew and their wives. 25 individuals alone were located under the seabed mud				✓		Simonds, 2017[12]
La Belle	1686	Matagorda Bay, Gulf of Mexico	1996	Skeletons – buried in the seabed beneath sand and mud		✓	✓	✓	✓	Ambers et al., 2020[16]
HMS Swift	1770	South Atlantic Ocean	1998	One skeleton located in Captain's cabin covered by compact sediment	DNA testing unsuccessful					Maier et al., 2010[17]
Whydah Gally	1717	Cape Cod, United States	1984, 2021	One complete and five partial skeletons found in large concretions		?*	?*	?*		Boston Globe, 2018[5]; New York Post, 2018[18]
HMS Pandora	1791	Great Barrier Reef, Australia	1977, 1986, 1995-1998	Three sets of remains - >200 human bones and bone fragments		✓				Hughes-Stamm, 2013[19]
Batavia	1629	Abrolhos Islands and Beacon Island, Australia	1960-1964, 1994, 2001	10 skeletons found buried on Beacon Island in single and multiple burial graves		✓	✓			Yahya, 2008[3]
HMAS Sydney II	1941	Off coast of Carnarvon, Western Australia	1942 then 2006-2008	Unknown Sailor – body recovered in raft and buried on Christmas Island (later reburied)				✓		Australian Government: Defence, 2021[4]

Species = species determination; STR = short tandem repeat; Y-DNA = Y-chromosome DNA; mtDNA = mitochondrial DNA; FDP = forensic DNA phenotyping.
*DNA recovered from a femur sample was reported to originate from a male individual 'with general ties to the Eastern Mediterranean'. Comparison with known relatives suggest the individual was not Captain Samuel Bellamy [18].

characteristics (EVC) and whole mitochondrial genome (mtGenome) sequencing to be applied to shipwreck remains [16]. Such DNA profiling techniques mean that identification does not rely strictly on comparison with ante mortem data and investigators can be directed towards potential decedents, or relatives for comparison [20]. This paper reviews the current and emerging tools available for recovering and revealing genetic information from historic shipwreck remains.

Environmental exposure and impact on decomposition

Survivors of the *Batavia* shipwreck faced mutiny followed by mass killings with victims buried in mass graves on a nearby island. Relevant to these remains, in ancient bone and teeth specimens, a number of factors including temperature, humidity, pH, geochemical properties of the soil, the amount of postmortal organic substances and the general degree of microbial infestation in the soil can affect the chances of successfully amplifying DNA [21]. Bones and teeth reach a chemical equilibrium with the depositional environment via mineral leaching and the uptake of different solutes from the soil [22]. This can lead to bone degradation and chemical changes of the hydroxyapatite which can in turn affect the rate and degree of DNA degradation [22]. However, human decomposition in marine environments has been shown to be distinctively different from surface and subsurface decomposition. Environmental exposure is subject to its own unique factors such as decomposition processes, faunal predation and impact on DNA [23].

Decomposition in seawater

Due to the cooler temperatures and absence of necrophagous insects, decomposition generally progresses slower in water than on land [24-26]. Furthermore, decomposition in the marine environment proceeds slower than in fresh water as fresh water is absorbed

into the circulatory system causing organs to swell and rupture, whereas in salt water fluids are drawn out of the blood (by osmotic pressure) while bacterial activity is slowed due to the high salinity [27]. Likewise, submersion in salt water is thought to slow DNA degradation by reducing the levels of microbial activity [22].

The anaerobic nature of decomposition may result in adipocere which results from incomplete transformation of lipids by bacteria [28]. Adipocere formation has been studied in a variety of submerged remains contexts [28-31] and can persist over a long period of time (i.e., hundreds of years), depending on the bacterial activity of the surrounding environment [32-34].

Complete skeletonisation has been shown to occur in marine environments within three weeks [35]. Disarticulation usually occurs at major joints first, from distal to proximal, i.e., from wrist to elbow and then shoulder at the upper limbs, and from ankle to the knee in the lower limbs. The mandible disarticulates around the same time as the hands while the cranium is lost at a similar time to the forearms [36]. This sequence can be altered by the presence of clothing which has been reported to preserve soft tissue and inhibit disarticulation [26, 37], particularly in tight and heavy clothing such as boots [35, 38]. Where remains float, current and wave action weaken the soft tissue connection of the joints further contributing to disarticulation [36].

Alteration of bone in marine environments

Following skeletonisation, submerged bones are subject to four diagenetic processes: 1) bioerosion, the removal of bone by living organisms, 2) abrasion due to water, sand and sediment, 3) encrustation by sessile invertebrates and 4) dissolution of calcium carbonate [39] (for a detailed review, see Guareschi et al. [1]). These four processes can lead to fragmentation and the complete consumption of bone by the marine environment [40]. Microscopically, post mortem (PM) change in bone begins within three months with

sites of focal demineralisation on bone fragments [41] while changes such as peripheral tunnelling around the neck of a tooth occur after almost 400 years of marine submersion [42]. Fossilisation of bone can also occur [43], transforming bone into a more stable material [44] over several hundreds of years and lasting for thousands, and even millions, of years [45].

Alterations of bones submerged in saltwater can also include secondary concretions which can encompass adjacent bones, as well as bleaching and staining [46]. Whole and fragmented bone have been shown to display soft tissue adherence, exposed surfaces with brittle textures, adipocere formation from soft tissue fragments, battering and rounding of sharp edges, windowing, bleaching, mineral staining and the presence of adherent sediments or animal taxa [40]. Remains recovered from *HMS Pandora* displayed macroscopic bone features such as scavenger teeth markings, surface scratching, smoothing of sharp edges and exposure of cancellous bone [47].

Bones are rapidly covered by silt so they can also exhibit black discolorations on both the skeletal elements and surrounding silt [48]. Furthermore, differential preservation has been observed with remains in contact with sediment mostly skeletonised and remains suspended in debris virtually still intact [37]. The shipwreck itself can contribute to the preservation of human remains [47, 49]; including the solid structures of the wrecks or burial in sand, mud or sediment [1].

Marine predation

In the marine environment, remains are exposed to numerous forms of animal predation including scavenging on human corpses [50], both of which may cause external defects that mimic injuries [28]. Victims found drifting on the surface are reported to display large shark bites [51] and shark feeding patterns are well documented [52-59]. Shark attacks have also been postulated in archaeological remains (3000 years old) as a result of

characteristic damage to the bone including punctures, cuts and blunt force fractures [60]. Arthropods such as crabs, crawfish, sea lice and bivalve molluscs are responsible for smaller bites and damage [50 24, 36, 48, 61-64] including profound examples of sea lice [65]. Remains that sink have been shown to experience more severe scavenging and skeletonisation than those floating [66]. Remains at depth (i.e., 300 m) are predated upon by *lysianassid* amphipods which consume the internal organs then the skin and have been shown to completely skeletonise remains within four days [48]. Remains on the sea bed can exhibit circular lesions attributed to scavenging by cookiecutter sharks (*Isistius*) [50, 51, 67]. Amphipods and squat lobsters (*Galatheae*) gnaw on bone epiphyses and leave bone lesions on cancellous bone as well as the external table of the crania [26]. Bryozoa and Annelida taxa have been reported to encrust bone and rock-boring sponge can penetrate the bone matrix, disintegrating bone tissue. Filling of the medullary cavities of long bones with sand and reef debris and surface staining by oxidation of metallic alloys containing copper, zinc, iron, and lead has also been observed [47].

Bone as a source of DNA

DNA can be recovered from a range of biological sources, however; some sources are more ideal for the purposes of DNA-based identification. Factors such as resistance of the source to degradation or damage due to its natural structure can also affect DNA recovery [20]. These factors make bone a good target for recovering DNA, particularly from compromised remains.

DNA in bone

DNA is well preserved in bone cells and teeth [68], making them reliable sources of DNA, particularly in adverse environmental conditions and for long-term sampling [69, 70]. Current recommendations suggest the collection of bone is most appropriate for

compromised remains due to a higher success rate of DNA recovery from femur shafts and teeth [68, 69, 71-74]. This is due to the DNA being protected by the physical and chemical structure of compact bone within the calcium (Ca^{2+}) matrix [72]. Different skeletal elements have been found to vary in the way they preserve DNA and therefore, yield different amounts of DNA [68, 75] (see Watherston et al. [20] for a detailed review).

Optimal skeletal elements for DNA

There is no real consensus in the literature as to which bones yield the most DNA except perhaps that load bearing bones may be higher yielding because of bone remodelling. Weight bearing bones such as femur, tibia, pelvis, metatarsal and talus have traditionally been identified as some of the most suitable skeletal elements for sample collection [75]. While spongy and cancellous bone can be rich in DNA, preservation is not reliable and dense cortical bone is collected preferentially [69]. There is other evidence that optimal DNA recovery is obtained from the petrous portion of the temporal bone where the cranium is available [76, 77]. There is also research which indicates that small cancellous bones yield more DNA and short tandem repeat (STR) loci than cortical bones at increasing post mortem intervals [78]. On average, the small cancellous bones have much higher concentrations of DNA per unit mass than dense cortical bones such as femur [78]. High load bearing bones, particularly the bones of the feet, have been reported to be a preferable source of DNA in submersion cases [79]. Fredericks et al. [79] analysed remains of individuals submerged in sea water for 2 and 4 years and reported successful DNA amplification was dependent on the skeletal element and duration of submersion. The authors also report higher allelic dropout in low load bearing bones, noting the highest success from foot bones.

Teeth with the largest pulp volume provide the best source of DNA [80, 81] however, pulp may be limited or even absent in aged and/or diseased teeth [82]. Tooth

type together with health and chronological age of the donor will have an effect on the relative proportions of DNA present in the tooth [82]. In general, teeth with the largest root surface area (i.e. molars) should be targeted [82]. The unique composition of teeth and their location in the jawbone provide additional protection from environmental and physical conditions that accelerate PM decomposition and DNA decay [83, 84].

Challenges associated with DNA testing of bone

Polymerase chain reaction (PCR) is required to amplify DNA recovered from bones to detectable levels. PCR inhibitors in bone have been routinely reported [85, 86] with skeletal samples naturally containing calcium which inhibits *Taq* DNA polymerase (the DNA copying enzyme) by preventing its interaction with magnesium ions during the PCR [87, 88]. Some other PCR inhibitors include chondroitin sulphate chains in skeletal material [89], humic compounds in soil [90] and heavy metals such as iron, copper, cadmium and lead found with bone samples from mass graves [91]. PCR inhibition from bone exposed to water and/or soil is thought to be due to the presence of humic and fulvic acids, tannins, iron, cobalt and other materials that can enter the bone after long periods of exposure [90, 92-94]. PCR inhibition is the most common cause of PCR failure when sufficient DNA is recovered [95]. Using quantitative PCR to identify the presence of inhibitors and to inform the most appropriate method for their removal is important to avoid further depleting the amount of DNA [96]. Ethylenediaminetetraacetic acid (EDTA), used to dissolve the bone mineral matrix for DNA extraction, is also problematic as EDTA itself is an inhibitor [97].

Cytosine deamination is another major challenge associated with older bones and refers to one of the four DNA base pairs (cytosine) changing to another (thymine) via an intermediary (uracil) [98-100]. Deamination may not interfere with DNA analyses that rely on the length detection of PCR amplicons (as is the case with forensic STR

analysis) but high levels of deamination may interfere with sequence-based detection and ultimately, with primer binding, potentially leading to allelic dropout [99, 101].

Strand cleavage (DNA degradation) is another type of DNA damage resulting in shorter DNA fragments [98, 101, 102] which is problematic when they become smaller than the PCR amplicons required for STR profiling. DNA cleavage can be caused by endogenous or exogenous nucleases, acid hydrolysis or oxidation reactions.

Excavation and collection

Due to their ultra-structural organisation, sample permeability [103] and porosity [104], bones and teeth are easily contaminated prior to DNA testing [104-108] and aged bones are highly vulnerable to contamination from modern sources [109]. Porosity facilitates deep penetration by contaminants which makes bones particularly prone to water-borne sources of contaminant DNA [103]. Human teeth are less porous, seal their roots with age [110] and have an upper surface protected by impermeable enamel which makes them slightly less susceptible to contamination [103]. It has been reported that samples are most susceptible to contamination just after excavation when they are still damp from the burial environment [103]. This means foreign contaminant DNA usually originates from individuals who were involved in the initial washing and cleaning of bone rather than from those who collected the samples [111]. Contamination from comingled remains is another consideration [68].

Minimising the risk of contamination prior to DNA testing is crucial and this is best achieved by the use of personal protective equipment (PPE), clean sampling areas, use of clean instruments and the appropriate storage of collected samples [112]. Contamination can also be minimised by extracting material from the interior of a sample [113]. Elimination samples from personnel who handle the remains can assist to identify possible contamination events [114].

Storage

Bone sample is routinely stored at -20 ˚C for long terms [115]. Storage at higher temperatures has been shown to reduce the amount and reproducibility of DNA amplifications in ancient specimens [21] and long-term storage of bone powder has been reported to promote DNA degradation due to an increased exposed surface area and subsequent oxidative damage of DNA [116]. However, other authors have shown this to be negligible over a 10-year storage period at -20 °C and highlight the value of retaining surplus bone powder after extraction for application to future technologies [117].

During transport and storage, samples should not be exposed to conditions of elevated heat or humidity to the most practical extent possible [75]. Samples should also be completely dried prior to packaging and breathable packaging such as paper bags should be used. Wet samples placed in plastic sample bags encourages mould and bacterial growth [75]. Dryness, low temperature and the absence of microorganisms favours the preservation of DNA [21].

Sampling and preparation

Advances in biomolecular research means museums are now faced with the curatorial dilemma of conserving materials and evaluating them when new analytical methods become available [118]. Where proposals are received that involve destructive sampling, a committee is ultimately required to weigh up a gain in scientific knowledge against the loss of priceless and irreplaceable material [118]. Because different techniques, including those outside of molecular biological testing, yield very different information, it should be clear what scientific knowledge is gained from testing and if this adds information that can advance the overall knowledge around the artifacts pertaining to an historical event.

Healthy teeth (preferably molars) are primarily targeted, though in their absence, any available bones will suffice; preferably ~10 g of cortical bone with dense tissue is recommended [119]. While 5-15 g has been reported to be optimal, smaller samples of bone down to 4 g (and exceptionally less than 1 g) can still yield informative DNA results [75]. Preferred teeth and sample locations across various skeletal elements have been reported [75]. In general, areas of the bone that display damage or discoloration should be avoided as they may have resulted in DNA degradation within the bone [75]. When sampling long, compact bones such as femur, current guidelines suggest the collection of a 4-6 cm window section without shaft separation [69].

Determining the appropriate order in which to apply techniques should be defined prior to any testing and understanding the implications for the sample of the different techniques is crucial in preserving sample integrity. Any non-destructive examination by anthropologists, odontologists and/or pathologists should be carried out prior to DNA testing [120]. Because they are typically less destructive of samples, other techniques such as radiocarbon dating, organic residue analysis and any other archaeological examinations are also likely to require application prior to DNA testing.

Decontamination

Prior to DNA testing, chemical and physical decontamination procedures can be applied to bone to remove exogenous DNA [20]. Laboratories use a variety of techniques to clean the exterior surface of skeletal remains such as the complete removal of the exterior of the bone [121-124], washing using a diluted bleach solution [113, 125], acid washing [126-128] and ultra-violet (UV) irradiation [21, 129]. While sodium hypochlorite is highly efficient (up to 99%) at contaminant removal [130], it may damage endogenous DNA as well as contaminating DNA such that the latter cannot be distinguished from poor quality and/or quantity endogenous DNA[130]. A combination of cleaning by wiping with 10%

bleach, sterile water and 70% ethanol, followed by at least 12 hours of drying in a fume hood has also been reported [78]. In general, physical and chemical cleaning followed by UV irradiation has been recommended as the best way to decontaminate bone prior to powdering in a freezer mill, commercial blender or drill [120, 131].

For archaeological remains, Ambers et al [16] also report the need to utilise standard contamination prevention measures for archaeological and ancient DNA specimens. These include the use of PPE; bleach and UV-irradiation decontamination; physical and/or chemical treatment of bone surfaces; extraction of bone samples in designated low yield areas; PCR amplification in a physically separated area; use of appropriate negative and positive controls, reagent blanks; and replicate testing [103, 113, 132-135].

Minimally-invasive sampling

More recently, skeletal elements such as the petrous portion of the temporal bone [76, 77, 136] have been shown to provide optimal DNA recovery, but sample collection often involves destructive sampling. This is often not appropriate for historical remains and/or museum specimens because the petrous bone is also useful for other analyses. Austin et al [118] highlight its value in stable isotope analysis as a supplement or proxy for teeth in reconstructing diet during early life [137], important morphological signals of population histories [138] and morphological information regarding sex and childhood disease [139].

Minimally-invasive, or in-field, approaches to sampling could offer an alternative solution for successfully recovering DNA. Successful DNA recovery from the small cancellous bones has been demonstrated [78] and other studies have since shown their viability for DNA-based identification offering a less invasive alternative to the femur and petrous bone [140, 141]. While metacarpals and metatarsals (epiphyses) have been reported to outperform all other bones in DNA yield from WWII victims [142, 143],

the 1st distal phalanx of the hand has been reported to contain the highest DNA across 70 fresh and 22 casework bones [144]. The small cancellous bones of the feet have also been shown to outperform other bones in terms of DNA yield and STR profile completeness in buried remains [145]. Minimally-invasive methods for other PM sample types have been described with a method reported for sampling the petrous bones from the cranial base [146]. The value of small cancellous bones and the generation of bone drillings from the femur has also been demonstrated in combination with efficient DNA protocols [141, 147].

DNA profiling

DNA extraction

Demineralisation is a DNA extraction protocol for bones and teeth involving the use of an EDTA-based buffer to dissolve the bone mineral matrix and inactivate DNAses by chelating bivalent cations such as Mg^{2+} or Ca^{2+} [148, 149]. The ratio of bone powder to EDTA is important for optimum digestion and 1 g of bone powder should be demineralised in 15 mL of 0.5M EDTA [150]. In most cases 5-6 hours is sufficient to completely demineralise 0.5 g of bone powder though an overnight dissolution is usually applied for convenience [150, 151]. Increasing the EDTA incubation time to >48 hours can induce DNA damage or degradation [2, 152, 153].

Current recommendations suggest bone and tooth powder should be subject to total demineralisation [120, 148]. Coupled with proteinase digestion this method significantly increases DNA yields and DNA typing results by completely breaking down the hard bone material [148, 149, 151, 154, 155]. This allows access to larger, high-quality fragments of endogenous DNA that are held in dense crystal aggregates of the bone matrix [125] which is particularly important for smaller quantities of starting material [148,

[151]. Variability in the quantity and quality of the DNA is to be expected in degraded skeletal samples. Such uncertainty highlights the importance of using an extraction protocol optimised for smaller starting amounts of bone powder which facilitates re-extraction in the event of failure to recover a profile [72, 151]. The total demineralisation method of Loreille *et al*. [148] and the silica-based clean-up of Yang *et al*. [156] using QIAquick™ spin columns has been combined for more challenging skeletal samples and has been reported to recover more DNA, improve STR typing results and yield less PCR inhibitors from aged samples [149, 151, 157].

The ancient DNA method of Dabney [158] (demineralisation followed by MinElute™ PCR Purification Kit (QIAGEN) purification) has been shown to have an improved efficiency for retrieving shorter DNA fragments that is beneficial when highly degraded DNA is present [159], while the Loreille method [148] (demineralisation followed by 30 kDa Millipore Sigma Amicon Ultra Centrifugal Filter Unit) yielded higher overall DNA amounts facilitated by its tolerance of higher sample input. This makes the Dabney method preferrable in cases where there is evidence of significant DNA degradation while the Loreille method is sufficient when sample preservation is not an issue [159]. The results suggest that the choice of extraction method needs to be based on available sample, degradation state and targeted genotyping method. A further increase in DNA recovery has been documented for a recent ancient DNA extraction method for human remains using an organic DNA extraction with phenol/chloroform/isoamyl alcohol followed by concentration and buffer exchange using an Amicon Ultra-4 centrifugal filter unit (Millipore-Sigma) [160].

Target enrichment

Hybridisation-based DNA capture

MPS hybridisation-based capture is an approach directly applied after DNA extraction and library preparation [161]. Fragmented shotgun libraries are denatured by heating and subject to hybridisation with biotinylated DNA or RNA single-stranded oligonucleotides, referred to as 'probes' or 'baits', specific to regions of interest [162]. Non-specific unbound molecules are then washed away, leaving enriched DNA available for elution and then MPS [162]. The ultimate aim of MPS hybridisation-based capture is the sequencing of enriched nucleic acids and bioinformatic analyses of the reads [161]. DNA capture approaches have been shown to selectively enrich short endogenous DNA templates over longer exogenous contaminant DNA [163]; helpful for compromised samples contaminated with large amounts of exogenous DNA [164].The approach has been successfully applied to ancient DNA human remains samples which are highly fragmented and dominated by contamination of environmental and bacterial DNA [165] with often less than 1% of sequenced DNA being endogenous [166]. Library construction can also include cytosine deamination removal via a treatment step with uracil DNA glycosylase and/or endonuclease VIII [167].

For application to mitochondrial DNA (mtDNA), probe hybridisation assays use biotinylated DNA or RNA probes targeting hypervariable regions I and II (HVI/HVII) [164, 167-173]. Multiple rounds of in-solution hybridisation-based DNA capture can retrieve whole mtGenome sequences from highly degraded samples [164, 174], by capturing DNA templates that are damaged and fragmented (<100 bp in length) [175]. This DNA capture strategy, originating from ancient DNA studies, is based on the hybridisation of target DNA sequences to probes that are immobilised in solution or on a surface [176, 177] to generate complete mtGenomes [169, 178-180]. Primer extension capture methods also target

smaller mtDNA fragment sizes and have been found to produce reliable and plausible mtDNA haplotypes not possible with Sanger-type sequencing or MPS [172]. For Y-chromosome DNA, hybridisation capture enriches specific genomic regions of the Y-chromosome both on solid support [181] and in solution [182].

Targeting only mtDNA or Y-chromosome DNA, however, involves discarding a large proportion of informative sequences present in autosomal DNA. Carpenter et al. [166] report a whole-genome in-solution capture (WISC) method, using fragments of a modern DNA reference individual as baits covering the entire human genome. This method was applied to ancient human DNA libraries and when compared to shotgun sequencing, showed an enrichment of 6- to 159- fold for total sequences mapping to the human genome and 2- to 13- fold for unique (non-duplicated) fragments [166]. Hybridisation capture and low-coverage single nucleotide polymorphism (SNP) profiling for extended kinship analysis and forensic identification of historical remains has also been recently reported [183].

Targeted amplicon sequencing

Targeted amplicon sequencing refers to the PCR amplification of target regions of DNA that are flanked by PCR primers. It allows the isolation of specific and informative DNA sequences on the genome, ignoring the remainder. An MPS tiling approach for simultaneous mtGenome sequencing using 161 short overlapping PCR amplicons (average 200 bp) is available for degraded samples where PCR amplification of large fragments (several kb) may fail due to mtDNA fragmentation [184]. Commercial kits are now also available using this approach, namely the Precision ID mtDNA Whole Genome Panel (Thermo Fisher Scientific: TFS) and the ForenSeq™ mtDNA Whole Genome Kit (Verogen) [185].

DNA quantification and quality assessment

Following DNA extraction, extracts are quantified to determine the quantity and quality of sample DNA. Such information can inform decisions regarding the DNA profiling approach and aid in the conservation of sample. Amplifying samples with suboptimal input amounts of DNA can result in inefficient amplification of target loci [186]. The use of multiple target Taqman assays in real-time quantitative polymerase chain reactions (qPCRs), such as the Quantifiler™ Trio DNA Quantification kit (TFS), provides the concentration of total DNA and male DNA. An internal PCR control (IPC) helps to identify the presence of inhibitors and a 'Degradation Index', consisting of the concentration ratio of a smaller amplified target relative to a larger amplified target, indicates the extent of DNA degradation in a sample [187]. This information can also be informative for interpreting profiling results.

Most quantification kits recommend use of the smallest autosomal target concentration value to accurately estimate autosomal DNA concentration in a sample. However, the largest autosomal target concentration value could be considered when estimating the DNA concentration of compromised skeletal samples [188-190] because the size of the larger target more accurately reflects the average, or upper, size range of amplicons in current STR multiplexes or routine HVI/HVII sequencing [191]. Where samples produce a low quantification result, stochastic sampling, amplification effects and the presence of environmental inhibitors mean that DNA profiling could still be considered [191].

Recent STR testing kits include quality markers that can differentiate between degraded and/or inhibited DNA, assisting in DNA profiling decision making (see Watherston & Ward [192] for a detailed review). The quality markers differentiate between failed PCR amplification due to a lack of DNA and failed PCR amplification

due to the presence of inhibitors [193]. Sample information is enhanced by using an STR kit with quality markers in conjunction with a quantification kit, providing an objective measure of PCR inhibition and DNA degradation [192].

Detection methods

Capillary electrophoresis (CE)

Current DNA profiling is most commonly achieved by capillary electrophoresis (CE) where DNA fragments are separated based on a charge-to-size ratio. One significant advantage applicable to compromised human remains is that only a relatively small amount of sample is required for injection with separation in the capillaries achieved in minutes [194]. CE platforms can be used for both fragment length analysis, such as STR genotyping, and sequencing applications, such as Sanger sequencing of mtDNA HVI and HVII. In addition, SNaPshot® (TFS) is a single-base extension assay minisequencing method for SNPs commonly applied for its sensitivity and high multiplexing ability [195, 196]. SNaPshot® offers a low-cost and time-efficient alternative to MPS for smaller scale SNP genotyping requirements [196].

Massively parallel sequencing

MPS (or next generation sequencing: NGS) refers to the next generation of post-Sanger sequencing technologies. MPS is increasingly being applied within a forensic context due to its ability to type large batteries of markers in multiple samples simultaneously [197-205]. Recently, a number of contemporary and historic shipwreck remains have successfully yielded genetic identifications using MPS [16, 206].

Genetic markers

A variety of different genetic markers exist for interrogating different genetic information. For a detailed review of current genetic markers used in forensic DNA analysis, see Watherston et al. [20].

STRs

Autosomal STRs

Autosomal STRs are the most frequently employed markers for genetic identification and have a high power of discrimination [207]. Modern STR multiplexes such as the GlobalFiler™ (TFS) and PowerPlex® Fusion 6C (Promega) assays consist of upwards of 20 STR loci. Multiplexes can be applied to automated platforms and can be modified to alter the number of cycles, reaction volumes and input amount of DNA, depending on the equipment used and types of samples encountered in the laboratory [208-211].

The use of six-dye technology for labelling STR fragments enables the shortening of the overall amplicon lengths and minimises marker overlap [212]. For profiling highly degraded DNA, 7-12 mini-STRs are also included in the kits. Mini-STRs are very short fragments where only very little of the flanking regions on either side of the STR are included in the PCR amplicon. Chemistry improvements have seen amplification time reduced to 60-80 minutes whilst enhancing profiling success from low template and inhibited samples. Full STR profiles have been generated from as little as 100-250 pg of template DNA [213, 214]. Some kits have the ability to add up to 15 µL of DNA template to the PCR which can also improve DNA recovery.

Mendelian inheritance of STRs is exploited in kinship analysis. As first-order relatives are expected to share more genetic data than unrelated individuals, STR profiling has made it possible to identify potential familial relationships between an

individual in a DNA database and an unidentified human remains profile [215], known as familial searching. While the incorporation of additional loci in STR multiplexes can improve the distinction between related and unrelated individuals [216], STRs only enable short-range familial searching to first-degree relatives, i.e., to parents, children and siblings [217]. To confirm or refute biological relatedness, familial searching using STRs can be combined with lineage marker testing using Y-STRs and mtDNA [217]. Besides offering a complementary approach, lineage marker testing can confirm or refute maternal and/or paternal relatedness between individuals and allows reference samples to be collected from more distant relatives [68].

X-STRs

X-STRs can be useful as they are highly polymorphic, meeting Hardy-Weinberg and linkage expectations if not within the same linkage group [218-220]. When using siblings as reference samples for DNA identification, extra discrimination can be achieved by supplementing the analysis of autosomal STRs with X-STRs [220]. The Investigator® Argus X-12 QS Kit (QIAGEN) co-amplifies 12 X-STRs, D21S11, amelogenin and a Quality Sensor for predicting sample inhibition and degradation while the ForenSeq™ DNA Signature Prep Kit (Illumina) types seven X-STR markers [221].

Y-chromosome STRs (Y-STRs)

Y-STRs are useful when establishing paternal lineages because Y-STR profiles are expected to remain the same along a patrilineage, barring mutations [222]. Like X-STRs, it is sometimes necessary to supplement the analysis of autosomal STRs with Y-STRs to achieve extra discrimination [220].

mtDNA

mtDNA is of great advantage due to its high copy number per cell [223], making sequencing of mtDNA HVI and HVII particularly useful in unidentified remains cases [224]. Compared to two copies per diploid cell in nuclear DNA (nDNA), a mature oocyte is estimated to have thousands of mitochondria and greater than 100,000 copies of mtDNA [225, 226]. The circular nature of the mtDNA molecule makes mtDNA more resistant to degradation [227]. In highly degraded specimens, the use of mini-primer sets can improve the chances of typing success [228].

mtDNA molecules are inherited maternally [223, 229] so testing can confirm or refute maternal relatedness between individuals. Because mtDNA should remain largely the same, barring mutations and especially heteroplasmy, reference samples can be collected from distant maternal relatives. While not associated with a power of discrimination comparable to nDNA, >70% of the total variation within the whole mtGenome has been reported to exist outside of HVI and HVII [179], meaning sequencing the whole mtGenome can provide far greater resolving power for human identification [198, 230].

MPS allows the routine processing of mtGenomes, providing the highest level of maternal lineage discrimination. For high quality mtDNA, this is achieved using long-range PCR to generate two amplicons of approximately 8 kilobases (kb) in length [198, 231]. The general workflow for library preparation includes tagmentation (enzymatic fragmentation) of long-range PCR products, PCR amplification, clean up, quantification, pooling and sequencing [198, 232]. For low quality DNA, short, overlapping, segments of mtDNA are subject to PCR which produces amplified and tagged DNA fragments that span the complete mtDNA genome. mtGenome sequencing using MPS offers an increased ability to detect point heteroplasmy [233], to resolve point [234, 235] and

length heteroplasmy [236-238], to detect the presence of damage-induced lesions [235] and resolve mixtures [236, 239, 240].

The 16S and 12S ribosomal RNA (rRNA) genes have also been used in forensics for the identification of various species [241, 242] offering a genetic means of distinguishing between human and non-human remains recovered from a shipwreck. They are relatively conserved genes, evolving slower than the mtGenome as a whole [243 244]. Highly conserved regions nearby can be used as primer-binding sites, whilst mutations existing in variable regions are reported, making both genes suitable for species discrimination [245, 246].

While the European DNA Profiling Group (EDNAP) Mitochondrial DNA Population Database (EMPOP) can provide a statistical weighting for matches to mitochondrial DNA profiles, it is also used for the phylogenetic evaluation of sequences which can assist in determining haplogroups, providing inferences of ancestry and assisting with quality control assessment. Mitochondrial haplogroups are collections of similar haplotypes defined by combinations of SNPs in mtDNA inherited from a common ancestor [247]. These haplogroups are formed due to sequential accumulation of mutations through maternal lineages [248].

A phylogenetic approach to mtDNA sequence alignment has been formulated and forms the basis for haplotype annotation in the EMPOP database. Alignment and nomenclature is based on the phylogeny of mtDNA, where mutational events are inferred through comparison to closely related sequences [249]. Improved haplogrouping is achieved by using a maximum likelihood approach [250]. Phylogenetic evaluation of sequences can help to uncover human error (e.g. cross-contamination, misinterpretation of sequence raw data, phantom mutations, clerical errors) [251-254].

SNPs

SNPs are single base sequence variations at a particular point in the genome. Because SNP-targeted amplicons are usually short, they are particularly useful for degraded samples [68, 255]. SNPs are classified according to their forensic application: identity-informative SNPs (IISNPs) for human identification, lineage-informative SNPs (LISNPs) for inferring male (Y chromosome) and female (mtDNA) lineages, phenotype informative SNPs (PISNPs) for inferring EVCs (i.e., physical traits) and ancestry informative SNPs (AISNPs) for inferring BGA [196].

Assays for predicting EVCs such as eye, hair and skin colour have been developed as a result of well-established knowledge of the melanin synthesis pathway [256-260]. The first such assay for prediction of eye colour was the IrisPlex system (six SNPs) which includes a prediction model based on reference samples in multiple European populations [261]. The IrisPlex system has been vigorously assessed demonstrating its reproducibility, robustness and the accuracy of the IrisPlex model (for blue and brown eye colours, at least), with simple implementation [262]. The newer HIrisPlex system (24 SNPs, including all six IrisPlex SNPs) has since been introduced for predicting both hair and eye colour [258, 259] with its application demonstrated on WWII skeletal remains, [263]. The newest HIrisPlex-S system (36 SNPs, including 13 HIrisPlex and 6 IrisPlex SNPs) combines hair, eye and skin colour [260].

AISNPs capture the genetic differences among major global populations due to allele frequency divergences [264-266]. Custom assays for predicting BGA include the SNP*for*ID 34plex [264, 267], Eurasiaplex [268], Pacifiplex [269] and MAPlex [270, 271]. Two proprietary MPS panels also exist, namely the ForenSeq™ Signature Prep Kit (Illumina) [221] which utilises the Kidd panel [272] and also includes PISNPs; and the Precision ID Ancestry Panel (TFS) [273-275] made up of both the Kidd [272] and Seldin [276]

panels. While both panels have been found to perform well, the appropriate reference population data are essential when inferring ancestry [272, 277-279].

Y-SNPs can also play a useful role as lineage markers [280], even assisting in estimations of ancestral origin [281, 282]. Because the Y chromosome is inherited paternally in a conserved manner [222] and Y-SNPs are slowly mutating bi-allelic markers with a single base variation they are useful for predicting human ancestry and origins (as well as evolutionary migration patterns) [283-286]. This facilitates the reconstruction of male phylogenetic trees divided into 20 main haplogroups, from 'A' to 'T', and >9,000 subhaplogroups [287]. Certain Y-SNPs have since been identified that can be attributed to specific populations [288].

Microhaplotypes

Microhaplotypes are clusters of at least two tightly linked SNPs [255, 289] within a range of about 200 bp [255, 289]. Microhaplotype loci can be used for inferring ancestry, individual identification, kinship and the identification and deconvolution of mixtures [255, 289-291] due to their polymorphic nature. MPS makes it possible to genotype microhaplotypes by sequencing a cluster of SNPs in phase [255, 289-291]. Microhaplotypes are seen as a useful alternative to STRs because they are also polymorphic, they are often on smaller amplicons (useful for degraded DNA) and they are not subject to the formation of so-called "stutter" artefacts from PCR which can hinder the interpretation of STRs.

Autosomal identity and kinship informative SNPs

SNPs possess a lower mutation rate than STRs, and have been reported to be more stable in terms of inheritance and therefore, more suited for kinship analysis such as is performed in missing persons cases [292]. While their statistical discrimination has historically been a limiting factor [293], a number of very large SNP panels now exist for

genotyping on MPS platforms. Panels include the (now discontinued) International Commission on Missing Persons (ICMP) panel (QIAGEN) consisting of >1,200 tri-allelic SNPs [294] and the ForenSeq™ Kintelligence Kit (Verogen) [295] consisting of 10,230 SNPs to facilitate long-range kinship analysis and forensic genetic genealogy (FGG). High density SNP genotypes can be exploited to infer distant relationships, exceeding the range of first cousins [296]. Outside of the forensic domain, this has been achieved by direct-to-consumer (DTC) companies like Ancestry and 23andMe using microarrays to produce in excess of 500,000 SNPs dispersed throughout the genome. It has recently been demonstrated that this technology could have forensic applications [297] after initial attempts [298] were compromised by the high DNA template requirements of microarrays. Large databases of publicly-available SNP genotypes facilitate searching.

GEDmatch is a DTC database consisting of ~1.2 million SNP profiles (as of 2021) though dominated by users of European ancestry [296]. Founded in 2010, GEDmatch was created to supplement information from DTC companies and specifically, to assist with unknown parentage searches. The GEDmatch portal allows users to search for links with people who have profiles on different platforms from different DTC companies, and now offers a dedicated law enforcement portal called GEDmatch PRO™ [296]. During searching, uploaded SNP data are first assessed for viability after which they are "tokenised", creating a compressed site-specific binary format which is supposedly impossible to de-code in a security breach. As part of this process, health-related SNPs are removed. All comparisons in the database are made with the token files, available as de-identified kit numbers (not raw SNP data). The kit numbers are used to find familial/kinship links with other kit numbers on the GEDmatch PRO™ database using the One-to-Many tool. Linked individuals in

GEDmatch PRO™ are identified in the match list by their kit number, name and email address [296].

It has been reported that as few as 10,000 SNPs are sufficient for long-range familial searching [299]. While sequencing the whole genome of an individual is now a viable option, whole genome sequencing (WGS) methods cannot yet offer solutions for typing the range of biological samples seen in forensic casework [296]. However, WGS of human remains has been shown to be possible by using carefully constructed validation measures to ensure sufficient sequence coverage for robust SNP genotype calling [300]. This technology offers a promising tool for historic shipwreck remains cases.

Insertion-deletion markers

Insertion-deletion length polymorphisms (InDels) are a type of biallelic short DNA length variation [301-305]. InDels are well suited for analysing degraded DNA due to their short amplicon ranges, high multiplexing capability and low mutation rates [205, 306]. Proximal SNPs in InDel flanking regions can increase the power of discrimination of currently defined InDels and provide potential as markers for ancestry inference [307-309].

Insertion and null alleles (INNULs)

Short interspersed nuclear elements (SINEs), are non-coding genomic DNA repeat sequences, or mobile insertion elements, comprising approximately 40% of the human genome [310]. A novel primer design has overcome the inherent size differences associated with insertion and null alleles (INNULs) [311]. Markers in the InnoTyper® 21 Kit (InnoGenomics®) are bi-allelic, having two possible allelic states (insertion or null). Alu elements are primate specific SINEs that have reached a copy number in excess of one million in the human genome, making them particularly valuable for extremely degraded DNA samples and because they are identical by descent only with no

mechanism for parallel independent insertions to occur, they are ideal for kinship analysis of degraded human remains [310].

Typing strategies involving changes to standard protocols

Genotyping success for skeletal remains recovered from marine environments can be improved by employing enhancements to standard protocols. These can include the combination of two or more protocols or changes to DNA input amounts, reaction volumes, PCR cycles or reagent concentrations.

Replicate and complementary amplification

For challenging samples, current guidelines recommend using repeat amplifications to improve and confirm DNA profiling results [69, 312]. This is a strategy first applied to the amplification of so-called low copy number (LCN) DNA [313, 314]. Alternatively, amplifying the sample using at least two complementary kits offers another strategy [69] overcoming larger amplicon drop-out and primer binding variations [315, 316]. For a detailed review and application to aged skeletal remains, see Watherston & Ward [192].

A number of dual amplification strategies with the MiniFiler™ PCR Amplification Kit (TFS) and different STR multiplex assays have been reported for old skeletal remains [317, 318]. Combining Y-STRs with other genetic markers allows the complementary addition of a lineage marker. Marjanović et al [319] report using a combination of STRs, mini-STRs and Y-STRs to provide genetic identification for old skeletal remains. Current guidelines for missing person investigations recommend genotyping autosomal STRs (including mini-STR loci), Y-STRs and mitochondrial DNA (mtDNA) with available options to apply SNP and InDel markers [120]. The combination of STRs, mini-STRs, SNPs and InDels has been applied to degraded PM

samples [320, 321]. However, most new commercial multiplexes include up to 10 mini-STRs which may negate the need to implement a separate mini-STR multiplex.

Optimising amplification parameters

Assuming an input amount of ~1 ng of DNA, STR multiplex systems normally use 28-30 amplification cycles. However, compromised or aged bone may not yield 1 ng of template DNA [192]. Because the number of attempts to genotype degraded samples is limited by the volume of DNA extract [322], optimised amplification parameters are crucial. For a detailed review and application to aged skeletal remains, see Watherston & Ward [192].

Increased DNA input amount

An increased input amount of DNA can improve the chances of successful DNA recovery assuming samples do not contain a large amount of PCR inhibitors. Different STR multiplex kits offer different sample volumes of 10 or 15 µL, the latter facilitating an increased input of DNA [192].

Reduced reaction volume

Half reactions of commercial STR multiplex kits are commonly used by many forensic laboratories with user manuals often describing their application. As such, half-reactions have been validated extensively on a range of multiplex kits, reporting comparable or increased quality profiles, with a significant saving on the cost of genotyping [323-325]. Another advantage is less sample is consumed per reaction [192]. This approach has been applied to aged skeletal remains combined with a total demineralisation extraction protocol and increased number of PCR cycles [326]. Reduced

reaction volume with increased *Taq* polymerase also yielded more full and concordant STR profiles and less off-ladder alleles than other methods (including standard PCR) from a broad range of input DNA from hairs [210].

Increased number of PCR amplification cycles

Increasing the number of cycles is the simplest way to increase the number of amplicons and therefore sensitivity of testing [313], but it comes with the risk of increased numbers of artefacts interfering with the interpretation of STR profiles. Some manufacturers describe standard and increased sensitivity options in their user manuals for amplifying routine and compromised samples. For example, the GlobalFiler™ PCR Amplification Kit User Guide offers two PCR options with alternative DNA input amount and PCR cycle numbers [327]. Alternatively, laboratories have used increased cycle numbers for the processing of old and degraded skeletal samples; from 31-60 cycles [21, 326, 328-330], also in conjunction with an increase in *Taq* DNA polymerase concentration [331, 332]. A nested primer PCR protocol using an initial 40-cycle amplification with a subsequent 20-30 cycles has also been described [333].

Increased concentration of Taq DNA polymerase/bovine serum albumin (BSA)

While modern STR multiplexes continue to increase their tolerance to PCR inhibitors, inhibition can also be minimised by increasing the *Taq* DNA polymerase concentration [334]. BSA prevents inhibitors from interacting with *Taq* DNA polymerase [335] and the addition of BSA has been reported to overcome PCR inhibition [13] (see Farrell & Alexandre [336] for a detailed review of the effects of BSA on PCR). The benefits of both increasing the concentration of *Taq* DNA polymerase and adding BSA to PCR has also been reported for high humic acid-content samples [337].

Post-PCR purification

Post-PCR purification methods purify PCR products using a range of filtration and silica spin column methods to remove salts, ions, unused deoxynucleotide triphosphates (dNTPs) and primers from the PCR. A reduction in PCR product volume (e.g., 25 µL) to 10 µL also concentrates the DNA [338]. Several post-PCR clean up kits are available commercially with selection usually based on PCR product size range and elution volume.

Conclusions

Skeletal remains present some of the most challenging samples due to the presence of a large number and variety of PCR inhibitors and the often severely degraded nature of these samples when recovered. Historic shipwreck remains are further challenged by time and submersion in a marine environment. Approaches available to combat these challenges have included the application of multiplex STR profiling following an efficient DNA extraction [148], the use of mini-STRs for highly degraded DNA [320] and optimised amplification parameters such as increased *Taq* DNA polymerase [334], increased PCR cycle number [313, 328] and decreased PCR reaction volume [323-325, 339], with a combination of these approaches also applied [210, 326, 331, 332, 340]. More recently, ancient DNA methods like hybridisation capture using biotinylated oligonucleotide "baits" and MPS have also been applied [341].

A number of genetic markers and approaches for recovering available DNA are now available for application to historic shipwreck remains. Minimally-invasive sampling will be particularly important for testing such irreplaceable remains. DNA profiling techniques offer alternative means by which to interrogate and apply genetic information. These new forensic DNA techniques were applied to remains from the

1685 shipwreck, *La Belle*, and were able to reveal the decedent's hair and eye colour, and ancestry [16]. This application demonstrates the sensitivity of current forensic techniques for recovering DNA from archaeological human remains, specifically those from historical shipwrecks. FGG offers another promising tool for long-range familial searching via DTC databases.

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