THE BIOARCHAEOLOGY OF INITIAL HUMAN SETTLEMENT IN PALAU,

WESTERN MICRONESIA

by

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A DISSERTATION

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DISSERTATION ABSTRACT

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The initial settlement of Remote Oceania represents the world's last major wave of human dispersal. While transdisciplinary models involving linguistic, archaeological, and biological data have been utilized in the Pacific to develop basic chronologies and trajectories of initial human settlement, a number of elusive gaps remain in our understanding of the region's colonization history. This is especially true in Micronesia, where a paucity of human skeletal material dating to the earliest periods of settlement have hindered biological contributions to colonization models. The Chelechol ra Orrak site in Palau, western Micronesia, contains the largest and oldest human skeletal assemblage in the region, and is one of only two known sites that represent some of the earliest settlers in the Pacific. As such, Chelechol ra Orrak provides an excellent opportunity for direct study of population dispersals into Micronesia.

This dissertation draws on bioarchaeological data from Chelechol ra Orrak to address research questions related to the initial human settlement and subsequent adaptation of small island environments in Palau, and more broadly, Remote Oceania. The results of ancient DNA and radiocarbon dates are used to test hypotheses related to a potential place of origin for early Palauan people. I also present a case study from Ucheliungs, a mortuary and small-scale habitation site located in Palau that is

contemporary with Chelechol ra Orrak, to assess claims of insular dwarfing following initial settlement. The second half of the dissertation focuses on aspects of behavioral adaptation to Palau. Results of stable isotope analysis from Chelechol ra Orrak are used to reconstruct early human diet, while the role of habitual chewing of betel nut is explored within the context of temporomandibular joint osteoarthritis. Together, these case studies provide fundamental baselines for understanding initial human settlement and small island adaptation in Palau from a bioarchaeological perspective.

This dissertation includes previously published and unpublished co-authored material.

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CHAPTER I

INTRODUCTION

Widespread population dispersals have been a hallmark of modern humans throughout their evolutionary history (Cabana and Clark 2011, Campbell and Crawford 2012). These movements into new landscapes are not only driven by aspects of our ecology and culture, but the same factors are also impacted upon arrival in a new location. In turn, various related facets of human life, including political and economic systems, language, subsistence, settlement patterns, and resource abundance, among others, are affected by dispersal events. Population dispersals also have a genetic impact, affecting population structure through the process of gene flow, and, in the case of initial arrival into previously uninhabited areas, genetic bottlenecks (Fix 1999, O'Rourke 2012). As such, anthropological studies of the causes, processes, and results of dispersal events in the past are valuable contributions to addressing questions of what makes us human (Cabana and Clark 2011). An important step in understanding the underlying reasons and impacts of population dispersals is to identify potential motivations for movement, often referred to as push (negative) or pull (positive) factors. To help identify such factors, especially within archaeological contexts, information related to the context and structure of a migration event, including the point of origin, is critical (Anthony 1990, Beekman and Christensen 2015, Tsuda et al. 2015).

An inherent challenge in reconstructing past dispersals by humans is the ability to distinguish between these and other cultural events that result in the introduction of new ideas or technologies without the physical movement of people. For example, the appearance of sudden changes in material culture, such as new artifact types or stylistic elements, are sometimes interpreted as evidence for the arrival of new populations to an area or community, but could instead result from the diffusion of novel ideas or the exchange of objects. A bioarchaeological perspective of migration is particularly valuable because it emphasizes direct evidence of human movement by studying possible migrants, rather than the transfer of artifacts or ideas (Knudson 2015). Additionally, a bioarchaeological perspective can inform on the biological factors affected by human

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movement, including biodistance and genetic studies that shed light on regional population relationships and points of origin or the impacts of migration on diet or health (e.g., Blom et al. 1998, Kinaston et al. 2013, 2014, Redfern et al. 2018, Tung and Knudson 2011).

One form of population dispersal that is of particular interest for understanding different aspects of biological and cultural adaptation is initial colonization, or the arrival of human groups into previously uninhabited areas. Islands provide ideal model systems within which to study human colonization because of their boundedness and relative isolation compared to continental areas (DiNapoli and Leppard 2018, Fitzpatrick and Erlandson 2018, Kirch 2007, Vitousek 2002). Additionally, the initial settlement of islands is especially interesting because of the unique suite of skills and behaviors necessary for successful arrival and settlement of new areas. These skill sets include the use of watercraft and navigation (wayfinding), the translocation of (non)domesticated plants and animals, and development of long-distance exchange networks. The contribution of a bioarchaeological perspective dedicated to understanding the lifeways and challenges of the first people arriving on these new small and relatively remote landmasses can also provide a valuable perspective for understanding the processes by which humans adapted to small islands.

Remote Oceania, which spans much of the Pacific Basin, is a particularly interesting island setting in which to study this process given the rapid pace at which people crossed vast expanses of open ocean. In the Pacific, a transdisciplinary approach combining archaeology, historical linguistics, and various biological data—including biodistance studies and population genetics—has been successful in reconstructing basic chronologies and trajectories associated with initial settlement of the region (e.g., Bedford and Spriggs 2019, Carson 2013, Kirch 2010, Matisoo-Smith 2015). However, some major gaps remain, particularly in Micronesia, where comparatively little work has been done. Although archaeological research in the region has increased in recent years, particularly in western Micronesia, the comparatively small amount of biological work conducted has largely been attributed to a lack of available skeletal remains, particularly for individuals dating to the period immediately following initial colonization. In Palau, western Micronesia, however, the Chelechol ra Orrak archaeological site has yielded

evidence of skeletal remains belonging to more than 55 individuals dating to the earliest phases of settlement (Fitzpatrick 2003a, Nelson et al. 2015). This collection thus provides an ideal opportunity for bioarchaeological work to contribute significantly to our understanding of Palauan and western Micronesian settlement and how it relates to the greater Pacific Islands region.

In this dissertation, I aim to demonstrate that the application of a bioarchaeological perspective in Micronesia not only provides a critical component to studying island colonization processes, but also sheds important light on the past lifeways of the earliest inhabitants of this region, specifically in Palau. By applying a suite of bioarchaeological methods, including ancient DNA (aDNA), stable isotopes, and osteological analyses to the Chelechol ra Orrak skeletal assemblage, I address questions related to where these peoples may have originated from, regional population relationships, resource use, and adaptations that first settlers would have had in Palau— and more broadly—western Micronesia. In doing so, I have generated preliminary baseline data that provides a foundation for future research in Micronesia aimed at addressing more specific aspects of colonization and the settlement process vis-à-vis this multidisciplinary approach.

Background

Settlement of the Pacific

Historically, the Pacific Islands have been subdivided into three major subregions: Melanesia, Micronesia, and Polynesia. These categories were largely based on phenotypic differences observed among living populations such as skin color, but only Polynesia has remained a meaningful category when linguistic and biological data are taken into account (D'Urville et al 2003, Green 1991). In response to the racist connotations and lack of significance associated with the original subregions, Green (1991) instead proposed dividing Oceania into two subregions—Near and Remote—with the latter originating just east of the Solomon Islands and spanning the Pacific Ocean as far east as Rapa Nui (Figure 1.1). While both D'Urville and Green's classifications are used interchangeably today for geographic reference, Green's divisions of Near and Remote Oceania also draw on the region's settlement history and geography, as Near

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Oceania represents the limit of both Pleistocene settlement and increased intervisibility between islands, which has been argued to facilitate early seafaring (Green 1991).
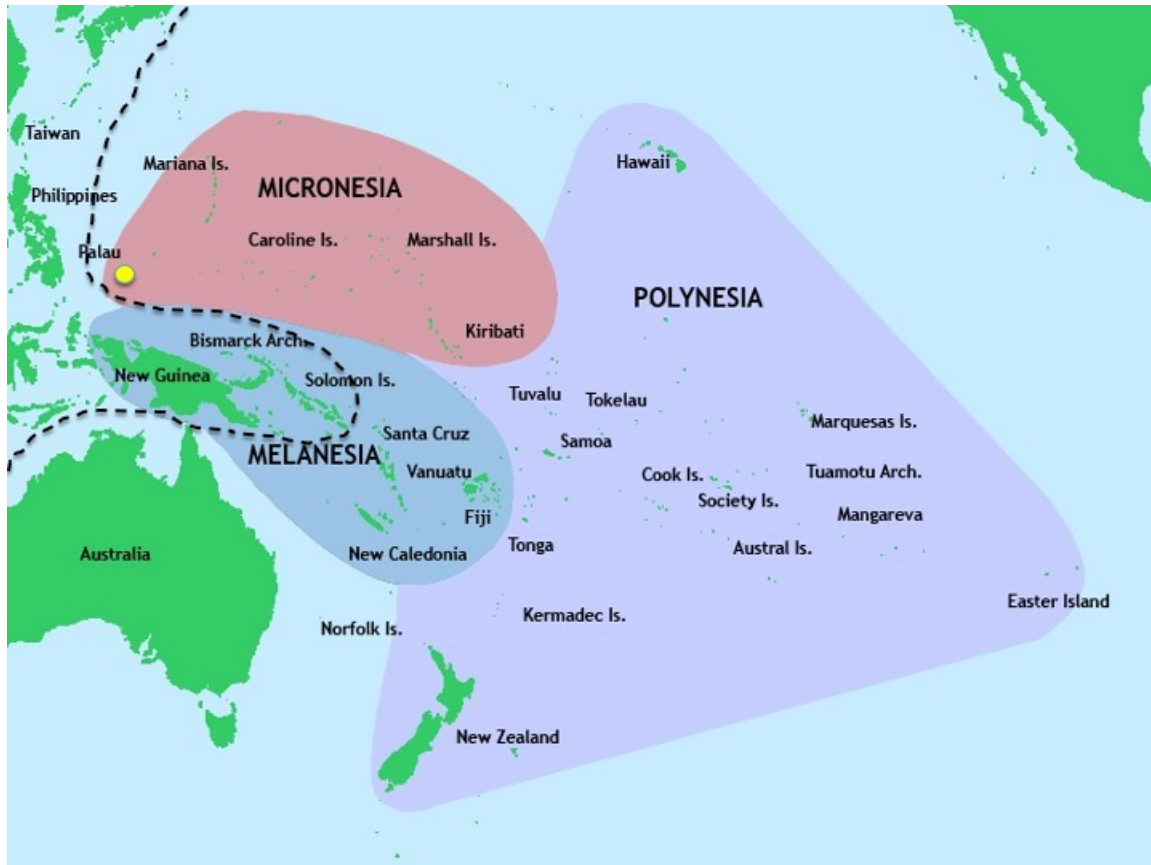
Figure 1.1. Map of the Pacific Islands depicting the subregions discussed above. The dotted line indicates the Near/Remote Oceania boundary, and Palau's location is marked by the dot (Image modified from Wikipedia.org).

As a result of lower sea levels during the Pleistocene, many of today's islands were joined, reducing the depth and number of water gaps that needed to be crossed for human settlement. Migration to the Pleistocene landmass of Sahul, the remnants of which include Australia and New Guinea, is particularly significant in human history as it represents the first ocean crossings by anatomically modern *Homo sapiens*, ca. 65-45,000 BP, though recent research in Australia is pushing this timing back to at least 65,000 BP (Clarkson et al. 2017, O'Connell et al. 2018). The route taken to these areas, the

watercraft used, and whether or not the crossings were intentional are still debated topics (Allen and O'Connell 2008, 2020, Bird et al. 2019, Kealy et al. 2016, O'Connor and Chappell 2003).

From Sahul, groups reached the Bismarck Archipelago, situated off the northeastern coast of New Guinea, by 40,000 BP (Leavesley 2006). Early sites were located in close proximity to the coast and reflect periodic use by small, mobile foraging groups that took advantage of marine shellfish and terrestrial fauna, and utilized unmodified chert (Allen and Gosden 1996, Leavesley 2006, O'Connor and Veth 2005, O'Connor et al. 2011). Subsequent settlement of the northern Solomon Islands by 32,000 BP involved seafaring in open ocean with no land visibility. This period is also associated with evidence for inter-island contact and the development of a regional exchange system between New Guinea, the Bismarcks, and the Solomons, which involved the movement of obsidian and translocation of terrestrial mammals, including the cuscus (*Phalanger orientalis*). These also overlap with the development of agriculture in the New Guinea highlands (Allen 1996, Ambrose and Green 1972, Anderson et al. 2009, Spriggs 1997, Wickler 1990).

Coastal and inland habitation sites, a regional system of obsidian exchange, and the domestication of major tree and tuber crops in the New Guinea highlands continued in Near Oceania until around 5000-4000 BP, when a second major wave of migration into Island Southeast Asia (ISEA) introduced Austronesian-speaking horticulturalists that likely originated from Taiwan, although recent genetic evidence has also suggested interaction with Mainland Southeast Asia (MSEA) during this time (Allen 1996, Allen and Gosden 1996, Ambrose and Green 1972, Bellwood 1995, 2013b, et al. 1995, Bulbeck 2008, Denham 2004, Shutler and Marck 1975, Soares et al. 2016). These horticulturalists, often referred to as Austronesian groups based on their linguistic associations, expanded rapidly through Near Oceania, eastward into Remote Oceania, and westward to Madagascar over the next two to three millennia (Blust 1995, Crowther et al. 2016, Gray et al. 2009).

By far the most significant event in Remote Oceania was the appearance of the first humans known as the Lapita Cultural Complex. Archaeological evidence of Lapita first appears in the Bismarck Archipelago around 3300 BP, at which point they moved

rapidly eastward through Melanesia and into West Polynesia, reaching Tonga and Samoa by 2800 BP, though apparently bypassing the Solomon Islands for reasons that are still not clearly understood (Bedford et al. 2019, Green 1979, Sheppard et al. 2015). Lapita material culture is marked by a suite of characteristics, including dentate-stamped ceramics, worked shell and stone artifacts, settlements located in coastal areas, and the translocation of both domesticated and non-domesticated plants and animals (pigs, dogs, chickens, and rats) (Bedford et al. 2019, Kirch 1997, Larson et al. 2005, 2007, Matisoo-Smith 1994, Matisoo-Smith and Robins 2004, Spriggs 1984). Over time, later Lapita sites demonstrate increased localization of material culture and a decrease in regional exchange (Green 1991b, 1992, Spriggs 2003). At the same time, islands in western Micronesia, including those in Palau and the Marianas, were also being settled by people likely originating from ISEA that do not share the archaeological characteristics associated with Lapita, suggesting that at least two contemporaneous migrations from ISEA to Remote Oceania were occurring between ca. 3500-3000 BP (see discussion below).

The first settlement of Polynesia occurred ca. 2850-2800 BP in Samoa and Tonga by Lapita groups, after which voyaging appears to have ceased for almost 2000 years, a period referred to as the "long pause". Explanations for this hiatus in movement vary from changing climatic conditions and sea levels (e.g., increased El Niño/Southern Oscillation events during the Late Holocene) to a need for first improving canoe technology and wayfinding skills to be able to venture to the farthest reaches of the Pacific (Anderson et al. 2006, Irwin 2008, Montenegro et al. 2014, 2016, Sear et al. 2020). The same sea level stabilization around 2000 BP also resulted in the emergence of atolls across central and eastern Micronesia that were settled almost immediately thereafter (Dickinson 2003, 2004, Weisler 2001, Weisler et al. 2012). The timing of the onset of Polynesian voyaging eastward is somewhat contentious, but conservative estimates place settlement of the Central Eastern Polynesian archipelagos, including the Society, Cook, Austral, Gambier, and Tuamotu Islands to between ~925-830 BP (Wilmshurst et al. 2011). The islands of East and South Polynesia, including Hawai'i, Rapa Nui, and New Zealand, appear to have been settled from the Marquesas and Society Islands ca. 800-700 BP (Hunt and Lipo 2008, Wilmshurst et al. 2011).

The Initial Settlement of Micronesia

Micronesia comprises more than 2,000 islands in the northwest tropical Pacific that stretch across an ocean area of over seven million square kilometers. This region reaches from the Near/Remote Oceania border, with its westernmost landmasses in the Palauan archipelago, and as far eastward as some Polynesian islands, with the easternmost Micronesian landmasses being located in Kiribati. Despite the large number of islands, the total land area is only 2700 km^2, hence the name meaning "sea of little lands" (Craib 1983, Kirch 2000: 165). To put this in perspective, Micronesia is about the size of the United States, but the total land area is about the same as Rhode Island.

Geographically, the region is divided into four major island groups: the Mariana Islands (Guam, Saipan, Rota, Tinian, and numerous smaller ones that stretch northward), the Marshall Islands, the Gilbert Islands (Kiribati), and the Caroline Islands. The latter are typically divided into eastern and western parts and politically includes the Republic of Palau and the Federated States of Micronesia (FSM; Yap, Pohnpei, Kosrae, and Chuuk). Originally named for the small, low-lying atolls comprising much of the central and eastern portions of the region, Micronesia also has a variety of island types, including high volcanic, continental, and raised coral limestone (Alkire 1977, D'Urville et al. 2003, Craib 1983). The region is tropical and varies in rainfall seasonally, with the majority of the area falling within the tropical typhoon zone.

Generally, traditional subsistence is based on introduced crops such as taro, yam, banana, coconut, and breadfruit, while protein sources primarily include fish, shellfish, crustaceans, and turtle from nearby reef and lagoon environments, in addition to some endemic terrestrial fauna (e.g., birds, bats, land crabs). Common Pacific terrestrial domesticates, including pig, dog, rat, and chicken were present prehistorically, but the distribution of these taxa varies across Micronesia and have only been found in relatively small quantities, suggesting that they were not staple resources following initial settlement. To date, only one Micronesian island has yielded archaeological evidence for the presence of all four taxa: Fais, a small uplifted coral island located northeast of Yap. Strontium isotope evidence from pig and dog remains excavated on Fais suggests that

this island is a unique example within Micronesia where these animals were raised locally (Alkire 1977, Clark 2004, Fitzpatrick 2018, Gakuhari et al. 2013, Intoh 2008).

Comparatively little archaeological research was conducted in Micronesia until the mid-1970s, and in many areas is still lacking relative to other areas in the Pacific. Originally, Micronesia was thought to be a region of stepping stones by which people reached and settled western Polynesia, but this claim was disproven as a result of the identification of Lapita (Buck 1938). This, coupled with the noticeable absence of Lapita in Micronesia led earlier researchers to reevaluate colonization models and conclude that Lapita had moved eastward from Melanesia into Polynesia. Reinterpretation of the biological similarities originally identified between Micronesian and Polynesian peoples, joined with linguistic and archaeological evidence, are now known to result from shared ancestry in Island Southeast Asia (ISEA) prior to dispersal into Remote Oceania (Bellwood 1979, Craib 1983, Howells 1970, Lum and Cann 2000, Pietrusewsky 1990).

Separate settlement histories for the eastern and western portions of Micronesia are also apparent. Western Micronesia (Mariana Islands, Palau, and Yap) appears to have been settled by groups from ISEA who reached the Marianas by 3500-3000 BP (Carson 2012, Carson and Kurashina 2012, Rieth and Athens 2019) and Palau by 3300-3000 BP (Clark 2004, Fitzpatrick and Jew 2018, Stone et al. 2017). The earliest archaeological evidence for human presence on Yap dates later than other islands in western Micronesia, ca. 2400 BP, but this discrepancy has largely been attributed to a lack of archaeological research on Yap and may shift as work expands (Napolitano et al. 2019). Although similarities in red slipped ceramics have been used to suggest that the Marianas were settled from the northern Philippines, wind and current patterns, along with experimental seafaring simulations, suggest a "homeland" further south for both the Marianas and Palau (Hung et al. 2011, Fitzpatrick and Callaghan 2008, 2013, Montenegro et al. 2016, Winter et al. 2012). With the exception of Palauan and Chamorro, the native language of the Marianas, all Micronesian languages belong to the Oceanic subgroup of Austronesian, which has been correlated with Lapita expansion (Pawley and Ross 1993). Palauan and Chamorro instead belong to the Western Malayo-Polynesian subgroup, which also includes languages from the Philippines and Indonesia, lending further support for an ISEA point of origin for the Marianas and Palau (Reid 1999). Within

Micronesia, the remaining languages except for Yapese and those of the Polynesian Outliers Nukuoro, Kapingamarangi, and Nauru, comprise an Oceanic subgroup known as Nuclear Micronesian that appears to have diverged early from languages in Melanesia. Together, this suggests that the colonization of Micronesia largely occurred from two major sources: the archipelagos of Western Micronesia from ISEA ca. 3300-3000 BP, and Nuclear Micronesian-speaking groups from Melanesia, ca. 2500-2000 BP (Athens 2018, Bender and Wang 1985, Jackson 1986).

Palau Environmental and Archaeological Context

Palau Environmental Context

Palau is an archipelago composed of hundreds of geologically diverse islands located about 600 km east of the southern Philippines in the Western Caroline Islands (Figure 1.2) and about the same distance north of New Guinea. The archipelago is oriented in a northeast to southwest direction that stretches for more than 160 km. Together, the islands of Palau cover a land area of about 400 km^2, with nearly 83% belonging to the largest, mostly volcanic, island of Babeldaob. South of Babeldaob are a series of additional volcanic islands, including Ngerakabesang, Malakal, and Koror, which is partially limestone and the location of the city of Koror, where the majority of Palauans live today (Corwin et al. 1956). Most of Palau consists of small uplifted coral limestone islands located in the central portion of the archipelago that are often referred to as the "Rock Islands". Weathering from freshwater exposure has created karst topography and caves in many of these islands, with some also containing marine lakes (Figure 1.3). The northernmost state of Kayangel includes the atolls of Kayangel and Ngaruangel and in the southern end are Peleliu and Angaur, two limestone platform islands. While politically part of Palau today, the Southwest Islands (Fanna, Sonsorol, Pulo Ana, Merir, Tobi, Helen Reef, and Transit Reef) are a series of low platform islands and atolls located over 300 km from the main archipelago and appear to have a separate settlement history. From Babeldaob to Peleliu, the archipelago is enclosed by a barrier reef that creates a breakwater to major ocean currents and a large lagoon habitat, with open channels north of Babeldaob and between the southern portion of Babeldaob and Koror. Additionally,

there are many fringing reef systems that surround individual islands (Corwin et al. 1956).

Figure 1.2. Map of Palau depicting locations of Rock Island sites discussed.

Like other Micronesian islands, Palau has a tropical climate with some seasonal variation in rainfall. The archipelago is also at the crossroads of three oceanic currents (North Equatorial Current, South Equatorial Current, and the Equatorial Counter

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Current). Current patterns vary significantly seasonally and annually, which also would have impacted navigation over the surrounding reefs upon initial arrival (Fitzpatrick 2003a). Vegetation ranges from upland forest and jungle to savannah grassland, which may have been the result of anthropogenic modification (Athens and Ward 1999). Mangrove swamp is common around the coasts of Babeldaob and Koror, and the Rock Islands tend to be densely forested. Edible plants in Palau are similar to those elsewhere in Micronesia and includes coconut and taro, along with cassava and rice, both of which were introduced historically. Betel nut palms (*Areca catechu*) and pepper leaf (*Piper betel*) are also common, especially around domestic areas, as they are used along with slaked lime to prepare betel nut quids, which are chewed habitually by many people for their stimulant properties (Fitzpatrick et al. 2003, see Chapter V). Like many Remote Oceanic islands, Palau has a relatively impoverished terrestrial fauna, including bats, birds, frogs, crabs, and snakes. Pigs, a terrestrial domesticate that were introduced to other Pacific Islands upon initial human arrival, were present late in prehistory, but apparently never in large numbers. At European contact no pigs were observed, suggesting that the earlier populations were likely extirpated and reintroduced historically (Clark et al. 2013). Since European arrival, additional mammals have been introduced, including cats, dogs, and, on Angaur, a population of macaques (*Macaca fasicularis*) that were brought to the island in the early 1900s by German phosphate miners (Poirier and Smith 1974, Wheatley 2011). The overwhelming majority of Palau's ecological diversity, however, lives in the widespread marine lagoon and coral reef habitats, including fish, shellfish, sea turtles, dugong, saltwater crocodile, and cetaceans.

The Archaeology of Palau

Archaeological research on Palau began in the 1960s with initial survey work and test excavations by Douglas Osborne (1966, 1979) at sites throughout the archipelago, followed by a group of researchers from Southern Illinois University led by George Gumerman through the 1980s and early 1990s (Carucci 1992, Gumerman et al. 1981, Masse 1989, Snyder 1989). A major contribution to archaeological work on Palau was a series of cultural resource management projects in the 1990s following Palau's 1994 Independence and the implementation of a Compact of Free Association with the United

States, when a number of public infrastructure projects were undertaken, including the construction of the Compact Road on Babeldaob and relocation of the Capitol Building. Survey and excavations across Babeldaob for these projects yielded a tremendous amount of new data and radiocarbon dates that suggested initial settlement occurred by at least ca. 2500-2000 BP (Liston et al. 1998, Masse 1990, Welch 2002). Additional radiocarbon dates from multiple Rock Island sites, including Chelechol ra Orrak, Ucheliungs, and Ulong Island, have provided further support for an even earlier settlement date ca. 3300-3000 BP (Clark 2004, 2005, Clark et al. 2006, Farley et al. 2018, Fitzpatrick 2002, Fitzpatrick et al. 2003b, Stone et al. 2017, see chapter III). Proxy evidence from paleoenvironmental cores around the coast of Babeldaob in the form of increased charcoal particulates, sedimentation, grassland conditions, and the identification of coconut, betel nut, and swamp taro pollen have been used to suggest a human presence in Palau even earlier, ca. 4500-4000 BP (Athens and Ward 1999, 2002). However, complementary archaeological evidence is lacking, and the identification of any possible archaeological material dating to this time period has been hindered by a combination of possible island subsidence, sea level fluctuations, erosion, and poor preservation due to volcanic soils and dense mangrove on the coast of Babeldaob (Clark and Wright 2003, Dickinson and Athens 2007).

The origins of Palau's earliest populations are still unknown. While ISEA is often cited as a homeland for initial Palauan populations, proposed points of origin vary and include the Philippines, Indonesia, Taiwan, and/or New Guinea. Computer simulations of drift voyaging suggested that the highest rates of successful landfall in Palau originated in the southern Philippines (Mindanao) or somewhere between here and New Guinea (e.g., Halmehara), with little chance of success from New Guinea, Taiwan, the Bismarcks, or the central/northern Philippines (Fitzpatrick and Callaghan 2008). More recently, results of seafaring simulations and shortest-hop trajectories demonstrated that downwind voyages from Taiwan, the northern and central Philippines, and the Bismarck Archipelago would likely be unsuccessful, while successful landfall in Palau likely involved voyages originating in the southern Philippines, Maluku Islands, western New Guinea, and/or the Mariana Islands (Montenegro et al. 2016). Ceramic similarities in the common use of grog temper in Type X pottery from the north coast of New Guinea and

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Palau have also been used to suggest contact between the two areas, but this appears to have been later in time, ca. 1000 BP (Specht et al. 2006). Early Palauan ceramics decorated with red slip, incision, and lime filling, are similar to contemporaneous sherds in the Marianas and northern Philippines (Clark 2005, Fitzpatrick 2014). Genetic evidence from modern Palauan mtDNA also suggests connections to New Guinea, but again, may be due to later admixture (see Chapter II, Lum and Cann 2000). Together, these various lines of evidence continue to support an origin somewhere in ISEA, but are unable to point to a more specific area.

Figure 1.3. Examples of island types in Palau. Clockwise from top left: Babeldaob (volcanic high island), Angaur (limestone platform), Omedokel (rock island), and Kayangel (atoll). Photographs of Babeldaob and Angaur taken by S.M. Fitzpatrick.

Archaeological evidence for the earliest period of settlement appears to be primarily limited to mortuary practice and/or small-scale habitation in the Rock Islands. Archaeologically-associated radiocarbon dates from this period are found as part of the cemetery component of Chelechol ra Orrak (described below), Ucheliungs Cave (see Chapter III), and Ulong Island. Across each of the three sites are evidence for some

combination of mortuary activity, marine resource use, and habitation, although the latter is variable in scale (Clark 2004, 2006, Fitzpatrick 2002, 2003, Stone et al. 2017).

Following this period, ca. 2500 BP, the construction of massive earthwork terraces, and later, associated "crown and brim" features, begins on Babeldaob and Koror (Liston et al. 1998). Construction on these features continued for about 1000 years in three phases: Early (2400-2150 BP), Middle (2150-1500 BP), when construction peaks, and Late (1500-1200 BP), when construction declines and the areas were eventually abandoned (Liston 2009). The features, which are built by cut and fill construction into existing hillsides, have been the focus of much discussion as their function is still debated. While oral histories do not describe terrace functions, possibilities raised by researchers include agriculture, defense, competition, or ritual use, but it is likely that they were multifunctional (Fitzpatrick 2008, Liston 2009, Liston and Tuggle 2006, Phear 2004, Wickler 2002). Although a significant amount of ceramic material and occasional human burials have been found in the fill of terrace formations, and the remains of stonework suggest some form of settlement may have taken place on the terraces, evidence is limited due to poor preservation of organic material in the volcanic soil (Lucking 1984, Wickler 2002).

Earthwork construction ceased ca. 1200 BP, at which point it appears that the terraces were abandoned and populations moved to coastal areas, where they constructed stonework villages along coastal margins and taro fields during what Liston (2009) refers to as a Transitional Era ca. 1200-700 BP. Evidence of defensive features, including placement of villages behind dense mangroves, and stone walls and platforms, suggest the move was motivated by population growth and competition for land or resources (Clark 2005, Liston 2009, Masse 1989). Occupation and construction of stonework villages on many of the southern Rock Islands also took place during this period, but these appear to have been abandoned by ~700 BP (Clark and Reepmeyer 2012). Villages on Babeldaob were still inhabited at European contact, which occurred in 1783 with the shipwreck of the British *Antelope*, on Ulong Island (Fitzpatrick 2014, Liston 2009).

Chelechol ra Orrak

The Chelechol ra Orrak ("beach of Orrak") archaeological site (B:IR-1:23) is located on Orrak Island, which is about 1.1 km long, 0.5 km at its widest, and located about 1 km off the southeastern coast of Babeldaob (Figure 1.4). The island was connected to Babeldaob prehistorically by a causeway constructed of coral rubble, but portions have since been washed out as a result of tidal activity over time or purposefully removed; the remaining areas are now covered with mangrove vegetation. Similar to other Rock Islands, Orrak's coast is primarily rocky and steep, with several beach formations. The island's interior contains two marine lakes and several other sites, including Upper Orrak (B:IR-1:27), which is a former quarry used by the Yapese to carve stone money (Fitzpatrick 2003a). Chelechol ra Orrak stretches across a series of small limestone caves and rockshelters fringed by dense vegetation that stretches for about about 200 m along the western shore. A modern dock and other structures built over the last 10 years or so, have altered wave action and sand deposition, resulting in increased beach erosion and sedimentation in offshore seagrass beds.

Initially, the site was investigated for its use as a quarry for the construction of Yapese stone money by Blaiyok (1993). Since 2000, the largest central rockshelter has been the primary focus of archaeological excavation, beginning with Fitzpatrick's (2003a) dissertation, which focused on the construction and exchange of stone money. Over the course of multiple additional field seasons in 2002, 2007, 2012, and 2015, a total of 15 m^2 have been excavated; however, the base of the site has not yet been reached and excavations are planned to continue.

Archaeological investigation has revealed multiple surface features (e.g., unfinished stone money, limestone and coral rock alignments and walls, and docks that have been attributed to Yapese or historic use of the site), while excavations show that there are multiple components to the site demonstrating human use that spans at least the last 3000 years (Fitzpatrick 2002, 2003a, 2003b, Fitzpatrick and Jew 2018). The upper layers (roughly, the top 50 cm of deposits) of the site reflect episodic habitation as evidenced by areas of repeated burning, dense faunal remains, and a wide variety of artifacts dating from ca. 1700 BP. The faunal assemblage is diverse, including crustaceans, echinoderms, elasmobranchs, bony fish representing over 20 taxa, shellfish

representing almost 100 taxa, and sea turtle. Analysis of a portion of the faunal assemblage from Chelechol ra Orrak has demonstrated that the site's inhabitants were utilizing a variety of marine environments for fishing. A preponderance of parrotfishes (*Scaridae* sp.) and wrasses (*Labride* sp.) suggests targeting of nearshore and lagoon habitats, but this may also be a product of archaeological preservation (Fitzpatrick and Kataoka 2005, Fitzpatrick et al. 2011). There is evidence for an overall decrease in fishing with a concomitant increase in shellfish consumption occurs ca. 1200 BP, but this does not appear to be a result of overfishing (Fitzpatrick et al. 2011, Giovas et al. 2016). The rich artifactual record includes stone and shell adzes, pottery, bone needles, glass beads, and shell ornaments. Pearl shell (*Pinctada margaritifera*) scrapers have been recovered in association with human remains as a likely grave good. Most often, these tools are associated with grating starchy crops such as taro and coconut, which is traditionally a female task, and they are often included in baskets prepared for pregnant women as part of traditional birth ceremonies. Ethnographically, they are known to be a form of women's money (*chesiuch*) (Fitzpatrick and Boyle 2003). At Chelechol ra Orrak, scrapers have been found in association with female burials and directly dated to 1925-1635 cal. BP, demonstrating cultural continuity of the artifact's significance for almost 2000 years and possibly longer.

Burial deposits are primarily found below ~1m depth and continue through the deepest known portions of the site in loose coral sand that becomes a hard calcrete in areas where repeated moisture from tidal activity has encroached (Nelson and Fitzpatrick 2006). To date, the remains of more than 55 individuals have been excavated from the site that represent males and females ranging in age from fetal to older adult (e.g., over ~50 years of age; Buikstra and Ubelaker 1994). Radiocarbon dates indicate that the mortuary component of the sites dates to at least 3000 BP and continued until ~1700 BP, making this portion of the site contemporary with the earliest archaeological sites in Palau, and the individuals interred here likely representatives of the first 10-12 generations of occupation (Fitzpatrick and Jew 2018). No evidence for habitation of the site is present during this time, and only appears once burial activity ceased. Because mortuary activity was consistent over such a long time frame, existing burials were often disturbed as new individuals were interred, resulting in a large number of fragmentary

and commingled individuals (Nelson et al. 2015). Many burials remain complete and fully articulated; these individuals are designated by burial numbers and are collectively referred to as "articulated burials" throughout this dissertation. There does not appear to be any standard burial orientation, but individuals are typically found in an extended position with their hands over their hips and feet crossed at the ankles (Fitzpatrick and Nelson 2011). With the exception of the abovementioned pearl shell scrapers, there are only two other examples of grave goods: a single male excavated in 2015 was recovered with marine mollusks placed over the torso and one pearl shell scraper, and an isolated adult neurocranium containing the purposefully placed frontal of a young child (Fitzpatrick and Nelson 2011, Nelson et al. 2015).
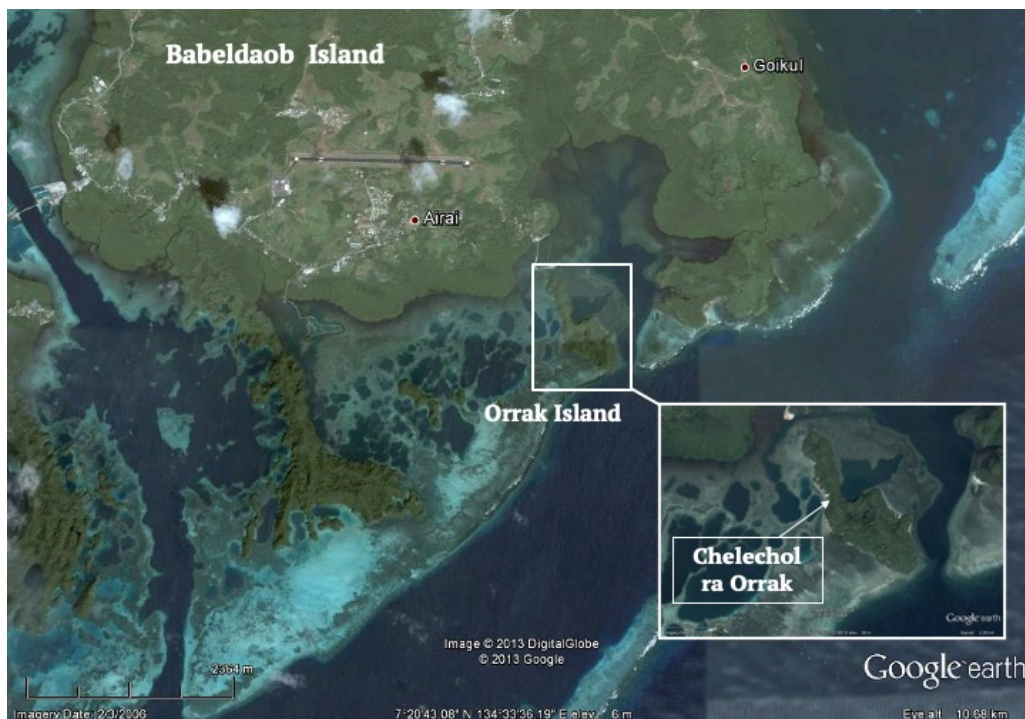
Figure 1.4. Map of Chelechol ra Orrak.

Project Overview

      This dissertation draws on bioarchaeological data from one of the most important archaeological sites found in Micronesia at Chelechol ra Orrak to address research

questions related to the initial human settlement and subsequent adaptation of small island environments in Palau, and more broadly, Remote Oceania. Questions regarding initial human settlement are addressed in Chapters Two and Three via genetic, archaeological, and osteological data. Chapter Two, which includes unpublished co-authored material with Caroline Kisielinski, Justin Tackney, Dennis O'Rourke, Nelson Ting, and Scott M. Fitzpatrick, discusses the results of ancient DNA research at Chelechol ra Orrak in testing hypotheses related to a potential "homeland" from where the earliest Palauan people originated. Additionally, direct radiocarbon dates on the individuals sampled are used to provide a temporal context within which to interpret the genetic data. Chapter Three, which has been published previously with co-authors Scott M. Fitzpatrick and Matthew F. Napolitano, uses a combination of archaeological and osteological data from the Ucheliungs site to test the hypothesis that early inhabitants of Palau underwent a process of insular dwarfing following arrival in response to an impoverished terrestrial resource base (Berger et al. 2008).

The next two chapters offer perspectives on early Palauan behavioral adaptations following initial settlement. Chapter Four, which was previously published with co-authors Scott M. Fitzpatrick and John Krigbaum, uses stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) from bone collagen and apatite to reconstruct the diet of individuals interred at Chelechol ra Orrak. Chapter Five, which was previously published with co-authors Greg C. Nelson and Scott M. Fitzpatrick, evaluates the possibility of a relationship between chewing betel nut, a common behavior in Palau that has been observed since initial human arrival, and high frequencies of osteoarthritis in the temporomandibular joint (TMJ) at Chelechol ra Orrak. In doing so, I begin to explore potential health tradeoffs with a common cultural behavior that has been continuously practiced in the area for more than 3000 years (Fitzpatrick et al. 2003). Taken together, these studies provide a fundamental baseline to understanding initial human settlement and small island adaptation in Palau from a bioarchaeological perspective. These data allow for more fine-scale resolution in understanding past lifeways in Palau and western Micronesia, generally, with important implications for examining dispersal processes within the larger context of Remote Oceania.

CHAPTER II

ANCIENT MITOCHONDRIAL GENOMES FROM CHELECHOL RA ORRAK,
PALAU: NEW INSIGHTS INTO THE INITIAL HUMAN SETTLEMENT OF
REMOTE OCEANIA

Introduction

The contribution of biological data to transdisciplinary models of Remote Oceanic settlement is significant because it allows for the direct study of human dispersals, regional population relationships, and adaptations following arrival upon previously uninhabited islands (Clark et al. 2017). Within bioarchaeology, the relatively recent addition of molecular techniques such as ancient DNA (aDNA) are playing an increasingly important role in reconstructing past lifeways and dispersal patterns in the Pacific. In recent years, bioarchaeological and genetic research has begun to shed light on dispersals, settlement, and adaptation associated with Lapita groups, who originated in the Bismarck Archipelago and rapidly spread into Remote Oceania as far as Samoa and Tonga in West Polynesia ca. 3000 BP (e.g., Buckley et al. 2008, 2014, Foster et al. 2013, Kinaston et al. 2015, Tromp et al. 2020, Valentin et al. 2016). Yet there remains a need to refine and integrate biological data from western Micronesia, which was settled by contemporary but distinctly non-Lapita people, to better characterize early Pacific Island population dynamics. Recent analyses of genome-wide data from Lapita individuals on Vanuatu and Tonga have demonstrated that shortly after initial human arrival, subsequent migrations to the islands rapidly shifted genetic ancestry despite linguistic continuity (Lipson et al. 2018, Posth et al. 2018, Skoglund et al. 2016). Therefore, in order to address questions regarding the dynamics of initial human arrival, biological data from the time period of interest is critical. To address early population dynamics in Palau, this chapter presents a preliminary look at western Micronesian and more specifically, Palauan settlement using complete and partial mitochondrial genomes from the mortuary site of Chelechol ra Orrak.

Ancient DNA in the Pacific Islands

Until recently, the use of aDNA in the Pacific Islands and other tropical environments has been limited due to issues of endogenous DNA preservation in hot and humid climates. With improvements to sequencing technologies and the development of enrichment methods, obtaining aDNA from these climes remains challenging, but is now feasible (Horn 2012, Knapp and Hofreiter 2010, Rizzi et al. 2012). In the Pacific, the majority of aDNA research has focused on using flora and fauna as proxies for human movement in an approach termed the "commensal model", which relies on taxa that are unable to reach island environments without human intervention. As such, the appearance of these domesticated plants and animals at archaeological sites serves as indirect evidence for human presence (Matisoo-Smith 1994). Applications of this approach with rats (*Rattus exulans*), pigs (*Sus scrofa*), chickens (*Gallus gallus*), and dogs (*Canis lupis familiaris*) have been successful in providing multiple sources of evidence that support Southeast Asian and ISEA connections to Remote Oceania via Lapita dispersals, ISEA-Western Micronesian connections, Lapita origins for Polynesian groups, and the possible introduction of chickens to the South American mainland by Polynesians (Allen et al. 2001, Gongora et al. 2008, Grieg et al. 2018, Larson et al. 2005, 2007, Matisoo-Smith et al. 1998, Matisoo-Smith and Robins 2004, Oskarsson et al. 2012, Savolainen et al. 2004, Storey et al. 2007, 2014).

The earliest Pacific aDNA studies directly involving human remains focused on identification of the "Polynesian Motif," a series of polymorphisms that now define mitochondrial DNA (mtDNA) haplogroup B4a1a1a, as a means to authenticate aDNA and assess relationships between Lapita and East Polynesian groups (Hagelberg 1997, Hagelberg and Clegg 1993, Hagelberg et al. 1994, Melton et al. 1995, Redd et al. 1995). Subsequent studies from the Gambier Islands in East Polynesia and historic era Solomon Islanders demonstrated consistency between ancient and modern populations (Deguilloux et al. 2011, Ricaut et al. 2010). More recently, ancient mitochondrial genomes and genome-wide data have been obtained from human remains dating to early settlement periods from several Pacific Islands (Fehren-Schmitz et al. 2017, Holdaway and Jacomb 2000, Knapp et al. 2012). Genome-wide aDNA belonging to a small number of Lapita individuals from Vanuatu and Tonga demonstrated that little to no Papuan ancestry was

present following initial Lapita dispersals, and admixture between the two linguistic groups occurred later than previously thought. Additional sequencing from individuals across a broader time period indicate that the contribution of Papuan ancestry seen in modern Vanuatu populations instead is the result of new Papuan migrants to the archipelago by the end of the Lapita period, ca. 2,400 BP and demonstrates both the importance of sampling individuals dating to the event of interest targeted by aDNA research, as well as the critical need for chronological control in aDNA studies (Lipson et al. 2018, Posth et al. 2018, Skoglund et al. 2016).

Genetic Evidence for the Colonization of Micronesia

Despite widespread work focused on the population genetics of the Pacific Islands region, Micronesia has been largely underrepresented in both global and regionally focused genetic studies. Research that does include the region often lumps individuals from islands across western, central, and eastern Micronesia into a single population even though these areas were settled by peoples from different points of origin (Athens 2018, Intoh 1997, Jackson 1986). Limited work focused specifically on Micronesian population relationships based on modern DNA samples has provided a foundation upon which hypotheses related to specific points of origin can be built. An analysis of mtDNA region V length polymorphisms from multiple Pacific Island and Asian populations found associations between linguistic and genetic groupings, and evidence for shared ISEA maternal ancestry for Oceanic-speaking Micronesian and Polynesian groups. Non-Oceanic speaking Micronesian populations (i.e., Palau and the Marianas), however, appeared distinct, and this point has been substantiated with additional research using biparental short tandem repeats (STRs) (Lum and Cann 1998, Lum et al. 2002). Similarly, craniometric studies have demonstrated closeness between Micronesian and Southeast Asian groups (Pietrusewsky 1970, 1990). Subsequent mtDNA work focused more specifically on the relationship between Micronesian and Polynesian populations found clear distinctions between the western and the central-eastern Micronesian islands, with a settlement history tracing back directly to ISEA for the west and to Near Oceania for central and eastern islands, mirroring archaeological evidence (Athens 2018, Carson 2012, Clark 2004, Fitzpatrick 2018, Intoh 1997). Among western Micronesian islands,

Palau was found to uniquely possess lineages shared with populations in New Guinea, though the timing of this admixture is unknown (Lum and Cann 2000, Lum et al. 2002). Together, this evidence suggests a complex colonization history consistent with settlement of western Micronesia directly from ISEA; however, the lack of biological data from individuals dating to this early period of colonization has prevented researchers from identifying more specific areas within ISEA as candidate source regions.

Based on these studies and complementary linguistic, archaeological, and computer modeling work, some general hypotheses for regional connections can be generated. Both modern genetic and archaeological evidence have suggested interactions with groups in New Guinea, which is typically associated with Papuan-speakers and mtDNA haplogroups P, Q, and some branches of M (M27, M28, M29) (Friedlander et al. 2008, Merriwether et al. 2005, Soares et al. 2011). Computer simulations of voyaging and commensal genetic evidence from pigs have suggested possible origins in the southern Philippines, where mtDNA haplogroups B4a1a, E1a1a, and M7c3c are common, or eastern Indonesia where mtDNA haplogroups B4a1a1, E, and F1a4 are more common (Tabbada et al. 2010, Tumonggor et al. 2013, Vilar et al. 2013). However, many mtDNA haplogroups, including lineages within B, D, E, and M, are widespread throughout ISEA, but are typically associated with populations that speak Austronesian languages. Therefore, identification of these lineages may aid in eliminating some of the above candidate source regions for Palau or may result in an increased likelihood of some source regions over others (Duggan et al. 2014, Friedlander et al. 2007, Lum and Cann 2000, Tabbada et al. 2010).

Materials and Methods

Sampling

Bone samples were selected from articulated burials excavated at Chelechol ra Orrak to avoid inadvertent repetitive sampling of the same individuals. Because rib fragments are limited in their utility for osteological analysis, they were chosen as the preferred element for sampling. Although research has demonstrated that the petrous portion of the temporal bone yields high amounts of endogenous DNA, sampling this area can result in the destruction of bone(s) that are critical for a number of osteological

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assessments including estimations of sex, age at death, and ancestry, among others (Buikstra and Ubelaker 1994, Harvati and Weaver 2006, Pinhasi et al. 2015, Ponce de Leon et al. 2018). While ribs may result in overall lower endogenous DNA yields, they have still been successfully utilized in aDNA studies, including this work. In cases where ribs were not available, other elements that are considered less osteologically informative, such as carpals or long bone fragments, were selected. Burials that were excavated prior to 2015 were sampled at the University of Oregon Island and Coastal Archaeology Laboratory. These remains had been previously washed, dried, and handled by researchers since their excavation. Burials excavated during the 2015 field season were sampled under sterile conditions in the field (Figure 2.1). During sterile sampling, all surrounding excavation work ceased and personnel stepped away from the excavation units until sampling was completed. A single individual, wearing a hair cover, sleeve covers, mask, and gloves, used sterilized tools to remove a bone or bone fragment, that was placed in a sterile 15 mL Falcon tube that remained unopened until the bone was used for DNA extraction in an aDNA lab facility. To account for potential contamination prior to aDNA work, modern DNA controls were collected prior to aDNA lab work from personnel that had handled samples using Oragene OG-500 saliva collection kits. Informed consent was obtained and procedures were approved by the University of Oregon Research Compliance Services.

DNA Extraction

All aDNA lab work was performed in dedicated aDNA clean lab facilities that follow established procedures to prevent contamination. Work conducted prior to August 2017 was performed in the Ancient DNA Laboratory at the University of Utah, while lab work conducted in August 2017 and later took place in the Ancient DNA Laboratory at the University of Kansas. DNA was extracted from 80-120 mg of drilled bone powder from elements that first had the outer surface removed with a Dremel rotary tool. Bone powder was digested in a 1mL buffer containing 0.5M EDTA, 250 μg/ml proteinase K, and 40 mM DTT in two stages. First, a pre-digestion step was performed at 55°C for 1 hour and discarded to remove non-target DNA, followed by a secondary digestion step at 37°C for 18-24 hours (Damgaard et al. 2015). The extraction buffer was then purified

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with an in-house silica column protocol that combines aspects of a previously published methodology (Gamba et al. 2016) with the commercially available GENECLEAN For Ancient DNA Kit (MP Biomedicals). DNA extracts were stored in Eppendorf LoBind tubes at -20°C. To minimize the potential for contamination during DNA extraction, no more than five samples were run at a time, and one water extraction blank was processed with each set of extractions as a negative control. Sequencing was limited to samples that had a corresponding non-amplifying extraction and (described below) PCR blank.

Figure 2.1. Comic illustrating the field sampling protocol (drawn by John Swogger).

HVR-I Amplification and Sequencing

Traditionally, mitochondrial DNA has been the target of aDNA studies, and it is the marker used for this study. Unlike nuclear DNA, which is billions of base pairs in length and inherited from both parents, the mitochondrial genome is comparatively smaller (16,569 base pairs) and maternally inherited. Critical to aDNA studies, which face issues of preservation, each mitochondrion can contain hundreds of copies of

mtDNA, and with numerous mitochondria present in each cell, the likelihood that target DNA is present increases substantially (Alonso et al. 2004, Hagelberg 1994, Raff et al. 2010). Additionally, the rapid mutation rate in mtDNA allows for examination of genetic history within a time scale relevant to archaeological studies (Giles et al. 1980, Paijmans et al. 2013). Substitutions in mtDNA result in a number of single nucleotide polymorphisms (SNPs) that can be found across individuals with shared ancestry. These larger groupings, referred to as haplogroups, are designated by a single letter of the alphabet, followed by number and letter combinations to designate more refined haplogroups (e.g., B4a1a1a).

Initially, lab work for this study focused on the amplification and sequencing of a portion of the mitochondrial control region known as the first hypervariable region (HVR-I), an area where many haplogroup-defining SNPs can be found. DNA extracts from 17 individuals were amplified using the polymerase chain reaction (PCR) in 50 μL reactions (see Raff et al. 2010 for additional details). Three primer pairs allowed for genotyping of fragments that provide coverage of nucleotide positions 16043-16161, 16183-16277, 16288-16402, respectively, while a fourth primer pair (HVRI_CarP1 and HVRI_CarP2) provided total coverage of nucleotide positions 16043-16277 + 16288-16402 (Table 2.1) (Tackney et al. 2019). The extraction blank and numerous water PCR blanks were processed at the same time as negative controls. Amplicons were visualized on agarose gels. After successful amplification, both the forward and reverse strands of the amplicon were cleaned using either QIAquick PCR Purification Kits (Qiagen) or UltraClean PCR Clean-Up Kits (MoBio Laboratories) and were either sequenced using Sanger sequencing at the DNA Sequencing Core Facility at the University of Utah using a 3730 DNA Analyzer or by Genewiz, using an ABI 3730xl DNA Analyzer (https://www.genewiz.com/en/Public/Services/Sanger-Sequencing). Sequences with ambiguous calls (e.g., double peaks) were either repeated with replicate PCR or sequencing reactions or noted in Geneious, version 7. Replicate amplifications were also used to confirm base calls.

Library Preparation, Enrichment, and Sequencing of Complete Mitogenomes

To allow for more refined haplotype calls, seven individuals were selected based on the results of HVR-I work for sequencing of complete mitochondrial genomes using Illumina next-generation dual indexed sequencing libraries constructed from 25 µL of DNA extract using the blunt end NEBNext Fast DNA Library Prep Master Mix Set (New England BioLabs Inc.) with Illumina blunt end adapters and SPRI bead cleanup (Meyer and Kircher 2010). Primary amplification cycles were determined using a quantitative polymerase chain reaction (qPCR) of 1:500 diluted preamplified library. Primary amplifications were performed in 50 µL reactions, with 10 µL of unamplified library, Amplitaq Gold 360 Mastermix, and Illumina indexing primers (Kircher et al. 2012). Primary amplified libraries were visualized on an Agilent Tapestation 2200, and quantified with a qPCR run using a 1:20,000 diluted library aliquot. Each primary amplified library was pooled and diluted as appropriate and shotgun sequenced to determine endogenous DNA content on an Illumina NextSeq 550 at the KU Genome Sequencing Core facility using a mid output 150 cycle (MO-150), PE-75 flowcell.

Table 2.1. Primer sequences used for HVR-I amplification and sequencing. All primer sequences previously published in Raff et al. (2010), except HVRI-Car_P1F and HVRI_CarP1R, which were published in Tackney et al. (2019).

Primer ID	Sequence (5' – 3')
HVRI_P1F	GTT CTT TCA TGG GGA AGC AG
HVRI_P1Rc	TTG ATG TGG ATT GGG TTT TT
HVRI_P2Fb	AAA ACC CAA TCC ACA TCA AA
HVRI_P2R	GGG TGG GTA GGT TTG TTG G
HVRI_P3F	CCC ACT AGG ATA CCA ACA AAC C
HVRI_P3R	ATT GAT TTC ACG GAG GAT GG
HVRI_CarP1F	CGG TAC CAT AAA TAC TTG AC
HVRI_CarP1R	GAT AGT TGA GGG TTG ATT G

Based on these results, libraries with endogenous DNA content above 0.5% were targeted for mitogenome hybridization capture. Libraries then underwent a secondary amplification in four 50 µL reactions with Accuprime Pfx and 4 µL library input that was then pooled and SPRI purified. Custom hybridization probes for the human mitochondrial

genome were designed off of the rRSRS sequences in 80 base fragments at 1.5X coverage (Behar 2012, Malyarchuk 2013). IDT xGEN Lockdown Probes and universal Blocking Oligos were selected for production. IDT-suggested wash buffers were utilized with the provided protocol, except slight changes were made to the volume of the initial hybridization buffer and the hybridization time and temperature were increased to 60ºC for 48 hours. An additional qPCR with 1:50 diluted captured libraries was performed. Based on these results, captured libraries were then amplified again using Accuprime Pfx in 50 μL reactions with 15 μL library input and quantified as before with Tapestation electropherograms and qPCR. Libraries were then pooled and sequenced on a NextSeq 550 as described above.

Data Processing

Demultiplexed reads were trimmed and adapters removed using CutAdapt v.2.4 (Martin 2011). Paired-end reads with a minimum overlap of 11 bp were merged into a single fragment with AdapterRemoval v.2.2.4, and merged trimmed reads were then mapped to the human reference genome (revised Cambridge Reference Sequence, or rCRS) using Burrows Wheeler Aligner (bwa, v.0.7.17; Li and Durbin 2010, Schubert et al. 2016). Reads were filtered and those with a mapping quality <30 were excluded using samtools v.1.9. Duplicate reads were also removed using samtools v.1.9 (Li et al. 2009). aDNA damage patterns were assessed using mapDamage2, and the resulting rescaled BAM files were used for the process of variant calling and generating a consensus sequence using bcftools-1.9 (Danecek et al. 2011, Jónsson et al. 2013, Li 2011). Mitochondrial haplotypes were assigned using Haplogrep 2.0 and manually verified in Geneious, version 7 (Weissensteiner et al. 2016).

Radiocarbon Dating

Radiocarbon Dating Methods

Because burial activity at Chelechol ra Orrak spans more than 1200 years, obtaining direct radiocarbon dates on the burials sampled for aDNA was necessary to provide temporal control as migration trajectories likely varied over the course of this period. Bone samples weighing between 2–18 g from osteologically uninformative

elements such as long bone, rib, or vertebral fragments were sent to Beta Analytic for dating. Previously published samples were dated at the Keck Accelerator Mass Spectrometer Laboratory at the University of California in Irvine. All dates, including those on articulated burials that were previously reported, were calibrated using OxCal v.4.3 with a 50% mixed marine/terrestrial curve to account for marine dietary contributions (see Chapter IV, Bronk Ramsey 2009, Fitzpatrick 2003, Fitzpatrick and Jew 2018, Reimer et al. 2013). Multiple marine reservoir corrections (ΔR) are available for Palau (Masse et al. 2006, Petchey and Clark 2010, Yoneda et al. 2007), but because none are present for the southern coast of Babeldaob or the northern Rock Islands, no ΔR was applied in the calibration of these dates (Table 2.2) (Fitzpatrick and Jew 2018, Petchey and Clark 2010).

Radiocarbon Results

With the addition of 11 new radiocarbon dates run as a part of this project, there are now a total of 14 direct radiocarbon dates on articulated burials. Together, these dates span 2765-1625 cal. BP, with the majority clustering between ~2700-2300 (Figure 2.2). Burial 14 is the oldest articulated burial thus far, and dates to 2765-2690 cal. BP. A cluster of burials (12, 20, 21, 25) overlap with the latter half of the date range for Burial 14, beginning ca. 2700 cal. BP. Three individuals (Burials 18, 26, and 38) all date noticeably later, from ~2000-1600 BP. Interestingly, these individuals were also excavated from the same area spanning two 1×1 meter units (E2S4 and E3S4). Although there is too much overlap between the remaining dated individuals from across the excavated areas of the site, there does appear to be a rough general pattern of the dated burials decreasing in age as one moves from west to east across the areas excavated thus far. This suggests the possibility that there may be some coarse spatio-temporal clustering of burials across the site, though additional work is needed to assess this possibility. No burials dated thus far are older than 2765 cal. BP (the older end of Burial 14's age range), therefore genetic results presented in this chapter may reflect additional interaction in the first centuries following initial settlement given that the earliest dates in Palau cluster around 3000 cal. BP (Clark 2004, 2005, Fitzpatrick 2003b, Fitzpatrick and Jew 2018, Stone et al. 2017).

Table 2.2. Radiocarbon results for articulated burials (*previously reported in Fitzpatrick and Jew 2018).

Burial	Lab Number	Provenience	Element Sampled	Sample Weight (g)	Radiocarbon Age (BP)	$^{13}C/^{12}C$ (‰)	Calibrated Age (2 sigma BP)
Burial 11		E3S1	Vert. arch	5.4	failed testing	failed testing	failed testing
Burial 12	Beta-521981	E3S1-E3S2	Tooth	2	2610 ±30	-15.6	2680-2365
Burial 13	Beta-497455	E1S5-W1S5	Ulna, Rib, Occipital, Thoracic Vert.	15.48	2550 ±30		2495-2340
Burial 14	Beta-541135	E1S4-W1S4		9.56	2760±30	-16.1	2765-2690
Burial 15*	PL2 (UCIAMS-151858)	E2S1-E2S2	Scapula, Clavicle, Long Bone	13.99	2475±25		2360-2300
Burial 16*	PL1 (UCIAMS-151857)	E1S4	Ribs	9.75	2465±25		2360-2295
Burial 18	Beta-523825	E2S4-E3S4/E3S5	Parietal	11.08	2100±30	-14.1	1955-1815
Burial 19	Beta-53840	E1S5-E1S4	Ribs, Humerus	12.2	2490±30	-16.1	2425-2300
Burial 20	Beta-521983	E1S4-E1S3	Sphenoid	7.13	2630±30	-15.3	2700-2415
Burial 21*	PL3 (UCIAMS-151859)	E1S4	L. Radius	11.91	2605±25		2675-2360
Burial 24	Beta-538337	E1S2-W1S2-W1S1	R. Fibula, Vert.	11.49	2540±30	-15.1	2485-2335
Burial 25	Beta-538338	E1S1-SE	Vert. arch, L. ulna	17.61	2640±30	-15.4	2705-2440
Burial 26	Beta-538339	E3S4-E2S4	Ribs	8.35	2200±30	-14.7	2100-1900
Burial 38	Beta-497456	E2S4	R. Radius	12.06	1960±30		1810-1625

It is important to note for the genetic analyses presented here that Burial 37 was not directly dated. As this is the only articulated juvenile burial recovered thus far, we chose not to complete a second destructive analysis and directly date this individual. This burial is also significant because of its context: Burial 37, an infant around the age of birth, was found placed directly on or between the femora of Burial 24, a young adult female, suggesting this was a mother-infant pair. Therefore, the radiocarbon date presented for Burial 24 has been used to provide temporal context for Burial 37.
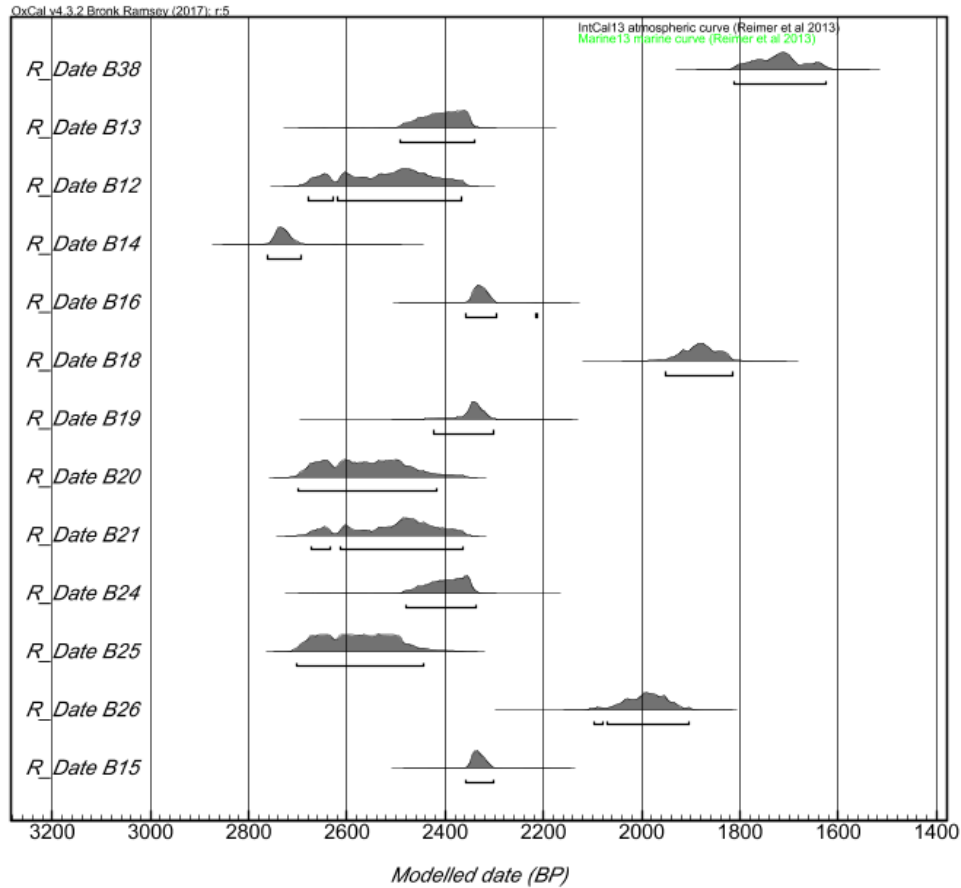
Figure 2.2. Plot of calibrated ¹⁴C ranges for each of the articulated burials.

aDNA Results

HVR-I

Each of the 17 individuals sampled for aDNA resulted in successful amplification and sequencing of at least one fragment, demonstrating the feasibility of aDNA research at Chelechol ra Orrak despite taphonomic conditions that are not conducive to endogenous DNA preservation. However, amplification and sequencing of at least three of the four HVR-I fragments was only successful for seven individuals, and of these, only three could be assigned to tentative haplogroups. These results suggest that partial HVR-I sequences may not be sufficient for haplogroup assignment in regard to this population

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and this level of endogenous DNA preservation. The tentative haplogroup assignments based on HVR-I SNPs are presented in Table 2.3.

Table 2.3. HVR-I variants and haplogroup assignments, *indicates double peaks, these are tentative calls.

Individual	HVR-I SNPs (+16,000)	Haplogroup
Burial 13	223, 257	
Burial 18	185, 223, 260, 298*	
Burial 20	192, 223, 254, 271, 316, 362	D4 or M7
Burial 21	223, 245	
Burial 25	086, 129, 297, 324	M7b1a2a
Burial 37	189, 192, 223*, 297*	Possibly M7b1a1
Burial 38	362	

Burial 25 is the only individual that could be unequivocally assigned to a haplogroup, M7b1a2a. The remaining two individuals with tentative haplogroup assignments are Burials 20 and 37. The SNPs associated with Burial 20 are likely some combination of haplogroup-defining variants and mutations private to this individual, but at this level of resolution the distinction between the two cannot yet be determined. Depending on which variants are deemed private, Burial 20 can be assigned to either D4 (based on variants at positions 16192, 16223, 16316, 16362) or M7 (based on variants at positions 16223, 16271, 16362). Although Burial 37 has been assigned to the M7b1a1 haplogroup, half of the SNP calls are tentative, and the possibility remains that this individual could be re-assigned to a different haplogroup with increased genomic coverage. The remaining individuals do not exhibit sufficient sequence variation to assign haplogroups at this stage; sequencing of additional portions of the mtDNA genome would likely aid in addressing this issue.

Although partial sequences were not informative in regard to genetic ancestry, some did prove useful for resolving questions related to the commingled nature of much of the burial assemblage. Burial 18 is represented by a cranium and cervical vertebrate excavated in 2012, and during the 2015 field season, postcranial remains were found in the same excavation area that were thought to belong to Burial 18. In order to collect an aDNA sample for this individual under sterile field conditions, a second postcranial

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sample was taken in 2015. This sample was used to generate a new DNA extract for mitogenomic work as the original DNA extract was located in Utah. Comparison of the HVR-I results from both samples confirmed that instead the cranial and postcranial samples belong to two distinct individuals (Burials 18 and 38) despite apparent archaeological association.

The low success rate of haplogroup assignment based on HVR-I may also reflect the need to modify primer annealing locations, as the primers used for this study were originally designed for Arctic North American populations. As a result, annealing locations for these primers covered areas of HVR-I where potentially informative SNPs may have been located. However, the accessibility and cost of next generation sequencing improved drastically over the time that this HVR-I work was performed and provides increased resolution by allowing for coverage of the full mitochondrial genome. As a result, follow-up work targeted a subset of individuals that using these methods rather than redesigning HVR-I primers.

Mitochondrial Genomes

Of the seven individuals sequenced for complete mitochondrial genomes, four yielded an average read depth > 5X and sufficient coverage to assign likely or tentative haplogroups. Coverage varied from 9% to almost 100%, demonstrating the wide range of preservation across the site (Table 2.4).

Among these four individuals, results revealed the presence of four distinct mitochondrial haplogroups that are presented in Table 2.4. These results share some similarities with the tentative haplogroup assignments from the HVR-I data. Burial 25, which yielded nearly 100% mitogenomic coverage, has remained consistently assigned to M7b1a2a. Neither Burial 20 nor Burial 18 could be assigned to haplogroups based on HVR-I work, but despite relatively poor mitogenomic coverage, could be tentatively assigned using the next-generation sequencing data. HVR-I results assigned Burial 20 to either haplogroup M7 or D4, which was further resolved with next-generation sequencing results to D1 or D4. Of the defining mutations that define haplogroup D1, only one (at position 2706) is present. Given the consistency of haplogroup D4 between both data sets, the implications of a tentative assignment to D4 will be discussed, however the

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possibility that Burial 20 could be reassigned to a different haplogroup if additional sequencing provides improved coverage must be considered.

Table 2.4. Library and Sequencing Metrics. Haplogroup assignment based on estimate from Haplogrep 2.0, with HVR-I haplogroup assignments in parentheses (Weissensteiner et al. 2016).

Sample	Barcoded Reads	Mapped Reads	Unique Reads	Coverage	Bases Missing	Average Depth	Mapped Read %	Haplogroup
Burial 12	15,385,848	1,559,559	92	8.90%	15,094	4.46	16.55	
Burial 16	28,058,444	13,201,424	49	1.91%	16,252	14.93	55.01	
Burial 18	27,710,073	15,617,024	803	50.82%	8,148	8.14	71.86	B5b1c
Burial 20	11,500,756	5,714,091	224	20.85%	13,115	6.09	69.85	D1 or D4 (D4 or M7)
Burial 21	20,864,444	0	0	0	0	0	0.00	
Burial 25	23,030,639	17,265,126	4,469	99.85%	25	21.42	91.53	M7b1a2a1 (M7b1a2a)
Burial 37	13,381,106	3,348,408	304	28.29%	11,881	5.59	32.99	E1a1a (Possibly M7b1a1)

Burial 18, which could not be assigned to a haplogroup based on HVR-I, can be tentatively assigned to haplogroup B5b1c based on this work. All five haplogroup-defining SNPs for B5 are present with one exception that is missing due to a lack of coverage at that site (Table 2.5). Of the remaining variants identified, the best possible fit is B5b1c, however, a number of defining mutations are missing due to a lack of coverage. As such, this assignment must remain tentative. Similarly, analysis of Burial 37's results best fit haplogroup E1a1a; but, given the number of missing haplogroup-defining mutations due to poor coverage, this assignment also remains tentative.

Table 2.5. Defining mutations for B5 haplogroups based on Burial 18. Positions in brackets do not exhibit the expected variant. *missing due to a lack of coverage.

Haplogroup	Defining mutations
B5	709, 8584, 9950, 10398 [16140*]
B5b	[103*, 204, 1598*], 8829, [12361, 15223*, 15508*], 15662, [15891*], 15927, [16243]
B5b1c	[152*], 3480, [3819*, 5836*], 7771, [8467*, 10274*]

Discussion

Although these results are tentative and only represent a small number of individuals at Chelechol ra Orrak—and more broadly, prehistoric Palau—some general conclusions can be made. Of the four individuals that yielded sufficient genomic coverage to assign haplogroups or tentative haplogroups, four distinct maternal lineages are represented in individuals that date from 2700-1815 cal. BP, with the majority dating from 2700-2365 cal. BP (Table 2.2). Although the radiocarbon dates indicate that genetic data has not yet been obtained from individuals dating to the first ~300 years following initial human arrival, the majority of these individuals represent those that were within the first ~10 generations. The mtDNA diversity found among four individuals demonstrates that Chelechol ra Orrak was utilized as a cemetery by multiple maternally-unrelated families, and that bioarchaeological data from the site is more likely to be representative of a broad population of early Palauans rather than one family group. This information may also aid in future work at the site focused on kinship at the site.

An inherent challenge in the interpretation of these comparisons is the lack of aDNA research conducted in ISEA to date; as such, the overwhelming majority of comparisons with ISEA mtDNA data are based on modern population genetics studies. A single study involving early Metal Age burials from the Gua Harimau site in Sumatra identified M7b1a and E1a1a haplogroups, but these samples are either contemporary with those at Chelechol ra Orrak or date to slightly later in time (Matsumura et al. 2018). Although this study demonstrates mtDNA haplogroup continuity between Palau and ISEA from ~3000-1700 BP, samples dating to an earlier time period would better inform potential areas of population origin for Palau.

When placed in a regional perspective, these results are generally characteristic of Austronesian-speaking populations that likely originated in ISEA and supports previous linguistic and archaeological evidence (Figure 2.3). No haplogroups that are typically associated with Papuan-speaking groups (P, Q, M27, M28, M29), particularly those identified in New Guinea, have been observed among these individuals (Friedlaender et al. 2008, Merriwether et al. 2005, Soares et al. 2011). Based on the absence of these haplogroups, the hypothesis that New Guinea may have been a point of possible origin for early Palauans is not supported. This conclusion mirrors findings from computer simulations of drift voyaging, which found that voyages from northern New Guinea had a minimal (<1%) chance of successful landfall in Palau (Callaghan and Fitzpatrick 2008). Haplogroups within B, E, and M are found throughout ISEA, but the specific haplogroups identified at Chelechol ra Orrak appear less frequently represented in population genetics studies to date. Therefore, a discussion of the frequency of each haplogroup identified will be discussed.
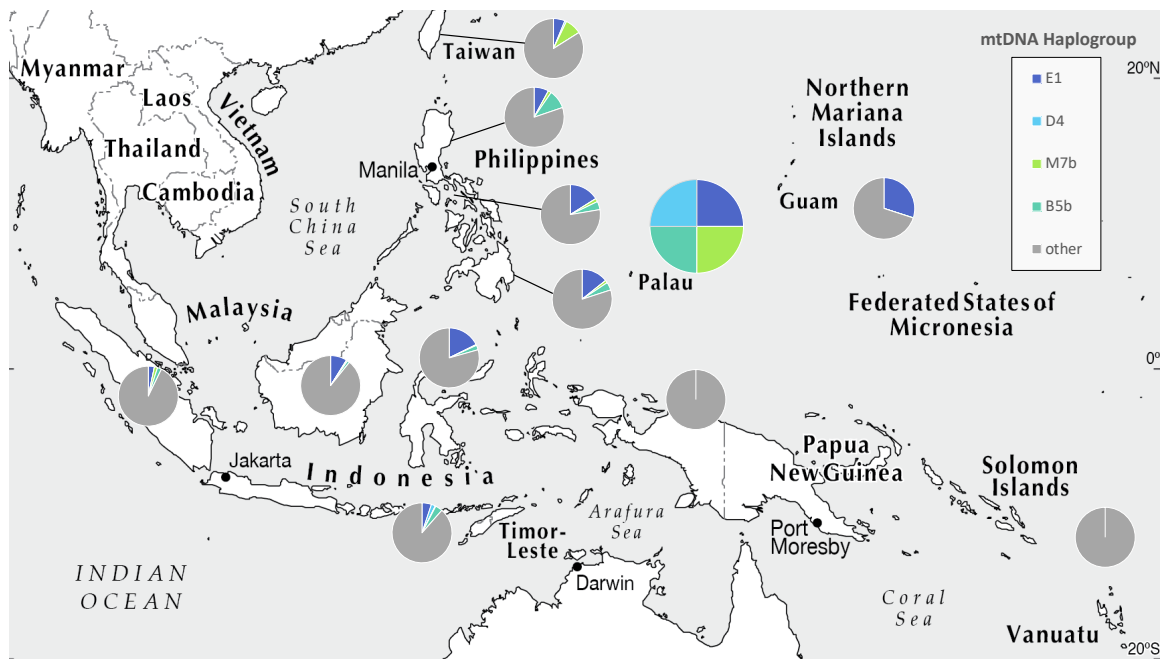
Figure 2.3. mtDNA haplogroup frequencies of potential source regions compared to Chelechol ra Orrak. All comparative data is from modern sources with the exception of Vanuatu, which is represented by Lapita aDNA (Skoglund et al. 2016, Posth et al. 2016).

Burial 18

Haplogroup B5b has been interpreted as a marker of an Early to mid-Holocene dispersal event from MSEA into ISEA and has been observed among both Austronesian-speaking ancient and modern MSEA populations (Brandão et al. 2016, Duong et al. 2018, Hill et al. 2007, Lipson et al. 2018, Soares et al. 2016). Within ISEA, B5, and more specifically, B5b, are widespread throughout the Philippines and Indonesia, with the highest frequencies of these haplogroups observed in the western islands of Indonesia, with slightly lower, but noticeable clusters in the northern Philippines and southern Sulawesi (Brandão et al. 2016, Gunnarsdottir et al. 2011). In the Philippines, B5b1c is found at the highest frequencies in the northern islands of the archipelago (Delfin et al. 2014). Given the later radiocarbon date from Burial 18 (1955-1815 cal. BP), the possibility remains that the presence of this haplogroup could be the result of admixture events following initial settlement. If so, these results may serve as evidence for sustained interaction with ISEA.

Burial 20

Haplogroup D4 has been found to be widespread among modern and ancient Austronesian-speaking populations in MSEA (Duong et al. 2018, Peng et al. 2010, Lipson et al. 2018, Summerer et al. 2014). A study of mtDNA diversity among indigenous Taiwanese groups also identified low frequencies of haplogroup D4 among tribes in the northern and central regions of Taiwan (Trejaut et al. 2005). However, haplogroup D4 is noticeably rare in ISEA. Given that the coverage for Burial 20 is low, it is important to note that this haplogroup assignment could change with additional data. However, if an assignment of D4 were to remain consistent, this assignment may be indicative of earlier mtDNA regional diversity in ISEA that has been lost.

Burial 25

Haplogroups within M7 are common and widespread across ISEA. Haplogroup M7b1 is also found outside of ISEA, in Southwest China, Taiwan, and both ancient and modern individuals from MSEA, suggesting that this haplogroup is a marker of long-term mainland and island SE Asian interaction among Austronesian-speaking populations

(Delfin et al. 2014, Gunnarsdottir et al. 2011, Tumonggor et al. 2013, Tabbada et al. 2010). The haplogroup is present at low frequencies in both the northern and central Philippines but is slightly more common in the central portion of the archipelago (Tabbada et al. 2010). Within Indonesia, M7b1 is more common in the central and western islands, including Java and Bali, which researchers have suggested is the result of dispersals from MSEA or interaction during the Pleistocene (Tumonggor et al. 2013). Together, these results can confirm a Palauan connection to ISEA, but given the widespread distribution of the M7b1 haplogroup, are generally uninformative regarding a more specific location in the location. One possible exception that warrants further comparisons is the observation of M7b1a2a1, the same haplogroup assigned to Burial 25, in modern samples from the northern Philippines, suggesting a possible connection to the area near and around Luzon (Tabbada et al. 2010)

Burial 37

Haplogroup E appears to have evolved entirely within ISEA during the Late Pleistocene. Lineages belonging to E1 and E2 also found in Taiwan, which has been interpreted as a later introduction to the island from ISEA (Brandao et al. 2016, Hill et al. 2007, Soares et al. 2008, 2016). A recent aDNA study of a single individual dating to ~8000 BP from Liang Island, located between mainland China and Taiwan, was found to belong to this mitochondrial haplogroup E and likely E1, demonstrating its presence in Taiwan prior to Austronesian dispersal to ISEA (Ko et al. 2014). Within ISEA, haplogroup E is relatively common across the Philippines, Sulawesi, the Maluku Islands, and eastern Indonesia, with the overwhelming majority of individuals within haplogroup E belonging to E1a1a (Tabbada et al. 2010). This distribution has been attributed to the long-term presence of the haplogroup within the region and interaction between these islands (Friedlaender et al. 2008, Gunnarsdottir et al. 2011, Hill et al. 2007, Tumonggor et al. 2013). Interestingly, this haplogroup is noticeably rare in the Pacific Islands with the exception of the Mariana Islands, where a study of 105 modern Chamorro individuals from Guam, Rota, and Saipan found that 92% of the individuals sampled belonged to haplogroup E, with 28% belonging to E1. Chamorro-specific mutations were also found,

which were attributed to a founder effect following initial arrival in the Marianas from ISEA (Vilar et al. 2013).

Comparisons with Lapita and modern Palauans

Although tentative, the results presented in this chapter appear drastically different when compared to aDNA results from three studies on Lapita remains. The first, which included three individuals from the Teouma mortuary site on Vanuatu and one individual from Talasiu, Tonga, found all four individuals shared the haplogroup assignment of B4a1a1a (Skoglund et al. 2016). Two separate follow-up studies, including additional Lapita individuals from Vanuatu across a broader time span, found the addition of mtDNA haplogroups commonly associated with Papuan-speaking populations (e.g., P, Q) (Lipson et al. 2018, Posth et al 2018). The haplogroup B4a1a1a, originally described as the "Polynesian Motif," is often described as a marker of Austronesian dispersal into Remote Oceania, and even among modern groups, is found at increasingly high frequencies as one moves eastward across the region. The identification of B4a1a1a in ISEA has also been used to link Austronesian speakers from the region to the Pacific (Duggan et al. 2014). Therefore, the absence of this haplogroup among early Palauans thus far is notable, and this haplogroup may instead be indicative of Lapita dispersal, rather than Austronesian dispersal into Remote Oceania.

B4a1a1a has been identified among modern Chamorro and Palauan people, but currently, these results suggest the presence of this haplogroup could be the result of later admixture events (Lum and Cann 2000, Vilar et al. 2013). Modern Palauan samples have also demonstrated Papuan-associated haplogroups that have been attributed to New Guinea. Given the absence of Papuan haplogroups in these results, the appearance of haplogroups such as P and Q similarly appear to be the result of later admixture events. The similarities between Type X pottery from New Guinea and grog-tempered ceramics from Palau has been used to suggest possible interaction between the two areas ca. 1000 BP that could be the source of this admixture, but genetic data from this period of time is needed to test that hypothesis (Specht et al. 2006). The identification of haplogroup E1a1a in Palau is also noteworthy, as this haplogroup is rarely found in Remote Oceania with the exception of the Mariana Islands. The presence of E1a1a in modern Chamorro

people has been interpreted as evidence for a direct population dispersal from ISEA to the Marianas. The addition of an ancient Palauan presence of E1a1a not only lends more direct support for ISEA as a place of origin for western Micronesian people, but also raises questions about the potential connections between early groups in the Marianas and Palau.

Conclusion

Although a significant amount of archaeological and linguistic evidence has suggested that western Micronesia, and more specifically, Palau, were likely settled from somewhere in ISEA, there has been a paucity of direct biological evidence to support this claim. The results of aDNA work presented in this chapter involving partial and complete mitochondrial genomes from Chelechol ra Orrak provide the first biological data from Palau focused on the population origins of the archipelago's earliest inhabitants. Taken together, these data lend the first direct biological support for the hypothesis that Palau was directly settled from somewhere in ISEA by Austronesian-speaking people. Based on the absence of Papuan-associated haplogroups, the hypothesis that initial populations arrived in Palau from New Guinea is not supported; however, the presence of these haplogroups in modern Palauans suggests a later or even modern admixture event. That completely different haplogroups are represented in this study compared to Lapita aDNA research is also notable, as shared ancestry between Lapita and western Micronesian groups in ISEA prior to dispersal to Remote Oceania has been suggested. Instead, these results raise the possibility that two, or possibly three, distinct population dispersals from potentially different areas within ISEA reached Remote Oceania ca. 3300-3000 BP.

In the next chapter, I assess archaeological evidence for possible adaptive challenges that would have been faced by some of the first Palauans. Previous research at the site of Ucheliungs Cave claims that following initial arrival, a process of insular dwarfing occurred among early Palauan populations utilizing the Rock Islands. However, biological evidence has refuted this claim. In Chapter III, I test whether the conditions that are conducive to insular dwarfing are present at Ucheliungs, including isolation and a reduced resource base.

DISPROVING CLAIMS FOR INSULAR DWARFISM AT THE
UCHELIUNGS SITE

Introduction

The use of caves and rockshelters for disposing of the dead is the oldest form of mortuary behavior in the Palauan archipelago (Fitzpatrick & Nelson 2008). Numerous sites throughout the Rock Islands have been identified as locations where human skeletal remains were buried or deposited, all of which date back to as early as ca. 3000-2500 cal. BP. However, two sites in particular, Omedokel and Ucheliungs, have received considerable attention because researchers had earlier interpreted human skeletal fragments found here as being 'small-bodied', arguing that they "exhibit a number of characteristics normally associated with more primitive species of the genus *Homo*" and "exemplify the regularity with which small body size—physiological dwarfing—emerges in island contexts" (Berger et al. 2008: 9). The authors also suggested that the Rock Islands provided an environment that was conducive to insular dwarfism where, over the course of a few generations, an isolated population developed a series of unique morphological characteristics, including small body size. Fitzpatrick et al. (2008) disputed these results, but at the time, there had been no subsequent field research at these sites to clarify and examine the archaeological evidence for insular dwarfism in Palau.

In this chapter, I report on additional fieldwork undertaken in 2015 at the Ucheliungs site (B:OR-14:8), including surface examination and excavation of a 1×1 m unit adjacent to one excavated by Berger et al. (2008). The primary goal of this work was to provide additional archaeological context and radiocarbon dates for the site to assess whether the conditions were present at Ucheliungs to support a hypothesis of insular dwarfism. Generally, the results are contrary to previous findings that suggested the site

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was exclusively used for mortuary activity, with no evidence for associated fauna and few artifacts. Instead, thousands of faunal specimens and an assemblage of artifacts, including pottery and a bone implement, having been found during our recent investigation. Four new radiocarbon assays on marine shell provide additional early dates for Palau, supported by the recovery of volcanic sand tempered pottery that has also been recovered from contemporaneous sites in the Rock Islands. Both lines of evidence hint at long-term use of the site that seem to both precede and come after the deposition of human remains and refute previous findings and interpretations.

Background

The Island Rule

The "Island Rule" is an ecogeographical principle related to the pattern of shifting body size in response to the availability of resources in island environments (Foster 1964, Lomolino 2005, Van Valen 1973). Although the Island Rule is not universally followed in island species, the general principle states that in areas of resource scarcity, dwarfing is expected to occur, while in areas of resource abundance, increased body size, or insular gigantism, is expected to occur. Foster, who first described the Island Rule, also suggested that relaxed predation pressures further contributed to the process of larger body size in small-bodied animals (Foster 1964). Evaluation of the Island Rule has also demonstrated that larger-bodied species tend towards dwarfism, such as the pygmy mammoths found in the Channel Islands off the coast of California, while smaller-bodied species tend to evolve towards a larger body size, such as the giant rats and marabou storks found on the island of Flores in Indonesia (Agenbroad et al. 1999, Locatelli et al. 2012, Meijer and Due 2010). While there are many examples of shifts in body size in insular species of reptiles, birds, and mammals, there are also many exceptions (Boback and Guyer 2003, Clegg and Owens 2002, Itescu et al. 2014, Meiri et al. 2004, 2006, 2008, van der Geer et al. 2018). These cases have largely been attributed to variation in the primary determinants of the island rule: resource availability, absence of predators and intra- and interspecific competition, and genetic isolation (Case 1978, Lomolino 1985, et al. 2013). At Ucheliungs, the hypothesized cause of insular dwarfing in humans

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proposed by Berger et al. (2008) was attributed to isolation and a reduced resource base in the Rock Islands.

Environmental Context

Ucheliungs is a burial cave located in the northern Rock Islands, southwest of Babeldaob and east of Koror. The roof of the main cavern has collapsed due to dissolution of the limestone that comprises the island. This has allowed for the growth of vegetation over the collapsed rubble and has given Ucheliungs the nickname "Tarzan Cave" due to the vines that extend through the roof to the cavern floor (Figure 3.1). This unique morphology, and close proximity to Koror, has also led to the site becoming a popular stop on local kayaking tours. Two smaller caverns are located in the north-west and south-west corners of the main cave, the latter of which is covered in a bright white limestone. A small beach provides relatively easy access to the main entrance.
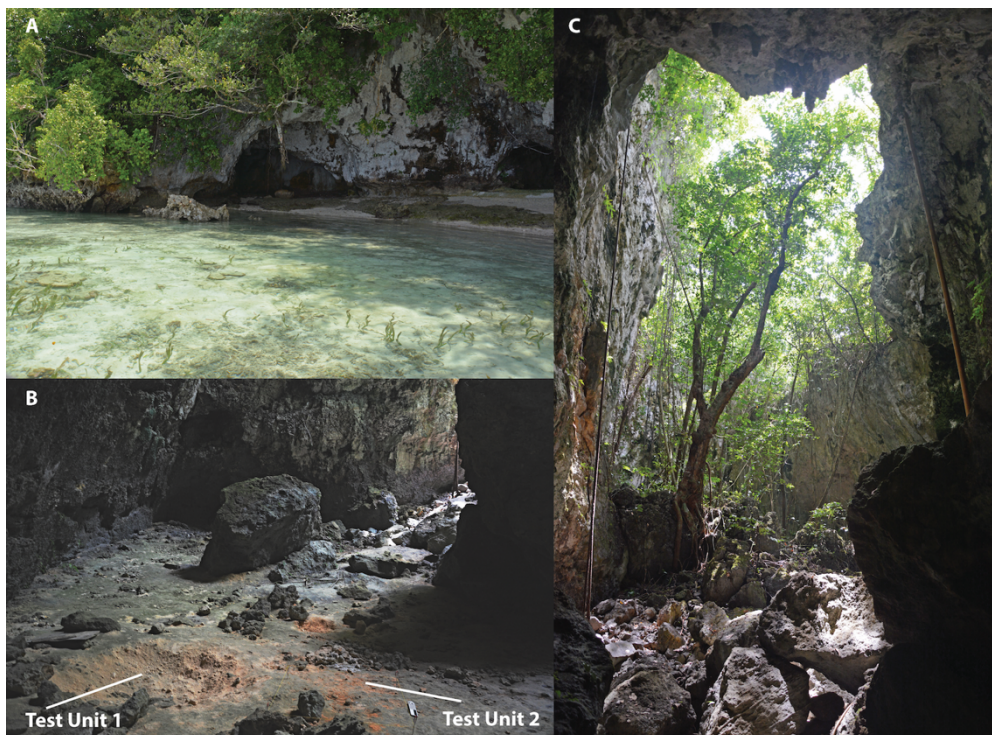
Figure 3.1. a. The entrance to Ucheliungs Cave. b. Facing north inside Ucheliungs. TU1 is to the left, and the location of TU2 is outlined to the right. c. Interior of Ucheliungs, facing east and showing the cave roof collapse.

Archaeological Context

Ucheliungs was first excavated by Berger and colleagues in 2006, who conducted surface collection of human remains from the cave interior and excavated a 1×1 m test unit (hereafter referred to as Test Unit 1), that together yielded a number of identified specimens (NISP) of more than 1000 human bone or bone fragments (Berger et al. 2008). Results suggested that the area was used exclusively for mortuary practice and contained little, if any, associated fauna or cultural material, but that the site likely contained large numbers of additional human remains. Radiocarbon dates on human bone were reported as ranging from 2890-1420 BP (Berger et al. 2008). As Fitzpatrick et al. (2008) noted, these dates were calibrated as if they were from terrestrial material; yet given the likelihood of a major marine dietary component for human inhabitants, which adds inbuilt age from marine carbon, recalibration to account for a mixed (50/50) marine and terrestrial diet shifts these dates by hundreds of years.

Methods

Test Unit 1 was placed in the western portion of the cave, and appeared not to have been backfilled after completion. The unit's location was compared to the site map published in Berger et al. (2008) to verify its position. A 1×1 m test unit (Test Unit 2) was placed east and directly adjacent to Test Unit 1 (Figure 3.1b). Test Unit 2 (TU2) was excavated by trowel in arbitrary 10 cm levels from the ground surface to a depth of approximately 50 cm, at which point a layer of dense flowstone was encountered. Arbitrary levels were chosen based on Berger et al.'s (2008) observation that the first 50 cm of sediment comprised a single stratigraphic layer. As excavation proceeded, this was found not to be the case. Our 10 cm levels closely followed a stratigraphic change observed at approximately 10 cm depth (Figure 3.2). Soil in the first 10 cm (Layer I) was a fine grained, pale brown sand (10YR 7/6). From approximately 10-20 cm, patches of finer, loosely packed yellowish sand (10YR 8/4) were encountered and continued to expand with depth to comprise a second stratigraphic layer (Layer II) by 20 cm that reached the flowstone deposit (Figure 3.2).
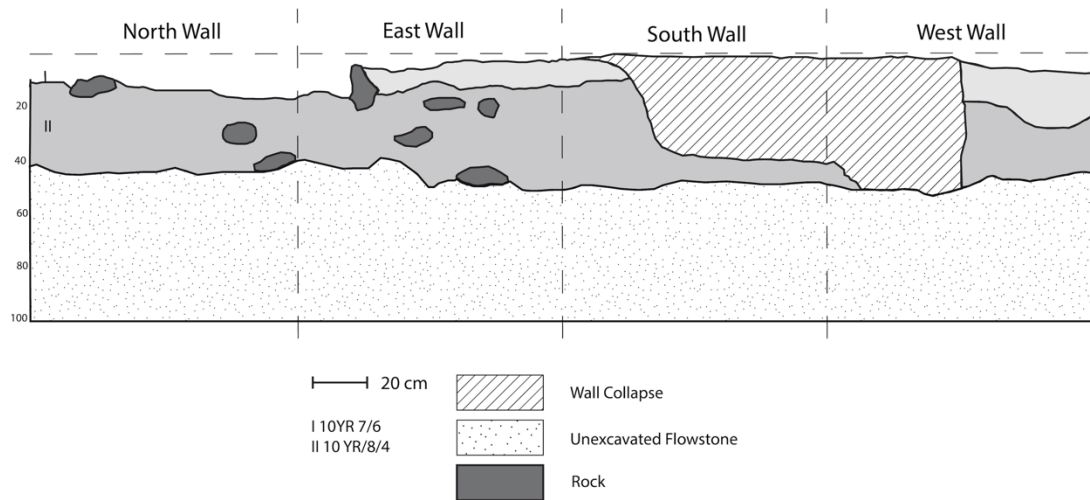
Figure 3.2. Stratigraphic profile of TU2.

All soil was dry-screened through 1/8 inch mesh. Human skeletal material and artifacts were also collected when encountered in surface contexts. All cultural material, including faunal remains, artifacts, charcoal, and human skeletal fragments were collected, sorted into basic categories, and entered into the InTerris Registries database management software, which utilizes a barcode label system to link all material and results of subsequent analyses to the original provenience. Further sorting and analysis was undertaken at the University of Oregon Island and Coastal Archaeology Lab.

Skeletal remains were identified to element, and when possible, standard osteological methods were used to estimate sex (e.g., morphology of the greater sciatic notch, supraorbital tori prominence and margin thickness) and age (e.g., epiphyseal fusion, dental development) (Buikstra & Ubelaker 1994; Scheuer et al. 2000). Pathology, trauma, and anomalies were also recorded when present (Buikstra & Ubelaker 1994; Scheuer et al. 2000). Faunal remains were sorted to the lowest possible taxonomic level and quantified using number of identified specimens (NISP), minimum number of individuals (MNI) based on non-repetitive elements, and weight (g) using standard procedures (Reitz & Wing 2008). Pottery sherds were weighed and preliminarily analyzed to identify temper, form, and any surface treatments. A representative sample

from each level (n=8), was selected for thin-section analysis based on stratigraphic location. A coarse analysis of temper constituents was conducted by Kathleen Marsaglia in the Department of Geological Sciences at California State University, Northridge.

Radiocarbon Dates

Seven samples of marine shell (n=4) and human bone (n=3) were submitted for radiocarbon dating. Marine shell samples were pretreated at the University of Oregon Island and Coastal Archaeology Laboratory with a 10% hydrochloric acid (HCl) solution "leach", dried, and drilled to obtain a powdered sample for submission. Bone samples were sent to two different laboratories; however, neither was able to obtain separable collagen following pretreatment procedures and dating of these specimens was unsuccessful. This is likely attributed to the mineralized nature of the human remains recovered, with results similar to those presented by Berger et al. (2008), who selected 25 samples for AMS dating and only reported six. All radiocarbon dates, including those previously reported, were calibrated using OxCal v.4.2 with a 50% mixed marine/terrestrial curve for bone samples and the Marine13 curve for shell (Bronk Ramsey 2009; Reimer et al. 2013) (Table 3.1). Given the wide range of marine reservoir corrections (ΔR) available for Palau, ^{14}C dates from Ucheliungs are presented with all ΔRs averaged for the archipelago (Table 3.2).

Although marine shell is sometimes viewed as a problematic material for radiocarbon dating due to a variety of issues, including inbuilt age from both global and localized oceanic carbon reservoirs, the "old shell" effect, and the possibility that natural deposits are being dated and interpreted as cultural events (e.g. Rick et al. 2005), the marine shell excavated at Ucheliungs is unlikely to be naturally deposited. Given the distance (approximately 20 m) and upward slope from the cave entrance and beach to TU2, and a lack of shell observed on the cave floor during excavations, it is unlikely that tidal activity or storm surges washed in beach material or that marine shell reached the cave interior via other natural mechanisms. As can be seen in Table 3.1, the new marine shell dates from Ucheliungs—which were taken from larger specimens of taxa known to have been used for subsistence and found at other Rock Island archaeological sites—span 4060-2710 cal. BP and are in stratigraphic order.

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Table 3.1. Radiocarbon dates from Ucheliungs. Sample numbers beginning with "B:OR-14:8" are dates from Berger et al. (2008) and have been recalibrated for this study.

Lab/Sample Number	Sample Type	Provenience	Radiocarbon Age	$^{13}C/^{12}C$ ratio	Calibrated Date (2 sigma BP)
B:OR-14:8-1200	Human Bone	not reported	2550±50	-15.1	2670-2320
B:OR-14:8-1201	Human Bone	not reported	2530±50	-15.3	2670-2300
B:OR-14:8-1202	Human Bone	not reported	2280±50	-15	2300-1950
B:OR-14:8-1203	Human Bone	not reported	2260±50	-14.7	2290-1930
B:OR-14:8-1204	Human Bone	not reported	2190±50	-15.9	2120-1880
B:OR-14:8-1205	Human Bone	not reported	2400±40	-14.4	2340-2130
B:OR-14:8-1206	Human Bone	not reported	1520±40	-17	1320-1180
B:OR-14:8-1207	Human Bone	not reported	1570±40	-14	1380-1250
D-AMS 017432	Marine shell (*Cypraea tigris*)	TU2, Level 3 (20-30cm depth)	3000±30	not reported	2850-2710
D-AMS 016831	Marine shell (Bivalve, pr. Cardiidae sp.)	TU2, Level 4 (30-40cm depth)	3450±30	-17.6	3410-3230
D-AMS 017433	Marine shell (*Fimbria* sp.)	TU2, Level 4 (30-40cm depth)	3370±30	not reported	3330-3150
D-AMS 017434	Marine shell (Bivalve, pr. Cardiidae sp.)	TU2, Level 5 (40-50cm depth)	3960±30	not reported	4060-3850
BOR-TU2-BOH	Human Bone (long bone shaft)	TU2, Level 4 (30-40cm depth)	No separable collagen	N/A	N/A
BOR-TU2-BOH1	Human Bone (Femur shaft)	TU2, Level 4 (30-40cm depth)	No separable collagen	N/A	N/A
BOR-TU2-BOH2	Human Bone (rib shaft)	TU2, Level 4 (30-40cm depth)	No separable collagen	N/A	N/A

The latter end of the date range overlaps with two of the human bone samples reported by Berger et al. (2008). The two marine shell dates from Level 4 (D-AMS 016831, D-AMS 017433) calibrate to the earliest known acceptable range of Palauan colonization and are generally coeval with those from Ulong and Chelechol ra Orrak, providing further support to the presence of Palauans in the Rock Islands just prior to and after 3000 BP. The sample from the lowest level (D-AMS 017434), which calibrates to 4060-3850 BP, extends beyond the earliest accepted archaeological dates in the archipelago. It is possible that the sample was subfossil shell or brought in as part of incidental debris, but this needs to be confirmed with additional dates. Regardless, the association of human bone with these dates implies that burial activity may have taken place at Ucheliungs earlier than Berger et al. (2008) suggested. This revised chronology

reduces the amount of time between initial colonization of Palau and use of the site, which does not allow adequate time for insular dwarfism to occur within the population following arrival in the archipelago.

Table 3.2. Calibrated marine radiocarbon dates (2 sigma BP) with various ΔR for Palau.

Lab Number	Radiocarbon age	ΔR -250±50[1]	ΔR -52±22[2]	ΔR 0	ΔR 34±44[3]	ΔR 75±68[4]	ΔR 168±43[5]
D-AMS 016831	3450±30	3800-3460	3490-3270	3410-3230	3420-3140	3420-3020	3270-2940
D-AMS 017432	3000±30	3250-2880	2930-2730	2850-2710	4830-4560	2870-2460	2730-2410
D-AMS 017433	3370±30	3670-3370	3390-3180	3330-3150	3340-3030	3340-2920	3160-2850
D-AMS 017434	3960±30	4450-4110	4140-3900	4060-3850	4070-3750	4060-3640	3870-3580

[1]Fitzpatrick 2002, Masse et al. 2006; [2]Petchey and Clark 2010; [3]Yoneda et al. 2007; [4]Petchey and Clark 2010; [5]Yoneda et al. 2007

Bioarchaeology

Human remains from TU2 consisted of almost 200 identifiable elements, including a small cache of isolates that had been collected from the surface by kayak tour guides and placed in a rock crevice to prevent looting by tourists. The remains are mineralized and highly fragmented, as evidenced by the recovery of numerous additional small fragments (n=987) that could not be identified beyond broader general categories (e.g. cranial, long bone, rib, etc.). With the exception of a single femur shaft located in Level 2 (10-20 cm) of TU2, the remains primarily consist of small, isolated elements that were recovered from each level of the test unit. The bulk of the remains were found in the upper levels, suggesting that individuals may have been originally placed on the surface of the cave floor or in shallow subsurface graves. This is also consistent with early mortuary contexts at other Rock Island burial caves and rockshelters, where both subsurface burial in beach sand and placement on cave floors are common practices (Fitzpatrick & Nelson 2008).

Because the assemblage consisted solely of isolated elements, no discrete individuals or articulated burials could be identified. However, a rough estimate of the

minimum number of individuals (MNI) present based on non-repetitive elements suggests that at least six individuals are represented, including three adults and three juveniles, ranging in age from infancy to adulthood. Unfortunately, no elements that can be used to accurately determine sex were recovered, but the presence of individuals across such a broad age range suggests that there were no age or sex-related interment restrictions in place at Ucheliungs. This is also consistent with the demographic composition of the Chelechol ra Orrak and Koror Quarry sites, which contain assemblages representing both sexes and a wide age range (Nelson et al. 2015, Rieth & Liston 2001, Stone et al. 2014). Pathological conditions were identified in 18 elements (1.5% of total skeletal assemblage), and are limited to degenerative changes, such as pitting and marginal growth along articular surfaces, and can likely be attributed to age or activity-related factors. No traumatic injuries were identified with the exception of a possible healed fracture on a proximal manual phalanx. A single instance of pedal symphalangism, or the fusion of the intermediate and distal foot phalanges, was the only skeletal anomaly identified. There is no evidence for pathological conditions that would contribute to dwarfism, nor are there any indications of small body size from the elements recovered. Although this is an extremely limited sample, the pattern observed at Ucheliungs appears similar to both Chelechol ra Orrak and Koror Quarry, where trauma and pathology are only minimally present (Nelson & Fitzpatrick 2006, Nelson et al. 2015, Rieth & Liston 2001).

Isolated teeth (n = 29) were also recovered, as well as a single mandibular fragment containing three teeth that was included in the surface cache collected previously by kayaking guides. Pathological conditions are comparable to other prehistoric Palauan assemblages, and include light occlusal wear, a lack of caries, and slight calculus formation, primarily located along the cementoenamel junction. Similar to Chelechol ra Orrak, a number of the teeth from Ucheliungs are also stained from habitual chewing of betel nut (*Areca catechu*), a common practice throughout Palau (Fitzpatrick et al. 2003a). Dental studies have suggested that chewing betel nut creates cariostatic conditions, possibly as a result of tannins in the drupe that possess antimicrobial properties or increased saliva production, which may explain the noticeable absence of carious lesions in this assemblage and others from Palau (de Miranda et al. 1996,

Howden 1984, Trivedy et al. 2002). However, unlike Chelechol ra Orrak where all but two burials exhibit staining, betel staining occurs in less than half of the teeth recovered (n = 12), though this may be a reflection of a small sample size. Deciduous teeth also exhibited a dark staining, but this appears to be taphonomic.

Zooarchaeology

Fauna recovered from TU2 consist almost exclusively of marine mollusks (88% of the total faunal weight), and were present in each level, with the bulk of the assemblage belonging to the upper three levels (Figure 3.3). The majority of the shell and all of the faunal bone recovered are bleached and mineralized in a manner similar to the human bone. This complicated identification of many taxa; as such, few are identified below the family level.

Bivalves and gastropods are represented relatively equally with a total of 55 taxa. While no single taxon dominated the assemblage, *Arcidae* sp., *Conus* sp., *Nerita* sp., and *Videna* sp. were all found in relatively high quantities (Table 3.3). Additionally, three species of land snail, including *Videna* sp., are found throughout all levels and represent a substantial portion of the gastropod assemblage (4% of the total gastropod weight and 1.4% of the overall shell weight; 49% of the total gastropod MNI, 31.5% of the total shell MNI). The shellfish assemblage at Ucheliungs is similar to what has been observed at other Rock Island sites, including stone money quarries and village sites, where taxa from intertidal and shallow reef environments are common, including those from the Arcidae, Conidae, and Cypraeidae families (Carucci 1992, Fitzpatrick 2003c).

In addition to shell, a small amount of vertebrate material was also identified, including two shark teeth, a single centrum of a fish vertebra, and a bird coracoid. Also present are a species of barnacle (*Cirripedia* sp.) found throughout all levels, small quantities of sea urchin (*Echinoidea* sp.), chiton, and crab (*Brachyura* sp.), which is the most abundant taxon apart from marine shell, comprising 9% of the overall weight. Together, the combined faunal assemblage from TU2 weighs 1530.52 g and represents 66 taxa, including many that are endemic to shallow reef environments, much like those immediately surrounding the area where Ucheliungs is located. Therefore, it appears that while terrestrial resources may have been scarce, marine resources were in fact abundant

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and in no way suggest that a reduced resource base, one of the contributing factors to insular dwarfing, was present at Ucheliungs.
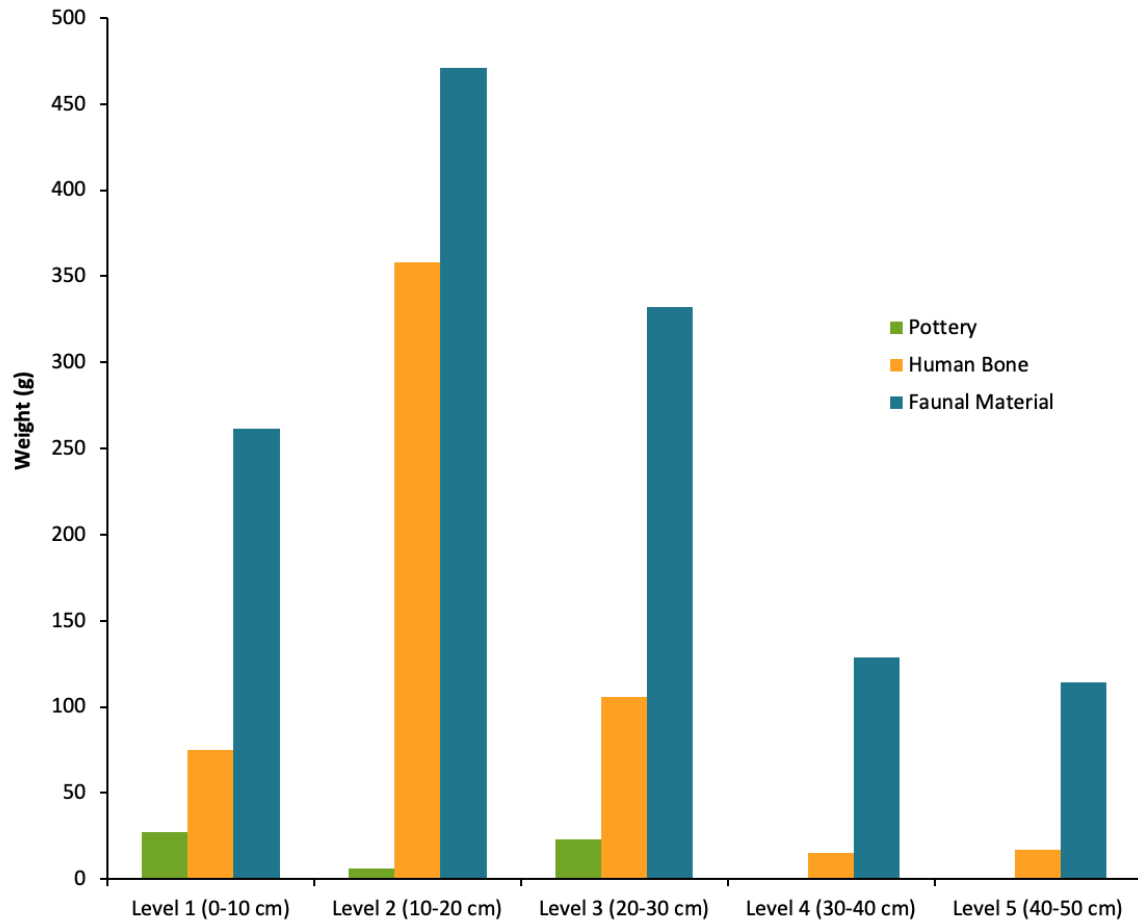
Figure 3.3. Relative contributions of faunal remains, human remains, and ceramics to the overall archaeological assemblage.

Table 3.3. Faunal remains recovered from Ucheliungs.

Taxon	Weight (g)	MNI	NISP
GASTROPODA			
Cantharus sp.	6.53	5	8
Cerithium sp.	1.9	1	1
Cerithidae sp.	0.98	1	1
Cerithoidea sp.	1	3	3
Conomurex luhuanus	0.11	1	1
Conus arenatus	0.3	1	2
Conus sp.	43.51	13	16
Cypraea sp.	23.26	14	14
Cypraea tigris	16.65	1	1
Erosaria helvola	6.08	1	1
Gibberulus gibberulus	12.71	6	9
Lambis lambis	14.16	1	1
Lambis sp.	0.56	1	1
Latirolagena smaragdulus	1	2	2
Monoplex nicobaricus	12.29	11	14
Nassarius sp.	0.64	1	1
Nerita polita	7.16	2	2
Nerita sp.	33.7	58	81
Oliva sp.	0.01	1	1
Patellidae sp.	1.71	4	4
Peristernia sp.	0.21	3	3
Pupuradusta microdon	0.7	1	1
Pythia scarabaeus	8.62	15	15
Rhinoclavis aspera	0.29	1	1
Strombidae sp.	13.84	5	10
Strombus sp.	4.99	2	3
Tectus niloticus	2.88	5	8
Terebralia sulcata	6.34	2	2
Thais sp.	2.08	3	3
Trochus sp.	52.13	15	38
Turitellidae sp.	0.05	1	1
Videna sp.	9.62	59	67
Land Snail A	1.47	20	41
Land Snail B	8.33	107	134
Turbo Opercula	6.44	1	1
Miscellaneous Opercula	5.82	8	8
Miscellaneous Gastropods	118.72		262
Total Gastropod	**461.77**	**377**	**763**
BIVALVIA			
Anadara sp.	17.89	7	7
Arca sp.	6.51	1	1
Arca ventricosa	48.97	13	16
Arcidae sp.	33.59	126	224
Bivalve, pr. *Cardiidae* sp.	11.72	2	2
Cardita variegata	0.5	2	2
Cardita sp.	0.05	1	1
Chama sp.	139.42	14	15
Codakia sp.	0.28	1	1
Fimbria sp.	2.68	1	1
Hippopus hippopus	42.43	1	1
Isognomon isognomon	5.18	1	8
Isognomon sp.	0.83	2	6
Limidae sp.	0.6	4	4
Lucinidae sp.	6.96	9	13
Spondylus sp.	71.2	20	21
Tapes litteratus	0.96	1	3

Table 3.3, continued.

Taxon	Weight (g)	MNI	NISP
Tellina sp.	0.13	2	2
Tellinidae sp.	0.02	1	1
Venericardia sp.	0.8	2	2
Veneridae sp.	0.37	3	3
Miscellaneous Bivalves	191.13		405
Total Bivalve	**582.22**	**214**	**739**
Miscellaneous Shell	305.09		1084
Total Shell	**1349.08**	**591**	**2586**
POLYPLACOPHORA			
Chiton	0.55	3	4
ARTHROPODA			
Crustacea	140.87		971
Cirripedia sp.	37.41		69
Total Arthropod	**178.28**		**1040**
Sea Urchin (Echinoidea)	0.24		6
VERTEBRATA			
Shark	0.76	1	2
Bird	0.57	1	1
Fish	1.04	1	1
Total Vertebrate	**2.37**	**4**	**4**
TOTAL	**1530.52**	**623**	**3640**

Artifacts

A total of 30 pottery sherds weighing 759.73 g were recovered from TU2 and the surface of the northwest cavern of the cave (Table 3.4). Sherds from TU2 were only recovered from the first three levels and all are small, undecorated body fragments. Multiple sherds appeared to be weathered and lacked an interior or exterior, which may be due to taphonomic processes that are known to contribute to post-depositional wear on sherd surfaces (Clark 2005). Body sherd thickness ranged from 3.96-10.18 mm, but the small sample size is not sufficient to address possible changes in manufacture across levels. Preliminary temper analysis indicates that sherds were produced with volcanic sand as temper, which is significant for the fact most Palauan pottery was made with grog temper (Fitzpatrick et al. 2003a, Osborne 1979). The total absence of grog temper, coupled with the AMS dates, supports earlier findings by Fitzpatrick et al. (2003a) in which volcanic sand temper pottery was associated with the earliest occupation of the Rock Islands (see also Clark 2005).

The only other artifact recovered in excavation was a single piece of carved bone recovered from the southeastern corner of TU2 at ca. 10 centimeters below surface. The artifact is of particular interest because it is decorated with linear and triangular carving

and may be a fragment of a harpoon tip used for fishing, but comparable artifacts have not been found at other Palauan archaeological sites. (Figure 3.4). Given the artifact's uniqueness, a follow-up project utilizing Zooarchaeology by Mass Spectrometry (ZooMS) to taxonomically identify the bone, is ongoing. ZooMS relies on the species-level variability in the dominant bone protein of Type I collagen to identify archaeological bone taxonomically through a process of non-destructive collagen fingerprinting, and has emerged as a particularly useful approach for distinguishing between taxa that are morphologically similar or bone fragments that do not display distinguishing features, such as this artifact (Buckley et al. 2009, 2011, 2014).

Table 3.4. Ceramics recovered from Ucheliungs.

Level	Catalog Number	Temper	Form	Thickness	Count	Weight	Comment
1	7	Volcanic sand	Body	5.1	1	7.58	
1	8	Volcanic sand	Body	7.55	1	7.6	
1	9	Volcanic sand	Body	7.32	1	6.54	
1	10	Volcanic sand	Body	9.63	1	5.58	
2	4	Volcanic sand	Body	—	1	2.94	
2	5	Volcanic sand	UID	—	2	1.97	refit
2	6	Volcanic sand	Body	3.96	1	1.58	
3	1	Volcanic sand	Body	10.07	1	5.5	
3	2	Volcanic sand	Body	5.31	1	3.67	
3	3	Volcanic sand	Body	10.18	1	13.81	
surface	11	Volcanic sand	Body	9.06	1	2.73	
surface	12	Volcanic sand	Body	8.78	2	42.85	refit
surface	13	Volcanic sand	Rim	6.24	1	6.51	
surface	14	Volcanic sand	Body	6.99	1	75.32	
surface	15	Volcanic sand	Body	6.05	1	44.64	
surface	16	Volcanic sand	Body	7.28	1	27.31	
surface	17	Volcanic sand	Body	7.21	1	51.08	
surface	18	Volcanic sand	Body	5.3	1	34.42	
surface	19	Volcanic sand	Body	8.82	2	20.19	refit
surface	20	Volcanic sand	Body	6.69	1	15.56	
surface	21	Volcanic sand	Body	6.47	1	23.6	
surface	22	Volcanic sand	Body	7.09	1	39.34	
surface	23	Volcanic sand	Body	6.79	1	30.64	
surface	24	Volcanic sand	Rim	8.57	3	185.64	refit
surface	25	Volcanic sand	Base, rounded	10.25	1	103.13	

Preliminary results suggest that this bone may be from a non-human primate, likely one belonging to the Hylobatidae family, but confirmation is still needed. Non-human primates were not present on Palau prehistorically, but tools made from non-human primate bones have been recovered from archaeological contexts throughout Island and Mainland Southeast Asia dating as early as the Pleistocene (Ignicco et al. 2020, Rabett and Piper 2012, Wedage et al. 2019). If confirmed, this artifact represents the only example of a prehistoric translocated non-human primate or primate material to Remote Oceania. Identification of the species is especially important, as it may help identify the source location and provide direct evidence for dispersal or early exchange routes.
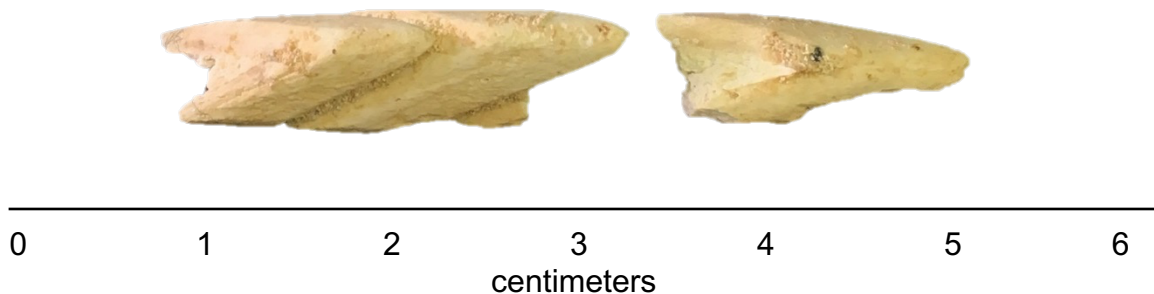
Figure 3.4. Carved bone artifact from southeastern wall of TU2.

Discussion

Analysis of archaeological and skeletal material recovered from recent excavation at the Ucheliungs site is significant for it presents a drastically different picture of prehistoric use when compared to previous research that claimed the site was used exclusively for mortuary practice by small-bodied humans (Berger et al. 2008). Our new results indicate that Ucheliungs was actually more diverse and used for a longer period of time than previously reported. The presence of faunal remains, artifacts, and dates on marine shell suggest that instead, use of the site occurred centuries earlier, ca. 3300 BP. Previous research argued that insular dwarfing occurs in tropical environments due to a

combination of factors that were also assumed to be present at Ucheliungs, including "relative genetic isolation, a reduced resource base, hot and humid climates, hilly topography, thick undergrowth of vegetation, and (in certain island contexts) an absence of terrestrial predators" (Berger et al. 2008:1). However, the presence of a diverse and abundant marine taxa assemblage as well as artifacts that were transported to the site (which are also commonly found on many other Rock Islands), suggest that genetic isolation and a reduced resource base were not factors affecting peoples that may have lived at Ucheliungs. Furthermore, the overall assemblage recovered from TU2 is similar what has been observed at other prehistoric Rock Island sites and does not indicate use of Ucheliungs by a population that would have been culturally or biologically distinct from other early Palauan groups.

Although the sample size is small, it appears that broad patterns in demography and pathology from other prehistoric Palauan skeletal assemblages are comparable to what has been observed at Ucheliungs. Given the early radiocarbon dates from TU2 that are associated with human remains, additional analysis of the existing skeletal assemblage and continued work at Ucheliungs has great potential to provide information related to the health of early Palauans and contribute to a more comprehensive collection of skeletal samples of the Rock Islands when combined with burials from Chelechol ra Orrak (Nelson & Fitzpatrick 2006, Nelson et al. 2015).

Conclusion

Berger et al. (2008: 3) argued that the Ucheliungs site contained the remains of smaller humans for which "the most parsimonious, and most reasonable, interpretation of the human fossil assemblage…..is that they derive from a small-bodied population of *H. sapiens* (representing either rapid insular dwarfism or a small-bodied colonizing population). A response by Fitzpatrick et al. (2008) demonstrated many fallacies inherent in previous interpretations, in part due to the presence of Palau's rich marine environment that would have provided excellent habitats for prehistoric populations to exploit (and as such, the inverse of conditions needed to induce insular dwarfism or a biological tendency for smaller bodies). Archaeological research at numerous sites throughout the archipelago also clearly demonstrate that interaction between islands through time was

frequent and intense as evidenced by the transport of pottery and other artifacts to the limestone Rock Islands, which lacked clay or tool-quality stone. This makes the notion of a population residing at Ucheliungs in isolation for hundreds or thousands of years unthinkable.

The material recovered in TU2—a unit the same size adjacent to TU1—includes the very evidence (marine taxa, non-local artifacts) that was used to support isolation for the cave's inhabitants, a key component to their interpretation that small-bodied individuals were present here. That so many indicators of human use or occupation were either ignored, dismissed, or unidentified demonstrates a failure to recover and analyze various site constituents that are commonly found in Palau's Rock Islands and other sites in the Pacific by previous researchers. While continued work at Chelechol ra Orrak is providing new and important data on Palau's prehistoric inhabitants from both archaeological and biological perspectives, Ucheliungs, which to date only contains very fragmented and widely dispersed skeletal remains, is significant for its potentially early dates and associated cave activities, but not for its contribution to human evolutionary processes that involved isolated populations or small-bodied individuals.

Future fieldwork at Ucheliungs will involve excavations with increased spatial coverage to provide a more representative picture of site use. Associated fauna will be particularly important for providing dietary resource information dating to the earliest period of settlement. These data will also complement other sources of dietary information from this time period such as the results of stable isotope analysis from human bone discussed in Chapter IV, which are the first direct dietary isotope data for Palau.

CHAPTER IV

STABLE ISOTOPE ANALYSIS OF HUMAN DIET AT CHELECHOL RA ORRAK

From: J.H. Stone, S.M. Fitzpatrick, and J. Krigbaum. 2019. Stable Isotope Analysis of Human Diet at Chelechol ra Orrak, Palau. *Bioarchaeology International*, 3(2), 142-156.

Introduction

In Remote Oceania, initial arrival upon previously uninhabited, relatively small, and remote islands would have presented early populations with a unique suite of challenges for survival, particularly those related to subsistence. Previous archaeological and isotopic research in Remote Oceania has largely focused on the subsistence strategies of Lapita colonizers with comparatively little research on prehistoric Micronesian subsistence following initial settlement (e.g., Beavan-Athfield et al. 2008, Green 1979, Groube 1971, Kinaston et al. 2014a, 2014b, 2015a, 2015b, Kinaston and Buckley 2013, Leach et al. 2003, Valentin et al. 2010). The subsistence strategies of early Lapita populations have long been debated based on faunal and botanical remains from various sites. Early studies proposed a "strandlooper" tactic focused on reef and nearshore marine resources, but the presence of plant and animal domesticates have led researchers to argue that the introduction of a "transported landscape," a term coined to describe the suite of plants, animals, that are both intentionally and unintentionally introduced to a new area alongside horticultural or agricultural human groups, was paramount to the successful settlement of Remote Oceania (Green 1979, Groube 1971, Kirch 1997). More recent isotopic analyses of Lapita-associated skeletal samples instead suggest that initial settlers utilized native resources from both inshore marine and terrestrial environments supplemented by terrestrial domesticates. However, it remains unclear to what extent these early Lapita groups relied on introduced taxa (Kinaston et al. 2013a, Kinaston and Buckley 2013, Valentin et al. 2010).

Unlike Lapita, early populations in western Micronesia are not associated with faunal evidence for a "transported landscape," raising numerous questions regarding the

extent to which these groups might have relied on endemic resources. Stable isotope paleodietary studies for western Micronesia are limited to the Mariana Islands, where samples have primarily been analyzed from Latte Period (post 1000 BP) sites. These studies suggest that prehistoric groups living on different islands were consuming varying amounts of marine protein and plants with C_4 photosynthetic pathways (Ambrose et al. 1997, McGovern-Wilson and Quinn 1996, Pate et al. 2001). However, the Latte Period is also characterized by increased social complexity, population growth, and agricultural intensification, and comparisons between Latte and Pre-Latte individuals demonstrate some dietary shifts over time (Carson 2012, Pate et al. 2001). Therefore, the results of these studies, however tentative, are unlikely to be informative regarding subsistence strategies following initial settlement of western Micronesia.

This chapter presents the first results of stable isotope analysis from human bone samples obtained from Palau, including Chelechol ra Orrak (ca. 3000-1700 BP). As the first isotopic paleodietary study in Palau, results are important for helping us understand early prehistoric subsistence here while also providing a much-needed comparison with other coeval sites in Remote Oceania.

Stable Isotope Analysis and Paleodietary Reconstruction

Stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) from human skeletal remains has become a common method in bioarchaeology for evaluating diet and subsistence, and is becoming an increasingly popular approach in the Pacific Islands (Commendador et al. 2013, Kinaston et al. 2013a, 2014a, 2015a, 2015b, Larsen 2015, Stantis et al. 2015a, 2015b). Because bone tissue incorporates multiple aspects of diet, $\delta^{13}C$ and $\delta^{15}N$ values of bone will reflect a long-term average isotopic composition of the foods that someone has consumed, thus allowing for a direct method of dietary reconstruction at the individual level. These values are measured in ratios ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) relative to an international standard (Vienna Pee Dee Belemnite, or VPDB, for carbon and atmospheric nitrogen, or AIR, for nitrogen) that are expressed in parts per thousand, or per mil (‰) using delta notation (δ) (DeNiro and Epstein 1978, Katzenberg 2008, Pate 1994, Schwarcz and Schoeninger 1991).

Carbon stable isotope ratios ($\delta^{13}C$) can be used to differentiate between marine and terrestrial proteins, and consumption of C_3 and C_4 terrestrial plants. Carbon in marine organisms is ^{13}C-enriched due to the presence of dissolved carbonate (~0‰) in marine ecosystems compared to atmospheric carbon (~-7‰) that is reflected in terrestrial species. These differences in source carbon are reflected in isotope partitioning between marine and terrestrial organisms observed in baseline data from Pacific Island taxa. For example, a sample of archaeological fruit bats from Vanuatu, used as a proxy for 100% terrestrial diets, yielded an average $\delta^{13}C$ value of -19.8‰, compared to samples of modern marine shellfish, parrotfish, or marine turtles, which average $\delta^{13}C$ values of -10.1‰, -9.7‰, and ~-9.1‰, respectively (Kinaston et al. 2014a).

Plants also vary in the ways that they incorporate CO_2 during photosynthesis, resulting in isotopically distinct pathways (Katzenberg 2008, Schwarcz and Schoeninger 1991). C_3 plants include temperate and tropical shrubs, trees, and tubers that are depleted in ^{13}C with more negative $\delta^{13}C$ values when compared to ^{13}C-enriched C_4 plants, which includes arid tropical grasses that display higher $\delta^{13}C$ values, typically averaging around -14‰. CAM plants, including cacti and succulents, reflect $\delta^{13}C$ values that are intermediate to C_3 and C_4 (Kohn 2010). In the Pacific, the majority of endemic plant resources utilize a C_3 pathway, with the exception of sugarcane, sea grapes, and some seaweeds (Kinaston and Buckley 2013). For example, $\delta^{13}C$ values of modern C_3 plants from Vanuatu average -26.2‰, while modern seagrasses average -9.3‰ (Kinaston et al. 2014a). As mentioned above, due to the presence of marine source carbon, both marine plants and animals are ^{13}C-enriched and exhibit higher $\delta^{13}C$ values than typical C_3 terrestrial resources, while freshwater resources display more depleted values (Schoeninger and DeNiro 1984, Schoeninger et al. 1983).

Nitrogen stable isotope ratios ($\delta^{15}N$) vary as a result of stepwise ^{15}N enrichment in bone collagen of approximately 2-4‰ with each trophic level, as well as between terrestrial and marine resources (Hedges and Reynard 2007, Minagawa and Wada 1984, Schoeninger et al. 1983). This ^{15}N enrichment is more complex in marine systems, due to the variation in N_2-fixation in primary producers. Additionally, marine ecosystems tend to have higher $\delta^{15}N$ values due to longer trophic systems compared to terrestrial environments (Schoeninger and DeNiro 1984). This trophic effect allows for $\delta^{15}N$ values

to be used to assess the relative contributions of marine and terrestrial foods to an individual's diet. However, coral reef and seagrass communities tend to have lower $\delta^{15}N$ than other marine areas due to N_2-fixation in shallow corals. The resulting effect is lower $\delta^{15}N$ values in organisms at higher trophic levels within coral reef environments when compared to pelagic ecosystems (Keegan and DeNiro 1988). For example, modern marine taxa collected from Vanuatu yielded $\delta^{15}N$ values of 5.4‰, 5.5‰, 7.3‰, and 9.2‰ for parrotfish, marine shellfish, tuna, and marine turtle, respectively (Kinaston et al. 2014a).

Because bone differs in how it assimilates dietary elements into its tissues, the bone fraction analyzed will reflect different dietary components. Bone collagen, which is principally composed of amino acids, primarily reflects dietary proteins consumed, while bone apatite reflects the "total" diet consumed, including protein, carbohydrates, and lipids (Ambrose and Norr 1993, Froehle et al. 2010, Krueger and Sullivan 1984, Tieszen and Fagre 1993). A meta-analysis of controlled feeding studies data has demonstrated that when protein sources are controlled for, significant relationships are apparent between $\delta^{13}C$ bone collagen and $\delta^{13}C$ of bone apatite ("total" diet) regardless of body size or the amount of protein consumed. The offset of $\delta^{13}C$ for bone apatite from consumed diet is debated but for humans is ~12‰, while the offset for bone collagen is ~5.2‰ (Froehle et al. 2010, Hedges 2003, Kellner and Schoeninger 2007). The combination of $\delta^{13}C$ values from both bone collagen and bone apatite provides a more comprehensive view of prehistoric diet (e.g., Froehle et al. 2012, Krueger and Sullivan 1984). Additionally, the difference in $\delta^{13}C$ between these two fractions allows for characterization of the carbohydrate sources by investigating the spacing ($\Delta13C_{ap-co}$) between collagen and apatite $\delta^{13}C$ values. Low $\Delta13C_{ap-co}$ spacing will reflect a diet of ^{13}C-enriched marine protein and terrestrial C_3 resources, while high spacing will reflect ^{13}C-enriched C_4 resources. Intermediate spacing for $\Delta13C_{ap-co}$ typically reflects a monoisotopic diet (Ambrose and Norr 1993, Kellner and Schoeninger 2007, Lee-Thorp et al. 1989).

Methods

Adult long bones and ribs from non-pathological elements were selected from 20 individuals from Chelechol ra Orrak. Additionally, samples from the Koror Quarry site (n

= 4) and Peleliu Island (n = 1) were included for comparison and to assess potential variation in diet across the archipelago. Koror Quarry, located in the northeastern portion of Koror, contains the remains of more than 30 individuals dating to between ca. 2500-1250 BP and was excavated as part of a salvage contract project (Rieth and Liston 2001). The single individual included from Peleliu, located at the southern tip of the archipelago, is of unknown age and provenience, but was interpreted as prehistoric by the original excavators, though it could possibly be historic. In order to assess potential demographic dietary differences, age and sex of each individual were estimated using standard morphological methods when possible (Buikstra and Ubelaker 1994).

For each sample, debris was removed mechanically with a scalpel followed by sonication in deionized distilled water and air-dried. Samples were then ground with a ceramic mortar and pestle and sieved into 0.25-0.5 mm and < 0.25 mm fractions for bone collagen and apatite analysis, respectively. Critical assessment of bone preservation of these prehistoric samples and their antiquity precluded lipid extraction procedures. About 500 mg of the larger (0.25-0.5 mm) bone collagen fraction was weighed and loaded into a 15 mL tube and demineralized with 0.1 M hydrochloric acid (HCl) for about seven days, with HCl refreshed every 24 hours. Once samples were completely demineralized and rinsed to neutral pH with DI-$H_2$0, 0.125 M sodium hydroxide (NaOH) was added for ~16 hours to remove exogenous contaminants and humic acids. Samples were then solubilized in 10^{-3}M HCl at 95°C for ~5 hours, spiked with 10 μL of 1.0 M HCl, and returned to the 95°C oven for another ~5 hours. After solubilization was complete, samples were removed and centrifuged, and the solute was placed in a 20 mL glass scintillation vial and reduced at 60°C to approximately 2 ml. Purified samples were then freeze-dried for 72 hours.

A number of quality-control measures can be undertaken to assess diagenesis in archaeological paleodietary studies. Because various factors, including alteration as a result of the surrounding depositional environment, can contribute to collagen preservation and potentially alter isotopic values in archaeological samples, C:N ratios are a consistent means to assess whether diagenesis may have contributed to the observed values. In this study, samples with a C:N ratio between 2.9 and 3.6 were considered acceptable (DeNiro 1985) in concert with evaluation of %C and %N. Diagenetic

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contamination in the hydroxyapatite portion of archaeological bone can be especially problematic, and crystallinity indices based on Fourier-transform infrared spectrometry (FTIR) are often utilized to assess the extent of diagenetic change (Shemesh 1990). However, a number of studies have demonstrated that this approach can have limited and variable utility, and as such, FTIR was not applied in this study (e.g., Stuart-Williams et al. 1996, Trueman et al. 2008). $\Delta 13C_{ap}$ data can potentially be precarious due to compromised biogenic preservation, especially with samples with low collagen yields and this must be considered as a caveat when interpreting these data.

Bone collagen samples were weighed and loaded in tin capsules and assessed for atomic C:N using a Carlo Erba NA 1500 Elemental Analyzer and and $\delta^{13}C_{co}$ and $\delta^{15}N$ using a Finnigan MAT DeltaPlus isotope ratio mass spectrometer (IRMS) in the Department of Geological Sciences, University of Florida. $\delta^{13}C_{co}$ and $\delta^{15}N$ were measured against Vienna PDB and Vienna AIR standards. Analytical precision for USGS 40 (n = 14) was 0.05 for $\delta^{13}C$ and 0.07 for $\delta^{15}N$.

The finer bone fraction, which comprised bone apatite samples, were weighed and chemically oxidized in a 50:50 solution of DI-$H_2$0 and sodium hypochlorite (NaOCl) and refreshed 2X until reaction was completed. Samples were then rinsed with DI-H20 to neutral pH, and 0.1 M acetic acid (CH3COOH) was added to removed secondary carbonates. Samples were again rinsed to neutral pH with DI-$H_2$0, freeze-dried for at least 72 hours, and loaded into a Kiel carbonate preparation device connected to a Finnigan 252 mass spectrometer in the Department of Geological Sciences at the University of Florida for $\delta^{13}C_{ap}$, which was measured against Vienna PDB standard. Analytical precision for NBS 19 (n = 17) was 0.05 for $\delta^{13}C$.

Results

Individual isotopic results are presented in Table 4.1. Of the 25 samples, 19 from Chelechol ra Orrak, three from Koror Quarry, and the individual from Peleliu all yielded C:N ratios that were considered acceptable for analysis (total N = 23). Bone collagen ($\delta^{13}C_{co}$) values for Chelechol ra Orrak averaged -15.9‰ (±0.83), ranging from -17.2‰ to -14.9‰, while $\delta^{15}N$ values averaged 11.0‰ (±0.89), ranging from 9.0‰ to 12.6‰. Bone apatite ($\delta^{13}C_{ap}$) values averaged -8.7‰ (±0.82), ranging from -9.9‰ to -6.9‰. When all

23 samples are pooled, $\delta^{13}C$ bone collagen values averaged -14.8‰ (±0.28), ranging from -17.2‰ to -14.5‰; $\delta^{15}N$ values averaged 11.4‰ (±0.16), ranging from 9.0‰ to 12.6‰; and bone apatite $\delta^{13}C$ values averaged -7.3‰ (±1.83), ranging from -12.9‰ to -5.2‰. $\delta^{13}C_{ap-co}$ spacing averaged 7.2‰ (±0.94), ranging from 5.8‰ to 9.2‰ for the Chelechol ra Orrak individuals, and 7.5‰ (±1.77), ranging from 5.8‰ to 9.5‰ for the pooled sample.

Sex could only be determined for nine Chelechol ra Orrak individuals, who represent five females and four males. One of the males yielded a poor C:N ratio and was excluded from analysis. Summary statistics for the remaining eight samples are presented in Table 4.2. Females yielded slightly higher $\delta^{13}C$ values, with an average $\delta^{13}C$ bone collagen value of -16.24‰ (±0.93) compared to -16.7‰ (±0.92) for males, and bone apatite $\delta^{13}C$ values averaged -9.9‰ (±0.26) for females and -8.9‰ (±0.55) for males. $\Delta^{13}C_{ap-co}$ spacing averaged 7.5 (±0.53) and 7.95 (±0.07) for females and males, respectively. Males yielded slightly higher $\delta^{15}N$ values, averaging 11.4‰ (±0.32) compared to a female average of 11.1‰ (±0.91).

Similarly, only seven samples could be assigned to specific age categories (adolescent, young adult, middle adult, and old adult, after Buikstra and Ubelaker 1994), one of which was excluded from analysis due to low collagen yield and an unacceptable C:N ratio. The remaining Chelechol ra Orrak samples belonged to adult individuals but could not be assigned to more specific categories. When all Chelechol ra Orrak adults are pooled into one category, $\delta^{13}C_{co}$ and $\delta^{15}N$ bone collagen values averaged -15.8‰ (±0.76) and 11.1‰ (±0.92), respectively, while $\delta^{13}C_{ap}$ bone apatite and $\Delta^{13}C_{ap-co}$ spacing average -9.25 (±0.07) and 7.95 (±0.07), respectively (Table 4.3). The two adolescents averaged slightly lower $\delta^{13}C_{co}$ and $\delta^{15}N$ values, -17.0‰ (±0.28) and 10.65 (±0.49), respectively, and bone apatite $\delta^{13}C_{ap}$ values of -9.0 (±0.28), and $\Delta^{13}C_{ap-co}$ spacing averaging 8.0‰ (±0). When the samples that can be further subdivided to age categories, including young, middle, and old adult, are compared, there is some slight variation across groups (Table 4.3). However, the middle and old adult categories are each represented by one person, and two females are present in the young adult category. As such, some of the variation that may appear to be due to age-related differences may instead be biased by sex or small sample size.

Table 4.1. Isotopic values for individuals sampled from Chelechol ra Orrak, Peleliu, and Koror Quarry. Italicized samples were not used because of unacceptable C:N ratios and low collagen yields. (Note: each sample represents a single individual.)

Sample	Provenience	UF BCL# (collagen)	UF BCL# (apatite)	Element	Sex	Age at Death	^{14}C Date (cal BP)	$\delta^{13}C_{col}$ (‰, VPDB)	$\delta^{15}N_{col}$ (‰, AIR)	%C	%N	C:N	$\delta^{13}C_{ap}$ (‰, VPDB)	$\Delta^{13}C_{ap\text{-}col}$
							Chelechol ra Orrak							
1	Test Unit 4, Layer 10	1205	242	os coxa	Male	Adult	2845-2340	-15.6	11.5	17.42	6.32	3.2	-8.3	7.3
2	Test Unit 1, Layer 9	1206	243	tibia	Female	Adult	2760-1420	-14.9	12.6	12.57	4.27	3.4	-8.8	6.1
3	Test Unit 1, Layer 9	1207	244	long bone	unknown	Adult	2760-1420	-15.0	12.3	12.68	4.45	3.3	-6.9	8.1
4	Test Unit 1, Layer 8	1208	245	long bone	unknown	Adult	2950-2010	-15.6	11.8	11.63	4.00	3.4	-6.9	8.6
5	Test Unit 1, Layer 8	1209	246	metatarsal	unknown	Adult	2950-2010	-16.6	11.4	7.74	2.69	3.4	-7.4	9.2
1A	E1S5	2242	1176	humerus	unknown	Adult	N/A	-15.0	9.0	25.49	9.07	3.3	-8.9	6.1
2A	E1S5	2243	1177	humerus	unknown	Adult	N/A	-15.7	11.8	34.26	11.87	3.4	-9.9	5.8
3A	E1S5	2244	1178	humerus	unknown	Adult	N/A	-15.0	11.2	34.89	12.15	3.4	-8.5	6.5
4A	E1S5	2245	1179	humerus	unknown	Adult	N/A	-15.6	10.0	30.85	10.85	3.3	-9.1	6.5
5A	E1S5	2246	1180	humerus	unknown	Adult	N/A	-16.0	9.7	27.81	10.07	3.2	-9.3	6.7
6A	E1S5	2247	1181	humerus	unknown	Adult	N/A	-14.9	11.5	35.26	12.09	3.4	-8.5	6.4
7A	E1S5	2248	1182	humerus	unknown	Adult	N/A	-15.9	11.2	34.49	12.06	3.3	-9.2	6.8
8A	E1S5	2249	1183	humerus	unknown	Adult	N/A	-15.2	10.6	N/A	N/A	N/A	-8.4	6.8
11	E3S1-E3S2, Layer 10	3046	3046	rib	Female	Young Adult	failed	-15.7	10.5	29.30	10.02	3.4	-9.0	6.8
13	E1S5-W1S5, Layer 10	3047	3047	rib	Female	Young Adult	2495-2340*	-17.2	11.1	29.37	10.13	3.4	-9.4	7.8
14	E1S4-W1S4, Layer 10	3048	3048	rib	Female	Old Adult	2765-2690*	-16.6	10.9	36.82	13.18	3.3	-9.2	7.4
15	E2S2-E2S1, Layer 10	3049	3049	rib	Male	Adolescent	2480-2325*	-17.2	11.0	21.37	6.85	3.6	-9.2	8.0
16	E1S5/E2S5-E1S4, Layer 10	3050	3050	rib	Male	Middle Adult	2465-2315*		11.6	28.82	10.14	3.3	-9.3	7.9

Table 4.1, continued.

Sample	Provenience	UF BCL# (collagen)	UF BCL# (apatite)	Element	Sex	Age at Death	^{14}C Date (cal BP)	$\delta^{13}C_{col}$ (‰, VPDB)	$\delta^{15}N_{col}$ (‰, AIR)	%C	%N	C:N	$\delta^{13}C_{ap}$ (‰, VPDB)	$\Delta^{13}C_{ap\text{-}col}$
						Chelechol ra Orrak								
19	*E1S5-E1S4, Layer 10*	*3051*	*3051*	*rib*	*Male*	*Young Adult*	*2425-2300**	*-20.8*	*2.2*	*9.14*	*2.89*	*3.7*	*-9.3*	*11.5*
21	E1S5-E1S4, Layer 10	3052	3052	rib	Female	Adolescent	2715-2465*	-16.8	10.3	4.37	12.96	3.5	-8.8	8.0
mean								**-15.9**	**11.0**				**-8.7**	**7.2**
std.dev.								**0.83**	**0.89**				**0.82**	**0.94**
						Peleliu								
6	Trench 1, Unit 15	1210	247	long bone	unknown	Adult		-14.8	10.8	23.09	8.07	3.3	-12.9	1.9
						Koror Quarry								
7	*Site 30, Chamber 10, Fea. 1*	*1211*	*248*	*long bone*	*unknown*	*Adult*				*2.76*	*0.28*	*###*	*-2.8*	
8	Chamber 7, Fea. 1	1212	249	long bone	unknown	Adult		-15.1	11.5	16.60	5.77	3.4	-8.6	6.4
9	Site 30, Chamber 1, Fea. 1	1213	250	long bone	unknown	Adult	1180-980	-14.7	11.2	27.73	10.02	3.4	-5.2	9.5
10	Chamber 3	1214	251	long bone	unknown	Adult		-14.5	11.4	24.41	8.76	3.4	-8.1	6.5
mean								**-14.8**	**11.4**				**-7.3**	**7.5**
std.dev.								**0.28**	**0.16**				**1.83**	**1.77**

UF BCL = Bone Chemistry Lab, Department of Anthropology, University of Florida

All radiocarbon dates were calibrated using OxCal 4.2 and are presented with 95% probability (2). A 50% Marine13 calibration curve was applied to bone dates to account for marine dietary contributions.

Dates marked with an * are direct burial dates. All others presented are associated date ranges from the same provenience as individual sampled, when available.

Adult age was assigned to the following categories following Buikstra and Ubelaker (1994): Adolescent (12-20 yrs.), Young Adult (20-35 yrs.), Middle Adult (35-50 yrs.), and Older Adult (50+ yrs.).

Provenience crossing multiple units is listed from head to foot.

Table 4.2. Descriptive statistics for isotopic values from Chelechol ra Orrak by sex.

Sex	n	Mean $\delta^{13}C_{col}$ (±1 SD) (‰, VPDB)	Mean $\delta^{15}N_{col}$ (±1 SD) (‰, AIR)	Mean $\delta^{13}C_{ap}$ (±1 SD) (‰, VPDB)	Mean $\Delta^{13}C_{ap\text{-}col}$ (±1 SD) (‰, VPDB)
Females	4	-16.24 (±0.93)	11.1 (±0.91)	-9.0 (±0.26)	7.2 (±0.78)
Males	3	-16.7 (±0.92)	11.4 (±0.32)	-8.9 (±0.55)	7.73 (±0.38)
Unsexed	12	-15.5 (±0.54)	10.95 (±1.01)	-8.45 (±1.00)	7.05 (±1.09)

Table 4.3. Descriptive statistics for isotopic values from Chelechol ra Orrak by age.

Age	n	Mean $\delta^{13}C_{col}$ (±1 SD) (‰, VPDB)	Mean $\delta^{15}N_{col}$ (±1 SD) (‰, AIR)	Mean $\delta^{13}C_{ap}$ (±1 SD) (‰, VPDB)	Mean $\Delta^{13}C_{ap\text{-}col}$ (±1 SD) (‰, VPDB)
Adolescents	2	-16.6 (±0.63)	10.7 (±0.37)	-9.1 (±0.26)	7.5 (±0.53)
Young Adults	2	-16.45 (±1.06)	10.8 (±0.42)	-9.2 (±0.28)	7.3 (±0.71)
Middle Adults	1	-17.2	11.6	-9.3	7.9
Older Adults	1	-16.6	10.9	-9.2	7.4
Adults	17	-17.2 (±0)	11.3 (±0.42)	-9.25 (±0.07)	7.95 (±0.07)

When all three sites are compared, the individual from Peleliu exhibits lower $\delta^{13}C_{ap}$ and $\delta^{15}N$ values and lower $\Delta^{13}C_{ap\text{-}co}$ spacing in contrast to the Chelechol ra Orrak and Koror Quarry samples (Figure 4.1). Typically, low $\Delta^{13}C_{ap\text{-}co}$ spacing suggests a ^{13}C-enriched diet of enriched marine protein supplemented with terrestrial C_3 carbohydrates, while more intermediate spacing is indicative of monoisotopic diets.

Discussion

Generally, the results are consistent with a diet that is primarily marine based with a variety of terrestrial plants, as evidenced by elevated $\delta^{13}C_{co}$ and $\delta^{15}N$ values from bone collagen (Figure 4.2) (Kellner and Schoeninger 2007). Although site-specific baseline data are not yet available for Chelechol ra Orrak, dietary baselines have been published for both modern and prehistoric plants and animals from the western Pacific (Kinaston et al. 2013a, 2014a).
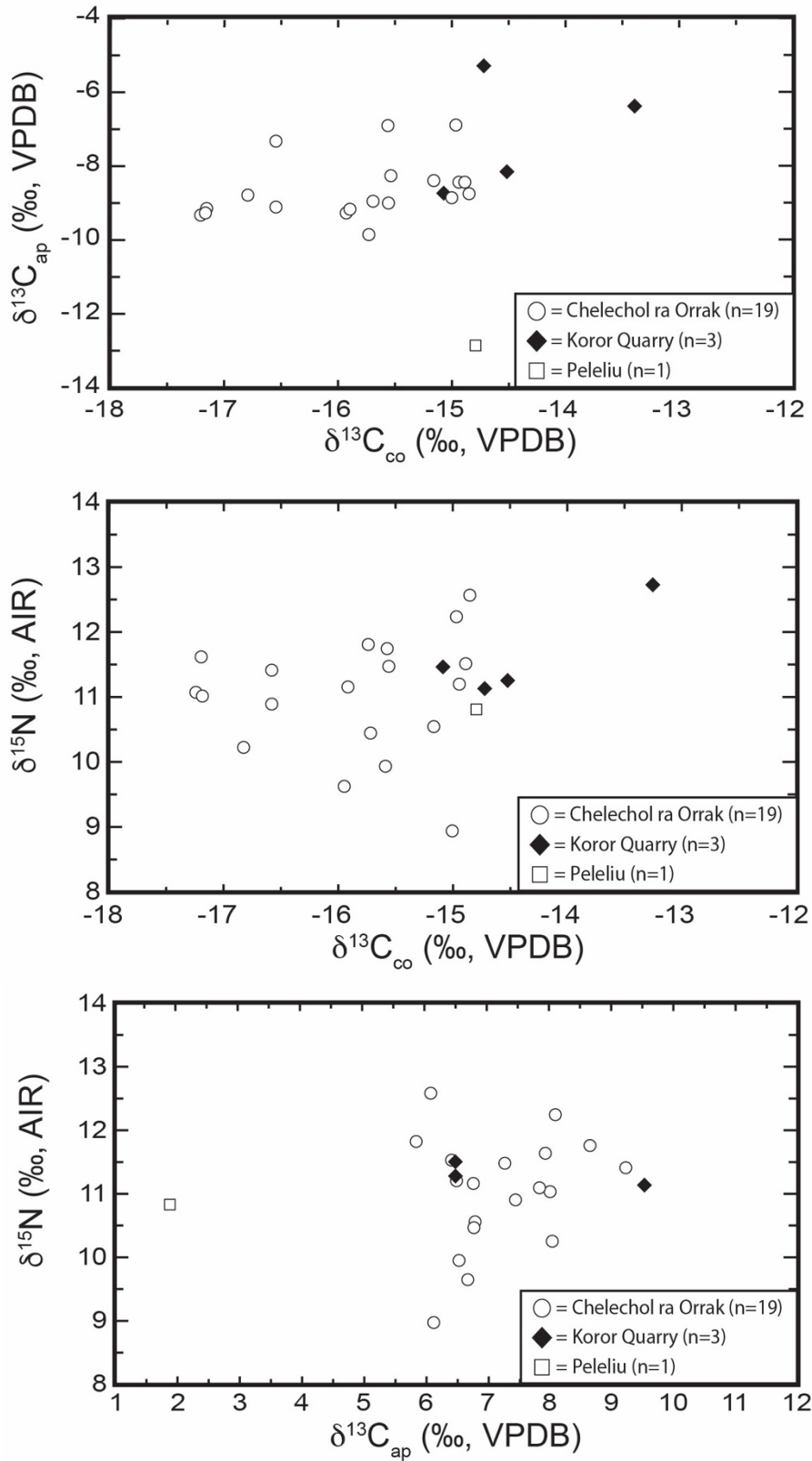
Figure 4.1. *Top to bottom*: δ¹³C collagen versus apatite values; δ¹³C collagen versus δ¹⁵N collagen values; δ¹³C collagen-apatite spacing versus δ¹⁵N collagen values.
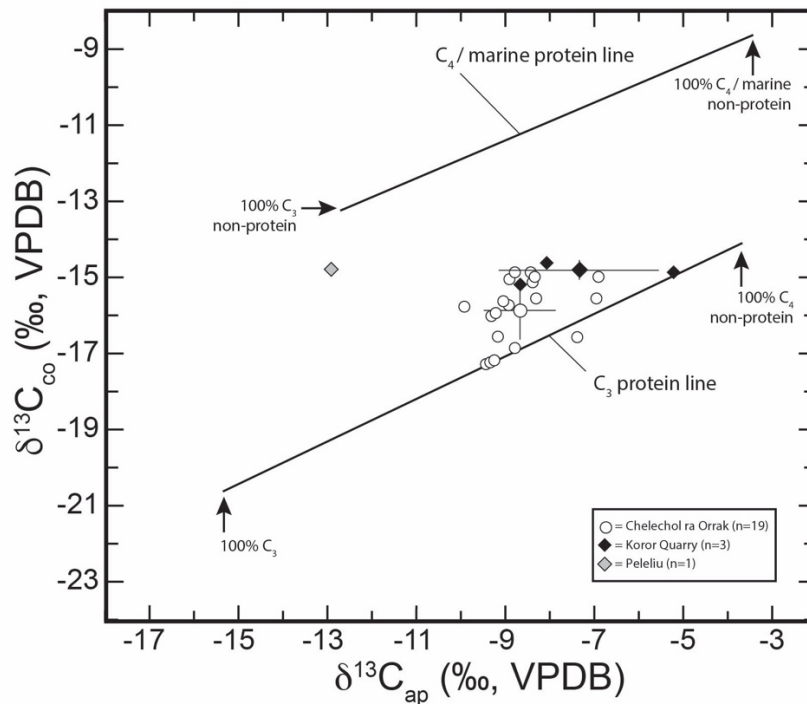
Figure 4.2. $\delta^{13}C$ collagen and $\delta^{13}C$ apatite data plotted against regression model developed by Kellner and Schoeninger (2007).

Additionally, Ambrose et al. (1997) generated modern baseline data from a number of faunal and botanical taxa from Guam and Yap (Figure 4.3). When compared to $\delta^{13}C$ values for fruit bats (-19.8‰), a proxy for a 100% terrestrial diet, $\delta^{13}C_{co}$ values for individuals from all three Palauan sites are significantly less negative, suggesting a major contribution of marine protein. Instead, diets are more in line with baseline data that include modern marine shellfish, such as scallops, oysters, and cowries reported for Vanuatu (Kinaston et al. 2014a). When $\delta^{13}C_{co}$ values are combined with $\delta^{15}N$ values, these results support a diet that includes taxa from reef and inshore environments. Elevated $\delta^{13}C_{ap}$ values for bone apatite suggest some ^{13}C-enriched source of carbohydrate, which may be due to consumption of marine plants, such as kelp or seaweed, or perhaps sugarcane. Although Kinaston et al. (2013a) considered sugarcane consumption unlikely as a dietary staple for Vanuatu, Froehle et al. (2012) reanalyzed data from Ambrose et al. (1997) and argued that the sample from Saipan is more consistent with consumption of sugarcane rather than seaweed.
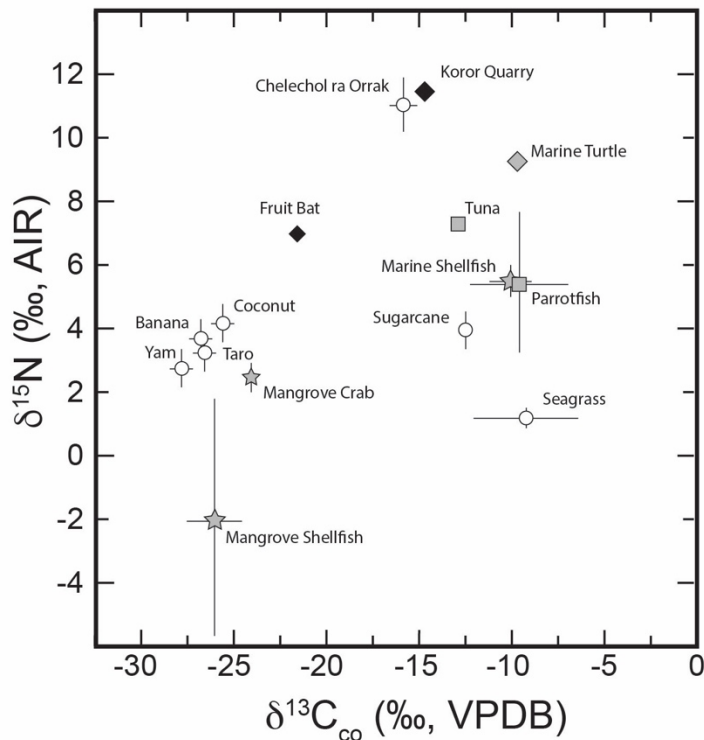
Figure 4.3. Mean $\delta^{13}C$ collagen versus mean $\delta^{15}N$ collagen values for Chelechol ra Orrak and common Pacific Island dietary resources. Values taken from modern samples analyzed in Kinaston et al. 2014a.

A diet focused on marine protein, however, is consistent with what has been observed in the faunal record, where assemblages tend to be dominated by mollusks and finfish remains (Clark 2004, Clark et al. 2006, Fitzpatrick 2003c, Fitzpatrick et al. 2011, Ono and Clark 2012). Shellfish assemblages at Rock Island sites, including stone money quarries and stonework villages, contain taxa commonly found in intertidal and shallow reef environments, demonstrating their importance for long-term survival (Carucci 1992, Fitzpatrick 2003b). At Chelechol ra Orrak the vertebrate faunal assemblage is dominated by fish from primarily nearshore reef and lagoon environments, including parrotfish (Scaridae), wrasses (Labridae), and surgeonfishes (Acanthuridae); however, these remains are associated with occupation of the site after burial activity had ceased and their ubiquity may be in part due to preservation bias (Fitzpatrick et al. 2011, Fitzpatrick and Kataoka 2005). The faunal assemblage from Ulong Island, which is contemporary

with burial activity at Chelechol ra Orrak, also consists of inshore taxa during the earliest phases of occupation that include parrotfish (Scaridae), surgeonfishes (Acanthuridae), triggerfish (Balistidae), sea bass (Serranidae), emperorfish (Lethrinidae), and eel (Muraenidae). Additionally, large bivalves such as *Tridacna gigas* and *Hippopus hippopus* were targeted during the early phases of occupation (Ono and Clark 2012). Together, these suggest that early foraging likely would have focused primarily on inshore fish and mollusk taxa.

The dental health of individuals from Chelechol ra Orrak is also suggestive of a diet based on marine protein with relatively low contributions of carbohydrates. Preliminary analysis of dental pathology found low caries rates, light tooth wear, and low rates of antemortem tooth loss. Enamel chipping is also frequent, particularly in the posterior teeth (Nelson et al. 2015). While low caries rates are typically associated with groups that consume low levels of cariogenic foods, such as starchy carbohydrates, the majority of the burials excavated from Chelechol ra Orrak to date exhibit staining from the habitual chewing of betel nut (*Areca catechu*). This practice has been shown to create cariostatic conditions in the mouth, possibly due to antimicrobial properties in tannins found in the plant or as a result of increased saliva production while chewing (de Miranda et al. 1996, Fitzpatrick et al. 2003, Howden 1984, Trivedy et al. 2002). Therefore, it is likely that low caries rates can be attributed to some combination of habitual betel nut chewing and a diet low in cariogenic foods.

The slight increases in mean $\delta^{13}C_{co}$ bone collagen and $\delta^{13}C_{ap}$ apatite values for females and $\delta^{15}N$ bone collagen values for males suggest that females may have consumed fewer marine protein resources from slightly lower trophic levels (Table 4.2). There is also a broader range in all values for females, which might suggest that females ate a more varied diet. However, the female ranges of values overlaps with males (e.g., Chelechol ra Orrak Burial 13), suggesting these differences may instead be a result of the small sample size of individuals of known sex rather than sex-based dietary distinctions. Sex- or age-based differences in diet may become more apparent as further individuals are analyzed, but the lack of observable differentiation in mortuary practice between individuals buried at Chelechol ra Orrak also suggests that demographic differences in status are unlikely or that access to specific food resources is dictated by other factors.

The only distinguishing grave goods found thus far at Chelechol ra Orrak are pearl shell scrapers associated with some females, and a single male individual that was found with mollusk shells and a single pearl shell scraper. There does not appear to be any apparent relationship between individuals with associated grave goods and an isotopic signature that is distinct from the rest of the assemblage, but this is also likely due to the fact that only one individual with associated grave goods has been sampled thus far. This is in contrast to what has been observed at the Lapita sites of Teouma, Vanuatu, where males displayed a higher range of $\delta^{13}C$ and $\delta^{15}N$ values and higher $\delta^{15}N$ values compared to females, and at Watom, where females display higher $\delta^{15}N$ values (Kinaston et al. 2015a). A number of possibilities have been presented to explain this trend at Watom, including gendered patterns of food acquisition or distribution, whereby males were consuming more varied foods and higher-trophic-level protein sources; maternal stress and poor health; the presence of female migrants from areas with distinct diet; or temporal changes in diet between the Middle and Late Lapita periods (Kinaston et al. 2014a, 2015a). Due to the broad time frame that encompasses mortuary activity at Chelechol ra Orrak, the possibility that temporal variation is present at the site is an important consideration. However, at this point in time, direct radiocarbon dates are only available for six of the individuals sampled, and when associated dates from the same provenience are included (available for an additional five individuals), too much temporal overlap is present to satisfactorily explore this possibility (Table 4.1).

When compared to the Chelechol ra Orrak samples, the individuals from Koror Quarry display slightly higher $\delta^{13}C$ values for both the bone collagen and apatite fractions (Figure 4.2). This could be attributed to consumption of fewer marine protein resources, or possibly increased consumption of C_3 plants, but is more likely due to the small sample size representing Koror Quarry. The individual from Peleliu displays noticeably lower $\delta^{13}C_{ap}$ apatite in comparison to both the Koror Quarry and Chelechol ra Orrak individuals, though given the lack of provenience information associated with this individual, the variation in $\delta^{13}C$ values could be explained by temporal differences that reflect a historic period diet.

Table 4.4. Mean bone collagen δ^{13}C and δ^{15}N values from other prehistoric Pacific Island sites (based on Kinaston and Buckley 2013); *n* reflects the number of bone samples that were considered acceptable for analysis based on C:N ratios.

Site/Location	n	Radiocarbon Dates (cal. BP)	Mean $\delta^{13}C_{col}$ (‰, VPDB)	Mean $\delta^{15}N_{col}$ (‰, VAIR)	References
Chelechol ra Orrak, Palau	19	3000-1800	-15.9	11.0	This chapter
Koror Quarry, Palau	3	2500	-14.8	11.4	This chapter
Ureia and Moturakau, Aitutaki, Cook Islands	18	740-100	-15.8	11.5	Allen and Craig 2009
Watom, Bismarck Archipelago	13	2800-2350	-18.1	11.2	Kinaston et al. 2015; Leach et al. 2003
Bourewa, Fiji	21	750-150	-15.1	8.6	Stantis et al. 2015a
Cikobia Island, Fiji	9	150-100	-17.2	9.5	Valentin et al. 2006
Lau Group, Fiji	9	2760-280	-16.3	9.4	Jones and Quinn 2009
Olo and Naitabale Waya Island, Fiji	13	2700-2300	-15.0	9.5	Field et al. 2009; Nunn et al. 2007
Nokonoko and Bukusia, Sigatoka Valley, Fiji	5	1300-280	-19.5	8.7	Field et al. 2009
Sigatoka Sand Dunes, Fiji	22	1435-1300	-16.3	9.3	Phaff et al. 2016
Kapingamarangi Atoll	2	post 700	-15.7	20.1	Leach et al. 2003
various sites, Rota, Mariana Islands	10	1000-	-18.1	9.0	Ambrose et al. 1997
various sites, Rota, Mariana Islands	12	2000-250	-18.1	9.0	Pate et al. 2001
Agana, Guam, Mariana Islands	5	1000-600	-17.4	9.5	Ambrose et al. 1997
Afetna, Saipan, Mariana Islands	10	1500-1300	-18.7	9.5	McGovern-Wilson and Quinn 1996
Duty Free, Saipan, Mariana Islands	4	700-600	-18.7	7.5	Ambrose et al. 1997
MacHomes and Nansay, Saipan, Mariana Islands	5	1000-	-18.1	8.4	Ambrose et al. 1997
Hanamiai, Marquesas Islands	4	925-100	-16.4	18.8	Richards et al. 2009
Kone, New Caledonia	1	2110-1990	-12.2	11.1	Pietrusewsky et al. 1998
Tina, New Caledonia	2	850	-15.1	9.8	Leach et al. 2003
Nebira, Papua New Guinea	28	800-300	-16.7	9.5	Kinaston et al. 2013
various sites, New Zealand	10	500 -	-17.8	13.0	Leach et al. 2003
Wairau Bar, New Zealand	28	650-	-17.5	15.9	Kinaston et al. 2013; Leach et al. 2003
various sites, Rapa Nui	41	800-	-18.5	13.4	Commendador et al. 2013
various sites, Rapa Nui	107	800-	-18.4	13.4	Polet and Bocherens 2016
Anakena and Ahu Tepeu, Rapa Nui	10	550 -	-18.6	14.5	Jarman et al. 2017
Fatu-ma-Futi, Tutuila, American Samoa	7	440-110	-18.0	11.3	Valentin et al. 2011
Lauli-i, Tutuila, American Samoa	6	535-380	-18.2	11.2	Valentin et al. 2011
Namu, Taumako, Solomon Islands	142	675-295	-16.5	11.6	Kinaston and Buckley 2017; Kinaston et al. 2013

Table 4.4, continued.

Site/Location	n	Radiocarbon Dates (cal. BP)	Mean $\delta^{13}C_{col}$ (‰, VPDB)	Mean $\delta^{15}N_{col}$ (‰, VAIR)	References
Atele, Tonga	41	1000-280	-17.6	9.3	Stantis et al. 2015b
Talasiu, Tonga	16	2700-2600	-15.7	10.7	Herrscher et al. 2018
Teouma, Vanuatu	49	3000-2800	-15.7	12.1	Kinaston et al. 2014a
Uripiv, Vanuatu	27	2800-150	-17.6	8.3	Kinaston et al. 2014b
Vao, Vanuatu	4	2300-1900	-17.9	8.7	Kinaston et al. 2015b

In contrast to other Micronesian paleodietary studies conducted in the Mariana Islands, the Palau signature observed in these data reflects a diet predominantly of ^{13}C- and ^{15}N-enriched foods that lead to elevated δ^{13}C and δ^{15}N values, suggesting a greater reliance on marine resources among Palauans (Figure 4.4). Ambrose et al. (1997) also analyzed $\delta^{13}C_{ap}$ and $\Delta^{13}C_{ap-co}$ and demonstrated some inter-island variability in the Marianas archipelago. $\delta^{13}C_{ap}$ values from bone apatite from Saipan are most similar to those from Palau, though other sites sampled from Guam and Rota are also broadly similar to results reported here, but with lower δ^{15}N values. However, this may be due to a temporal difference, as the majority of the individuals sampled from the Marianas date to the Latte Period, which postdates 1000 BP and, as previously mentioned, is typically associated with archaeological evidence for agricultural intensification and a shift to more targeted fishing of coastal reef and lagoon habitats (Carson 2012, Pate et al. 2001).

When compared to contemporary Lapita groups, the individuals at Chelechol ra Orrak exhibit broadly similar $\delta^{13}C_{co}$ values to what has been observed at Teouma in Vanuatu, where individuals also reflect a marine-based diet consisting primarily of reef fish and nearshore shellfish, and Talasiu in Tonga (Figure 4.5, Table 4.4) (Herrscher et al. 2018, Kinaston et al. 2014a, 2015b, Valentin et al. 2010). At Teouma, however, the presence of terrestrial faunal remains such as pig and chicken suggest that marine foods were likely supplemented by translocated resources (Kinaston et al. 2014a, Valentin et al. 2010). Conversely, on Watom Island in the Bismarck Archipelago, Lapita individuals instead reflect a diet based in terrestrial protein and C_3 plants supplemented by some marine foods. This has largely been attributed to the differences in Near and Remote Oceanic ecology and biogeography, as Near Oceania contains a wider variety of edible

terrestrial resources as well as islands larger in area that would have had available land for horticulture and animal husbandry (Kinaston et al. 2015a, Kinaston and Buckley 2013).
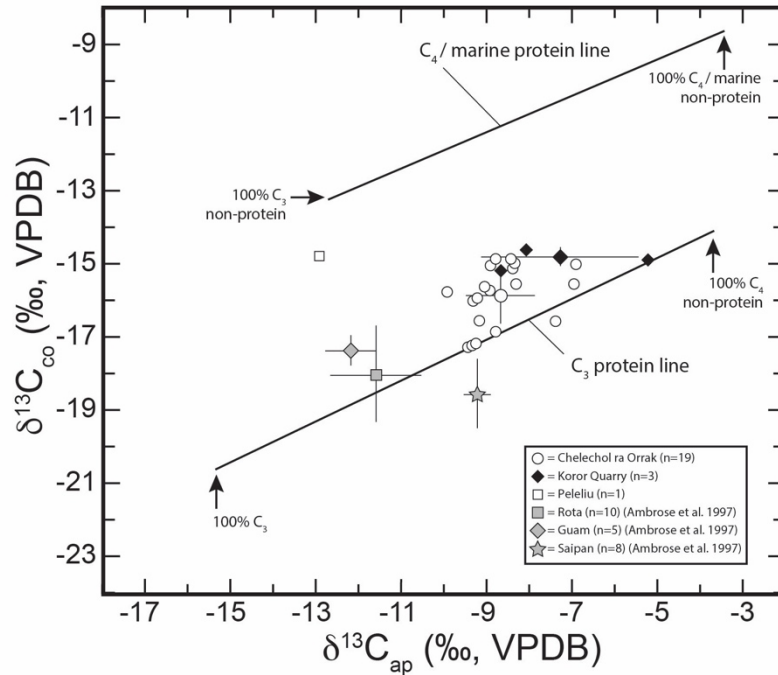
Figure 4.4. Mean $\delta^{13}C$ collagen versus $\delta^{15}N$ collagen values for human bone samples from western Micronesia, including Chelechol ra Orrak, other sites in Palau (Koror Quarry), and the Marianas Islands. Values from Table 4.4.

The reliance on marine protein resources seen at Chelechol ra Orrak and Teouma is broadly similar to what has been observed among other groups in Remote Oceania, including later and post-Lapita sites on Vanuatu, Fiji, Tonga, the Cook Islands, and the Marquesas Islands (Allen and Craig 2009, Field et al. 2009, Jones and Quinn 2009, Richards et al. 2009, Stantis et al. 2015a). However, there does appear to be a temporal trend toward increasing amounts of terrestrial plant and animal foods over time, especially among later and post-Lapita groups, which may be explained by a delay in establishing crops following settlement (Kinaston et al. 2015b).
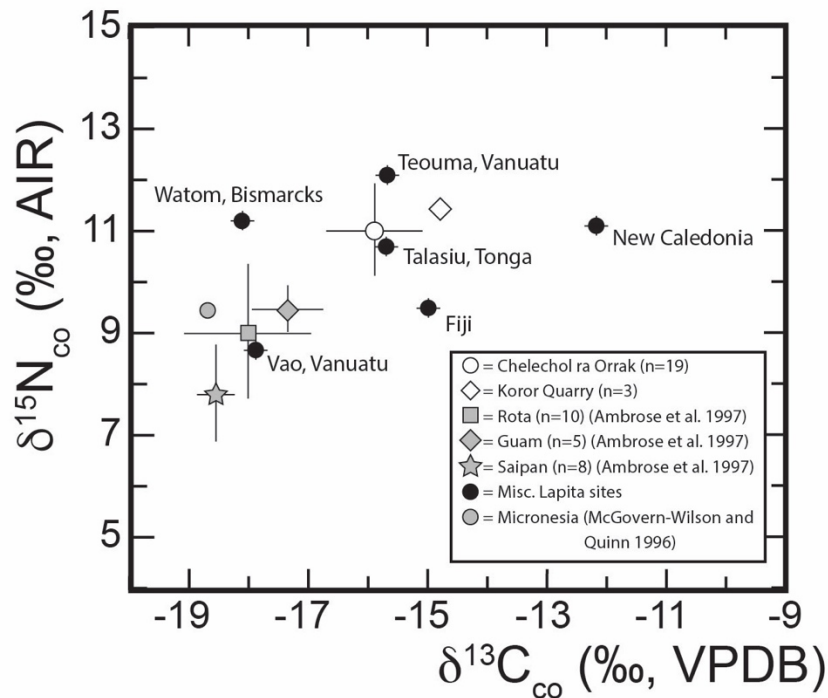
Figure 4.5. Mean $\delta^{13}C$ collagen versus $\delta^{15}N$ collagen values for human bone samples that are contemporary with Chelechol ra Orrak. Micronesia samples include Koror Quarry from Palau and Afetna, Saipan. Lapita sites include Teouma and Vao, Vanuatu, Kone, New Caledonia, Talasiu, Tonga, Watom, Bismarck Archipelago, and Olo and Naitabale, Waya Island, Fiji. Values from Table 4.4.

Conclusion

      Although baseline faunal data are needed, these preliminary results suggest that early inhabitants of Palau took advantage of readily available and diverse marine resources, including inshore marine protein and possibly seaweeds. Protein consumption appears to be relatively similar to what has been observed among Lapita populations, suggesting that both groups primarily relied on endemic resources following initial settlement in Remote Oceania despite the presence of translocated terrestrial fauna at Lapita sites (Kinaston et al. 2013a, Kinaston and Buckley 2013, Valentin et al. 2010). However, demographic patterning that has been observed at Teouma is not present among the Palauan samples, which currently lack any dietary distinctions based on sex and age (Kinaston et al. 2014a, 2015a). While this could be the result of differences in gendered patterns of resource distribution or health between Lapita and non-Lapita

groups, larger sample sizes of individuals of known sex and age, as well as a better understanding of how gender was represented in early Palauan groups, are needed to more fully investigate this possibility.

While it appears that endemic marine resources played a significant role in early Palauan diets, plants such as the areca palm (*Areca catechu*) were also important and led to habitual cultural behaviors that are still practiced today. In the next chapter, I look at possible impacts of habitual betel nut chewing on skeletal and dental health, including its role as a possible cause of osteoarthritis in the temporomandibular joint (TMJ).

TEMPOROMANDIBULAR JOINT OSTEOARTHRITIS AT CHELECHOL RA ORRAK

Introduction

Paleopathological studies of joint use and degeneration can provide a biocultural perspective on habitual activities practiced in the past (Jurmain 1991, Roberts and Manchester 2007). For example, processing fibrous plant materials using the dentition would have required substantial involvement of the jaw and associated temporomandibular joints (TMJ). In the case of colonization studies in the Pacific, where a number of habitual fibrous chewing activities are well known, such information has the potential to shed light on the consequences of cultural practices following initial settlement. In this chapter, I investigate the potential relationship between osteoarthritis of the TMJ (TMJ-OA) and the chewing of betel nut (*Areca catechu*), a common practice in Palau, at Chelechol ra Orrak.

The TMJ is essential to the human body because of its necessity in accomplishing a wide range of important functions, ranging from chewing to swallowing and speech (Levangie and Norkin 2001, Piette 1993). As a result of the joint's frequent use, disorders affecting the TMJ are widespread and have been the subject of much clinical research. The antiquity of TMJ disorders, such as osteoarthritis (OA), have also been demonstrated in archaeological populations (e.g., Fujita 2014, Griffin et al. 1979, Lovell 2014, Richards and Brown 1981, Tanaka et al. 2004). As such, the paleopathological record is uniquely situated to contribute to our understanding of TMJ osteoarthritis (TMJ-OA) by adding a deep time perspective to fluctuations in the frequency of bony changes across populations. However, paleopathologists also face an inherent challenge in diagnosing and assessing the impact of pathological conditions when compared to their clinical research counterparts. Critical information, such as the presence of additional soft tissue that comprises portions of the joint, patient history, or symptoms experienced, is rarely, if

ever, available. Studies of OA commonly cite activity and general joint use as playing a major role in the etiology of these disorders, but our understanding of activity in the archaeological record is challenging given the extremely limited preservation of soft tissue. Furthermore, both clinical and paleopathological research has demonstrated that the factors contributing to OA are diverse and can include sex, age, genetics, and trauma, among others (Sandell 2012, Waldron 2008, Weiss and Jurmain 2007).

In the case of the TMJ, frequent activities such as chewing, tool use, and speech can all impact the joint. However, in the archaeological record, the extent to which specialized parafunctional activities impacted a joint can be difficult to identify. One example of an activity that leaves an observable signature is betel nut (*Areca catechu*) chewing, which is a substance used throughout parts of Southeast Asia and the Pacific Islands for its stimulant properties. Habitual betel nut chewing requires substantial TMJ involvement and leaves characteristic staining on the dentition that typically preserves well in archaeological contexts.

Among some Pacific Island populations, the processing and consumption of psychoactive substances, such as betel nut and kava (*Piper methysticum*), is an activity with demonstrated antiquity, but little archaeological or epidemiological research has focused on the potential impact on the TMJ. While the relationship between kava processing and TMJ-OA has been evaluated in a prehistoric Fijian population (Visser 1994), the anatomical effects of betel nut have primarily focused on dental health in modern populations (e.g., Trivedy et al. 2002). At Chelechol ra Orrak, both a high frequency of TMJ-OA related bony changes and evidence for habitual chewing of betel nut in the form of tooth staining have been observed, thus providing a unique opportunity to explore this potential relationship. Because betel nut use is widespread throughout Southeast Asia and parts of the Pacific (Fitzpatrick et al. 2003; Zumbroich 2008), a better understanding of the substance's impact on TMJ health may influence clinical approaches to TMJ-OA treatment in living populations (Trivedy et al. 2002). Additionally, because OA is known to be multifactorial, other potential contributing factors, including tooth wear, antemortem tooth loss (AMTL), joint surface morphology, and demography are also evaluated.

Anatomy of the Temporomandibular Joint

The TMJ is a synovial joint comprised of three elements: the mandibular condyle, the articular eminence of the temporal bone, and an articular disc of dense fibrous tissue that subdivides each joint into two synovial cavities (Figure 5.1). The articular eminence, which forms the posterior surface of the zygomatic arch and the anterior surface of the mandibular fossa, is the non-moveable component of the joint and typically forms a concave sloping shape in profile. The mandibular condyle, or the moveable portion of the joint, can vary between individuals in size, shape, and angulation, but is typically elliptical in form when viewed superiorly (Herring 2003, Kreutziger and Mahan 1975, Piette 1993). The joint is unique in a number of ways. First, while the body contains two distinct TMJs (on the right and left side of the body), unlike most other joints, the individual sides cannot move independently. Second, movement of the joint is inherently associated with use of the dentition, resulting in greater repetitive use compared to other joints (Kreutziger and Mahan 1975, Piette 1993). Lastly, the joint surfaces are covered in fibrocartilage rather than the hyaline cartilage that is characteristic of synovial joints. Because fibrocartilage can remodel, joints with this tissue are more capable of withstanding repetitive high stress (Herring 2003, Levangie and Norkin 2001).
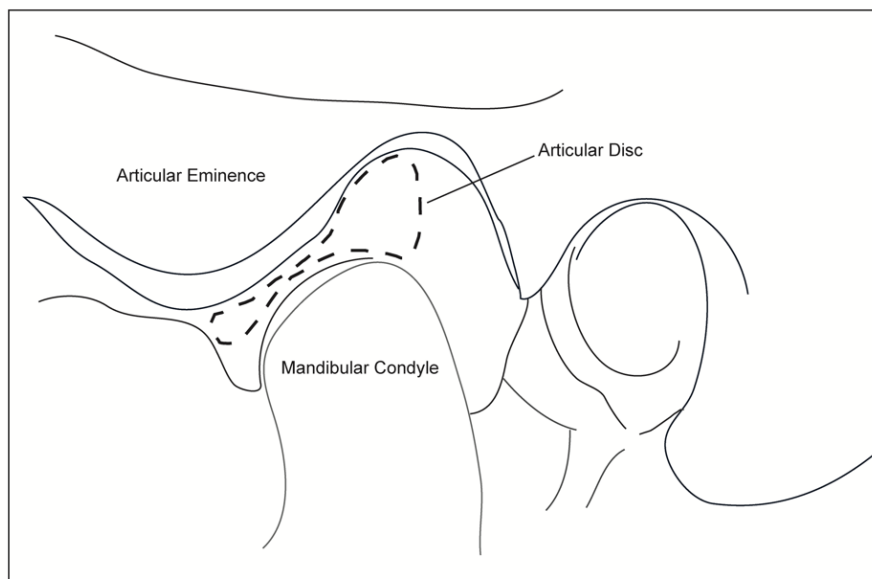

Figure 5.1. Illustration of temporomandibular joint, showing the elements discussed in the text.

TMJ disorders and factors

        TMJ disorders comprise a group of musculoskeletal issues that together are the second most commonly reported category of musculoskeletal pain (Shahidi et al. 2018). The disorders can vary significantly in prevalence across populations, and symptoms present in a wide variety of forms, ranging from myofacial pain to disc displacement, or OA, which is the most common pathological condition affecting the joint (Tanaka et al. 2008). Osteoarthritis of the TMJ (TMJ-OA) can trigger bony changes to the joint in response to a breakdown of cartilage. There are several factors contributing to the development of TMJ disorders, including demography, genetics, joint morphology, and activity. Clinical research suggests that adult women most frequently experience TMJ-related inflammation and pain, and that TMJ-OA increases in frequency and severity with age due, in part, to hormonal changes and age-related degeneration of articular disc cartilage and osseous tissue (Shi et al. 2017, Takano et al. 1999, Warren and Fried 2001, Yadav et al. 2018). Hormonal variation, especially of estrogen levels, has also been linked to sex differences in TMJ-OA prevalence (Magnusson et al. 2010, Mazzetto et al. 2014, Ribeiro-Dasilva et al. 2009, Wang et al. 2008, Yadav et al. 2018).

        The role of joint morphology in TMJ disorder prevalence is complex. Clinical studies have evaluated potential correlations between mandibular condyle morphology and TMJ-related disorders using both computer tomography (CT) and magnetic resonance imaging (MRI). While some associations have been observed, no significant correlations have been found (Cruz et al. 2017). Similar studies, focusing on articular eminence shape, indicate that despite a slight tendency for disc displacement to occur more frequently in joints with steep slopes, there does not appear to be a significant relationship (Hirata et al. 2007, Kurita et al. 2000, Rabelo et al. 2017, Shahidi et al. 2013). However, both MRI and experimental studies have identified a relationship between disc displacement and degenerative changes, but whether bony changes are a predisposing factor for disc displacement or vice versa, is unclear (Kurita et al. 2000, Yamada et al. 2004, Yasa and Akgul 2017).

        Due to TMJ involvement in use of the dentition, various tooth-related factors, including AMTL and tooth wear, appear to contribute to the prevalence of TMJ disorders. The loss of posterior support through antemortem molar loss has been

associated with increased OA severity, but longitudinal clinical and autopsy studies have not found significant correlations (Magnusson et al. 2010, Wang et al. 2009). Instead, there appears to be an indirect relationship, whereby AMTL can lead to drifting of the remaining teeth that results in changes in occlusion and the direction of mechanical loading on the mandibular condyle. This can lead to increases in temporomandibular disorders, including TMJ-OA (Kamelchuk and Major 1995, Wang et al. 2007, 2009, Whittaker et al. 1985). A study analyzing mandibular shape using three dimensional geometric morphometrics found that the combination of age and AMTL together have an effect on mandibular ramus shape, and the effect may further increase under high biomechanical stress (Jung et al. 2019). Similarly, studies of the association between tooth wear and the presence and severity of TMJ-OA remain inconclusive. This may be due to indirect consequences of varying dental attrition, such as changes in occlusion, and the effects of age and activity-related factors (Eversole et al. 1985, Griffin et al. 1979, Magnusson et al. 2008, Richards and Brown 1981). Therefore, it appears that changes in occlusion, as a result of tooth loss, wear, or mandibular shape change, may play a role in the etiology of TMJ-OA (Kamelchuk and Major 1995, Marklund and Wanman 2010, Solberg et al. 1986).

Lastly, mechanical factors, including trauma and parafunctional activities, have been associated with the presence of TMJ-OA. Trauma to the TMJ and surrounding tissues can result in inflammation and mechanical alteration to the disc, which can later lead to joint alteration and other arthritic changes. Additionally, excessive stress and joint loading has been shown to contribute to disc degeneration (Chisnoiu et al. 2015, Tanaka et al. 2008, Yun and Kim 2005). Parafunctional activities, such as repetitive chewing or grinding, can result in hyperactivity of the lateral pterygoid muscle, which inserts directly at the TMJ and has been found associated with TMJ-OA (Israel et al. 1999, Tanaka et al. 2008). Together, these results suggest a complex relationship between age, sex, dental occlusion, and activity that contribute to both the incidence and severity of TMJ-OA.

TMJ-OA in the Archaeological Record

Bioarchaeological studies focused on TMJ-OA are limited, but reflect clinical and epidemiological results; that is, reported frequency rates vary considerably, and the

relationship between parafunctional activities, dental traits, and the presence of TMJ-related osseous changes yield mixed results. For example, Lovell (2014) and Eversole et al. (1985) report no significant association between AMTL and TMJ-OA at Naqada in Egypt and in a modern American skeletal collection, respectively. In a British sample derived from multiple archaeological sites ranging from the Neolithic through the Late Medieval periods, AMTL and biological sex were not found to be associated with TMJ-OA, but significant associations with tooth wear were identified (Hodges 1991). Griffin et al. (1979) examined more than 300 crania across time and from different geographical locations, including Bronze Age, Iron Age Romano-British, and Anglo-Saxon remains from England; Christian Norse from the Orkney Islands; Medieval Germany; and indigenous eastern Australian individuals. Results demonstrated that individuals exhibiting substantial tooth wear displayed an increased propensity for TMJ-OA (Griffin et al. 1979). The authors suggest that antemortem molar loss or malocclusion that results in asymmetrical tooth wear may play a role in the presence of TMJ-OA and could possibly be attributed to preferential chewing on one side of the mouth. Similarly, prolonged retention of deciduous second molars likely contributed to TMJ-OA in a Late Edo (late 17th to the 19th century) period individual from the Suhgen temple site in Japan (Fujita 2014). Most recently, a study focusing on Late Holocene hunter-gatherers from southern Patagonia found that age, dietary patterns, and tooth wear were not statistically related to the frequency of TMJ-OA, but AMTL played a role (Suby and Giberto 2019). Additionally, masticatory and occlusal stress resulting from terrestrial food processing may have contributed to TMJ-OA in these populations

In Oceania, research focusing TMJ-OA has been limited to populations from Australia and Fiji (e.g., Griffin et al. 1979, Richards and Brown 1981, Visser 1994). Among indigenous populations from Australia, a relationship appears was noted between tooth wear and TMJ-OA frequency (Richards and Brown 1981, Richards 1990, Webb 1995). At the Sigatoka site in Fiji, high incidences of TMJ-OA in males were attributed to repetitive and forceful chewing behaviors, such as those associated with fibrous plant processing. Historic accounts of males processing kava with their teeth led the author to attribute the frequency of TMJ-OA to this activity, which simultaneously would have reduced TMJ pain due to the narcotic properties of the plant (Visser 1994).

The impact of parafunctional activities associated with processing and consumption of psychoactive substances has not been examined in detail, but habitual consumption of khat (*Catha edulis*), a small evergreen plant that is chewed for its stimulant effects, has been linked to TMJ-OA in habitual chewers (Almashraqi et al. 2018, Al-Maweri et al. 2018, Alshahidi and Moaleem 2017, Hill and Gibson 1987). In the Andean highlands, leaves of the coca plant (*Erythroxylum coca*) are chewed for a variety of purposes, including their stimulant properties and ability to treat symptoms of altitude sickness (Plowman 1986). The most common skeletal evidence for coca use is the presence of dental conditions such as high rates of dental calculus, dark brown or green staining on tooth crowns, antemortem posterior tooth loss, buccal alveolar bone changes, and carious lesions on the cervical segments of teeth (Indriati and Buikstra 2001). However, many of these conditions are general indicators of poor dental health caused by a multitude of factors. The relationship between coca and TMJ disorders has not been directly studied, but coca chewing was implicated as a possible etiological factor in the prevalence of TMJ disorders among Ecuadorian Quechua (Jagger et al. 2004).

In the Pacific, kava is commonly consumed in Polynesia, but not in Micronesia except on two islands (Pohnpei and Kosrae) in the Eastern Carolines that lie more than 1600 km east of Palau and more than 2000 km from Vanuatu, where kava is thought to originate. Instead, betel nut is found across the three island groups in the Western Caroline Islands: Palau, Yap, and the Mariana Islands, where archaeological (Carucci and Mitchell 1990, Douglas et al. 1997, Fitzpatrick et al. 2003b, Hocart and Fankhauser 1996), historical (Levesque 1993, Rooney 1993), and ethnographic (Paulino et al. 2011, Ysaol et al. 1996) evidence attest to its widespread use for millennia.

Betel Nut

Betel nut—sometimes referred to as the areca nut—is technically a drupe produced by the areca palm (*Areca catechu*) that grows throughout Southeast Asia, East Africa, and parts of the Pacific. The substance is combined with slaked lime (calcium hydroxide) from the burning of marine shell or limestone and wrapped in pepper leaf (*Piper betel*) to create a bundle, or quid, that is then chewed for its stimulant properties (Norton 1998). The effects of habitual consumption on oral health vary and have been associated with

elevated risk of mouth and esophageal cancers, increased dental wear, and tooth loss (Trivedy et al. 2002). However, dental research has also suggested that tannins present in the plant may have antimicrobial properties, which, when combined with the increased saliva production associated with mastication, contribute to a cariostatic oral environment (de Miranda et al. 1996, Howden 1984). Betel nut also possesses antihypertensive properties and is used in a variety of medicinal preparations (Inokuchi et al. 1986, Perry 1980).

The antiquity of betel nut consumption has been demonstrated through both palynological and osteological evidence. While chewing betel nut does not damage the tooth surface, staining does occur and preserves in archaeological record (Figure 5.2). Dental remains with a characteristic reddish-brown stain from habitual betel nut consumption have been recovered from sites across Southeast Asia, Island Southeast Asia, and the Pacific Islands, including Vietnam, the Mariana Islands, and Palau (e.g., Fitzpatrick et al. 2003b, Hocart and Fankhauser 1996, Oxenham et al. 2002, Zumbroich 2008). Paleoenvironmental evidence for betel nut in the form of *Areca* pollen on Palau have been found in soil cores dating to as early as 4250 BP (Athens and Ward 1999), though smaller particles are known to move within contexts and no archaeological sites in the archipelago predate ca. 3300 BP. As such, these earlier dates for betel nut are equivocal. More direct archaeological evidence for the use of betel nut in Palau is based on human dental remains that are characteristically stained and derived from both Chelechol ra Orrak and Ucheliungs (Fitzpatrick et al. 2003b, Stone et al. 2017).

Methods

Sampling

In order to assess the overall frequency of TMJ-OA, both the articular eminence of the temporal bone and the mandibular condyle were scored for each of the articulated burials for whom the joint surfaces were present. Additionally, temporals from isolated crania and isolated mandibles for whom mandibular condyles were present were also scored. In order to be included in this analysis, at least 50% of the articulating surface of the bone had to be intact. Only adult specimens were used for two reasons. First, juvenile remains were not expected to show arthritic changes, and second, no juvenile dental

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remains from the Chelechol ra Orrak assemblage demonstrate the characteristic staining of habitual betel chewing, mirroring historical and modern restrictions of this activity for sub-adults. Given that the primary focus of this research is on the relationship between betel nut and TMJ-OA, juvenile remains were expected to be uninformative. Adults were primarily defined as individuals with erupted third molars, but because third molar agenesis has been observed with some regularity in this assemblage, if third molars were not present, additional osteological characteristics were used to estimate age at death (see below). In these instances, any individual aged to at least ~20 years old was included in the analysis. In order for isolated material to be included in this sample (crania and mandibles), each mandible required the presence of a non-repeatable element to avoid repetitive sampling: a right mandibular condyle. Additionally, the provenience of all isolated mandibles and crania of similar age and sex were recovered from different excavation units, rendering association of mandibles and crania with a single individual unlikely.

Demography

For articulated burials containing associated postcrania, sex was estimated through assessment of dimorphic features of the os coxa (e.g., greater sciatic notch morphology, presence of a ventral arc) and skull (e.g., mastoid process, nuchal crest and supraorbital ridge development) (Buikstra and Ubelaker 1994). Age at death was estimated using a combination of epiphyseal fusion, dental eruption, cranial suture closure, and age-related changes of the auricular surface and pubic symphysis (Buikstra and Ubelaker 1994). Adult remains were then assigned to age categories of Young (20-35), Middle (35-50), and Older Adult (>50). In some cases, age at death estimates spanned two categories or could not be assigned to a specific age category; in these instances, they were labeled as "Adult" (Buikstra and Ubelaker 1994). For isolated mandibles, sex was estimated, when possible, using morphological characteristics (e.g., mental eminence, gonial eversion), while age was estimated using dental development and tooth wear (Scott 1979).
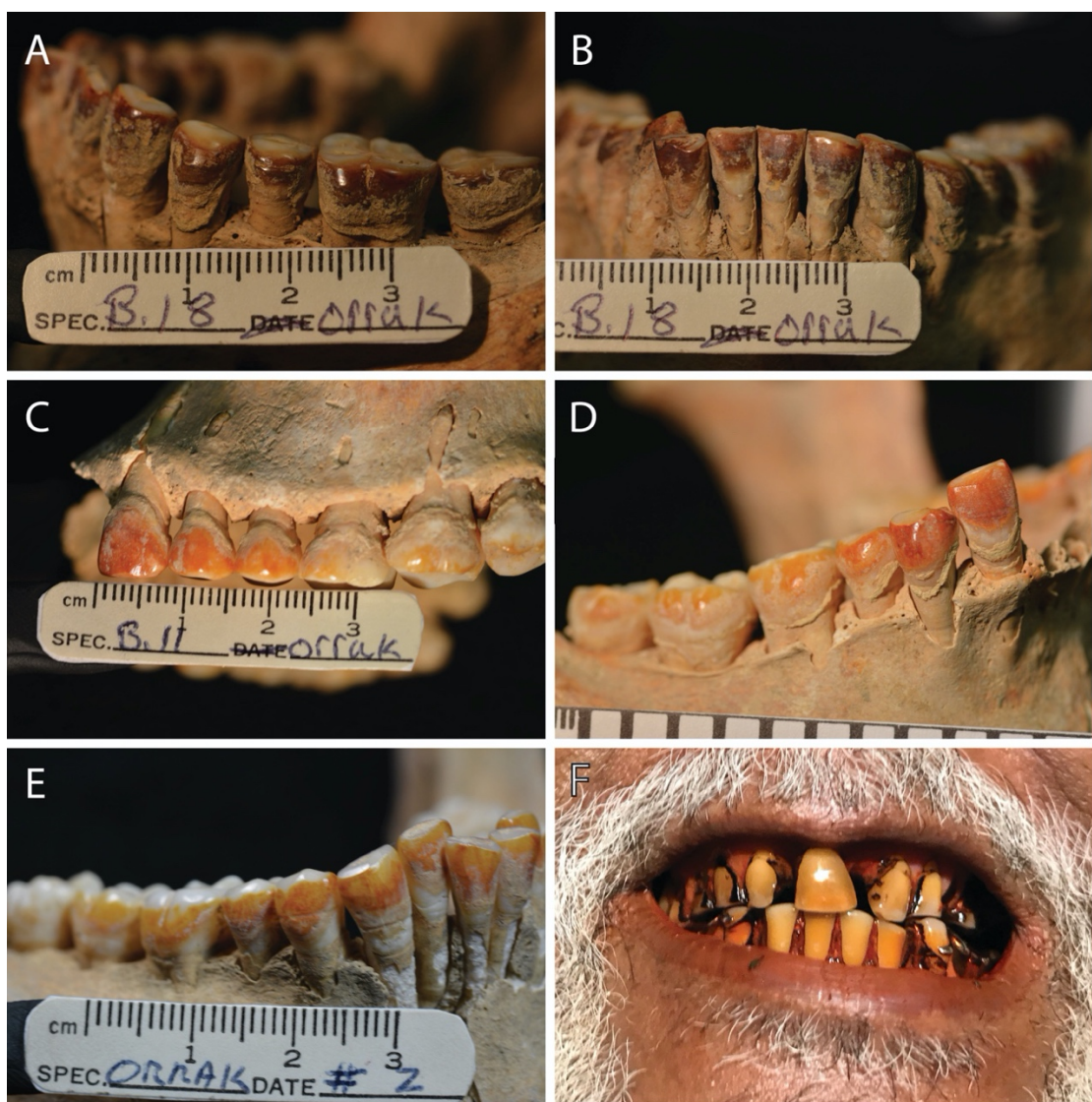
Figure 5.2. Archaeological and modern examples of the tooth staining associated with habitual betel nut chewing. The archaeological examples (2a-2e) are of individuals from Chelechol ra Orrak, while figure 2f depicts the dentition of Mr. Ngirngemengnged Hayes Malsol, Chief of Ngerubesang, Melekeok State, in the Republic of Palau (photo by Scott M. Fitzpatrick, Feb. 22, 2019). It is important to note that modern dental hygiene practices have impacted the degree of staining that is observable on many people that habitually chew betel nut today. In regard to the scoring scheme used for betel nut staining, Figures 2a and 2b represent a score of 5 ("very heavy"), Figures 2c and 2d represent a score of 4 ("heavy"), and Figure 2e represents a score of 3 ("moderate").

Osteoarthritis Diagnosis

Osteoarthritis was diagnosed using the methods outlined in Rando and Waldron (2012), which draw on a proposed methodology by Rogers and Waldron (1995), together

with an additional severity scale. This approach utilizes the presence or absence of five morphological characteristics: eburnation, marginal osteophytes, new bone growth on the joint surface, porosity, and alteration to the joint contour. If eburnation is present, the joint is diagnosed as osteoarthritic without the need for other criteria to be present. In cases where eburnation is not present, two of the four remaining criteria must be identified in order to confirm diagnosis. When positively identified, a diagnosis of TMJ-OA is indicated as 'yes'; if not present, TMJ-OA is indicated as 'no'. When diagnosed, severity was classified as light, moderate, or florid (severe) as illustrated in Rando and Waldron (2012).

Joint Surface Morphology

Both mandibular condyle and articular eminence morphology were also scored in order to assess whether joint morphology might correlate with arthritic changes (Figure 5.3). Morphology of the mandibular condyle was assigned to one of four types in the posterior view after Yale et al. (1966): concave, convex, flat, or rounded. Morphology of the articular eminence was classified by slope after Kurita et al. (2000), in which morphology was classified into one of four types: box, sigmoid, flattened, and deformed. While Kurita et al. (2000) assigned individuals to type using MRI, in this study we assigned types based on visual inspection of the joint profile. A box-type was defined as exhibiting a steep posterior slope, while gentler sloping was defined as a sigmoid-type. Flattened eminences displayed a fairly shallow fossa and overall flattened appearance, and any individual that failed to fit the three categories was defined as deformed.

Dental subset and activity-related factors

A subset of the sample comprised of individuals with associated dentition (hereafter referred to as the dental subset), representing 17 individuals, was selected to explore potential relationships between TMJ-OA and activity-related use of the dentition via scoring of tooth wear and betel nut staining of the tooth enamel. Tooth wear was used as a means for evaluating joint use and was scored using Scott (1979) on both the first and combined first and second molars. Any of the 17 individuals possessing associated first and second molars was included in this analysis. These scores were then averaged

for each individual and assigned to a category for statistical analysis (Table 5.1). Because habitual betel chewing results in staining of the tooth enamel, the degree of betel staining present was used as a proxy for habitual use. Staining was noted as present or absent, and graded on a 5–point scale based on the color and shade of stain on the enamel, as well the distribution across the dentition (Table 5.1). Any of the 17 individuals possessing associated anterior dentition was eligible to be included in this analysis. Although a threshold was not implemented for the number of teeth required to be included in the betel staining analysis, all individuals represented in this dental subset possessed at least 10 total teeth. Instances of AMTL were also noted and have been recorded with the results. Because this is an exploratory analysis, Pearson correlations and Spearman's rank order correlations were chosen to evaluate the potential relationships between TMJ-OA, age, betel nut chewing, and tooth wear on the dental subset. To test the Pearson correlations for significance ($p = .05$), a Bonferroni correction was applied. All statistical analyses were performed in Systat 13.

Table 5.1. Scoring criteria for each of the variables statistically analyzed.

Trait/Level	1	2	3	4	5
TMJ-OA Severity*	No expression	Light	Moderate	Florid	
Betel nut staining	No staining observed	Light (light reddish orange in color; somewhat translucent stain limited to anterior teeth)	Moderate (darker red in color; stain is opaque and extends to molars)	Heavy (stain is red and opaque; affects most or all posterior teeth)	Very Heavy (dark reddish brown, almost black in color; stain extends across molars)
Tooth Wear**	<10	10-17.99	18-25.99	≥26	

*Scores based on figures in Rando and Waldron (2012).
** Based on average Scott (1979) wear score for all molars for each individual. Minimum of one set of contiguous M1 and M2s.
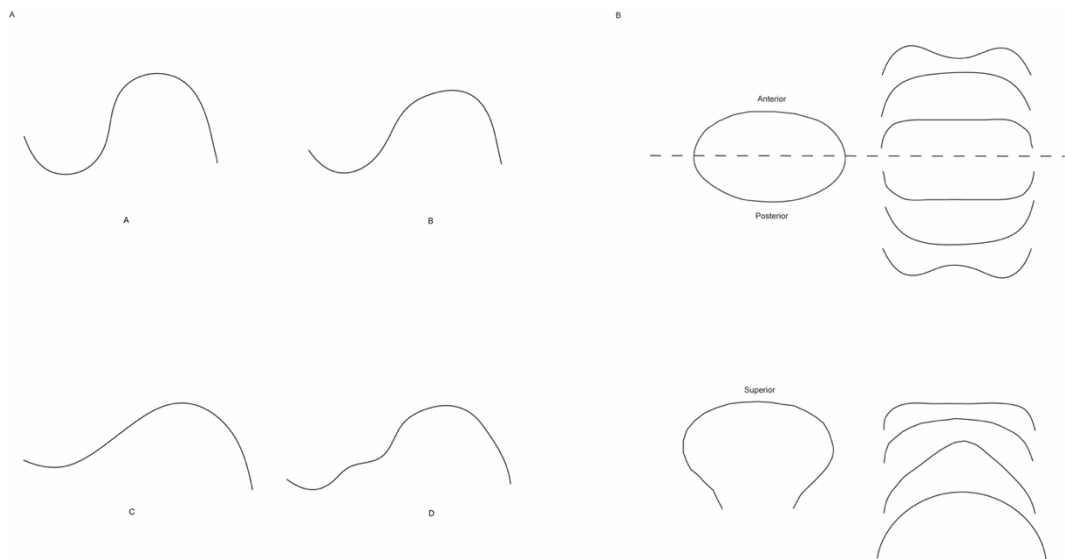
Figure 5.3a. Categories of articular eminence morphology after Kurita et al. (2000), including box (A), sigmoid (B), flattened (C), and deformed (D). **Figure 5.3b.** Categories of mandibular condyle morphology after Yale et al. (1966). The top image depicts the condyle from a superior view, with both anterior and posterior condyle shape shown as follows: concave (1), convex (2), and flat (3). The lower image depicts the condyle shape from a posterior view as follows: flat (1), convex (2), angled (3), and round (4).

Results

A total of 50 individual joint surfaces comprising 23 mandibular condyles and 27 articular eminences that represent a minimum of 22 adult individuals fit the criteria for analysis. Of the 23 mandibular condyles evaluated, seven (30.4%) present lesions diagnostic of TMJ-OA, while nine of the 27 temporals (33.3%) present lesions diagnostic of TMJ-OA. These results correspond to nine individuals (40.1%) from Chelechol ra Orrak with TMJ-OA on at least one joint surface (Table 5.2). Almost all cases were classified as light in severity with the exception of two individuals that presented florid cases: Burial 12, an adult male (Figure 5.4), and an isolated adult male cranium (#100). Of the nine individuals with the condition, only two are female (Burial 14 and isolated mandible #2056), while six are male, with another belonging to an isolated cranium of indeterminate sex (#103). Individuals with the condition represent all age categories, with the majority (n=4) belonging to the Middle Adult category, followed by Young Adult (n=3); however, these are also the two largest groups in the assemblage (Table 5.3).
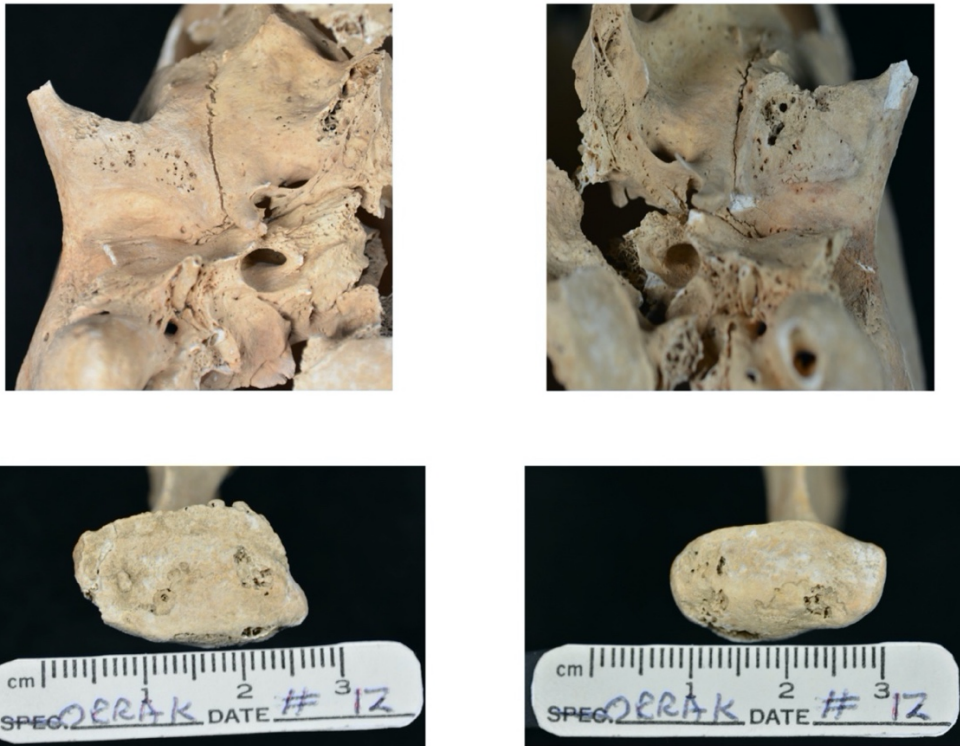
Figure 5.4. Photographs of the articular eminences (top) and mandibular condyles (bottom) of Burial 12, an adult male diagnosed with a florid case of TMJ-OA.

The Relationship of Joint Morphology to TMJ-OA

A total of 48 individual joint surfaces comprising 21 mandibular condyles and 27 articular eminences, representing a minimum of 21 individuals, could be scored for morphology. The majority of the mandibular condyles were convex in shape, and 25% of convex shaped condyles were diagnosed with TMJ-OA (Table 5.4). Of the remaining condyles that fell into alternative morphological categories, two of the three flat and two of the six angled condyles displayed lesions diagnostic of TMJ-OA. However, all of the condyles with any instance of non-convex morphology displayed some type of osseous change (e.g., osteophytes, porosity), with the exception of one, which belongs to Burial 25, a young female. Articular eminence morphology is more varied, and the majority of temporals scored were classified as either box-shaped or sigmoid-shaped. Although only four temporals could be assigned to the flat shape category, half of those displayed lesions diagnostic of TMJ-OA.

Table 5.2. Demography and scored results. "N/A" indicates joint surfaces that are absent or not scoreable due to breakage (<50% of surface present).

Individual	Provenience	Age at Death	Sex	Mandibular Condyle		Articular Eminence		Betel Nut Score	Tooth Wear	
				Joint Morphology (right/left)	TMJ-OA Diagnosis (right/left)	Joint Morphology (right/left)	TMJ-OA Diagnosis (right/left)		M1	M1 and M2
Burial 11	E3S1-E3S2	Young Adult	Female	Angled/Broken*	No/No	Sigmoid/Sigmoid	No/No	4	2	2
Burial 12	E1S5-W1S5	Young Adult	Male	Convex/Flat	Yes/Yes	Irregular/Irregular	No/Yes	4	4	3
Burial 13	E1S5-W1S5	Young Adult	Female	N/A/Convex	N/A/No	N/A	N/A	3	2	1
Burial 14	E1S4-W1S4	Old Adult	Female	N/A/Convex	N/A/No	Flattened/N/A	Yes^/N/A	3	AMTL	AMTL
Burial 16	E1S5/E2S5-E1S4	Middle Adult	Male	Convex/Flat	Yes/Yes	Sigmoid/Sigmoid	No/Yes	1	2	2
Burial 18	E2S4-E3S4/E3S5	Middle Adult	Male	Angled/N/A	Yes/N/A	N/A	N/A	5	2	2
Burial 20	E1S4-E1S3	Middle Adult	Male	Angled/Angled	No/Yes	Flattened/Sigmoid	Yes/Yes	3	3	3
Burial 24	E1S2-W1S2-W1S1	Young Adult	Female	Convex/Convex	No/No	Box/Sigmoid	No/No	3	1	1
Burial 25	E1S1-SE	Young Adult	Female	Convex/Angled	No/No	Flattened/Flattened	No/No	3	1	1
Burial 26	E3S4-E2S4	Adult	Male	N/A	N/A	Box/Box	No/No	4	3	3
Burial 27	E3S5-(E3S6)	Old Adult	Male	Broken*/N/A	No/N/A	Box/Box	No/No	5	3	2
Isolated Cranium #20	W1S4/W1S5	Young Adult	Male	N/A/Convex	N/A/No	Box/Sigmoid	No/No	2	2	1
Isolated Cranium #23	E3S1	Young Adult	Unknown	N/A	N/A	Box/N/A	No/N/A	2	1	1
Isolated Cranium #24	E3S1	Young Adult	Prob. Male	N/A/Convex	N/A/No	Box/Box	Yes/Yes	3	2	2
Isolated Cranium #100	E2S2	Middle Adult	Male	N/A	N/A	Sigmoid/Sigmoid	No/Yes	4	4	4
Isolated Cranium #101	E3S1	Middle Adult	Male	N/A	N/A	Sigmoid/N/A	No/N/A	N/A	N/A	N/A
Isolated Cranium #103	W1S4/W1S5 L. 9	Young Adult	Unknown	N/A	N/A	Box/Box	No/Yes	N/A	N/A	N/A
Isolated Mandible #2	E1S5	Young Adult	Prob. Female	N/A/Convex	N/A/No	N/A	N/A	3	2	2
Isolated Mandible #237	E1S1	Young Adult	Unknown	Flat/N/A	No/N/A	N/A	N/A	PMTL	PMTL	PMTL
Isolated Mandible #857	E1S2	Adult	Prob. Male	Convex/N/A	No/N/A	N/A	N/A	PMTL	PMTL	PMTL
Isolated Mandible #859	E1S2	Young Adult	Prob. Male	Angled/N/A	No/N/A	N/A	N/A	3	2	2
Isolated Mandible #2056	E1S4	Adult	Prob. Female	Convex/N/A	Yes/N/A	N/A	N/A	PMTL	PMTL	PMTL

Provenience crossing multiple units is listed from head to foot. All burials and elements recovered from Layer 10 unless otherwise noted.

^Diagnosed as TMJ-OA with light severity but appears to have remodeling that may be indicative of healing.

*Condyle is broken in a way to prevent morphology scoring but allows for full scoring of joint for TMJ-OA.

Table 5.3. Sample sizes for age and sex categories.

Age	Female (n)	Male (n)	Indeterminate Sex (n)	Total
Young Adult	5	4	3	12
Middle Adult	0	5	0	5
Old Adult	1	1	0	2
Adult	1	2	0	3
Total	7	12	3	22

Table 5.4. Morphology scores for all joint surfaces evaluated for TMJ-OA.

Morphological Category	Mandibular Condyles (n)	Articular Eminences (n)	Total
Flat	3	N/A	3 (14.3%)
Convex	12	N/A	12 (57.1%)
Angled	6	N/A	6 (28.6%)
Rounded	0	N/A	0
Box	N/A	11	11 (40.7%)
Sigmoid	N/A	10	10 (37%)
Flattened	N/A	4	4 (14.8%)
Irregular	N/A	2	2 (7.5%)
Total	**21**	**27**	**48**

Note: The discrepancy in mandibular condyle sample size is due to two condyles that were broken in a way to prevent morphology scoring but allowed for TMJ-OA evaluation.

The Relationship of Betel Nut Chewing, Age, and Tooth Wear to TMJ-OA

The dental subset, comprised of 17 individuals for whom associated teeth were present, were also evaluated for age, betel staining, and tooth wear in order to assess the potential relationships between chewing betel nut, tooth wear, and TMJ-OA. In this sample, seven of the 17 individuals displayed lesions diagnostic of TMJ-OA (41.2%), but 14 (82.4%) exhibited some form of bony change, meaning one of the two morphological characteristics required for TMJ-OA diagnosis could be observed. Both Pearson's correlation coefficients and Spearman's rank order correlation were calculated for relationships between TMJ-OA and each of the following variables: TMJ-OA severity,

degree of betel staining, tooth wear from the first molar and combined first and second molars, and estimated age. Interestingly, Pearson's correlation coefficients demonstrate a moderate to strong positive linear relationship between TMJ-OA severity and each of the variables evaluated except for betel staining, with the strongest relationships appearing between tooth wear and TMJ-OA (r =.815 and .849 for M1 and combined M1 and M2, respectively) (Table 5.5). Similarly, moderately positive relationships are observed between tooth wear and age, as well as between betel staining and age. When a Bonferroni correction is applied to explore significance, only the relationship between M1 tooth wear and TMJ-OA is significant (p=.001).

Table 5.5. Results of Pearson's correlations, with Bonferroni probabilities in parentheses.

	TMJ-OA Severity	Betel Staining	M1 Wear	Combined M1 and M2 Wear	Age
TMJ-OA Severity	1.000				
Betel Staining	0.160 (1.000)	1.000			
M1 Wear	0.815 (0.001)	0.471 (0.656)	1.000		
Combined M1 and M2 Wear	0.849 (0.000)	0.420 (1.000)	0.881 (0.000)	1.000	
Age	0.391 (1.000)	0.622 (0.077)	0.520 (0.387)	0.482 (0.589)	1.000

Similarly, results of the Spearman's rank order correlation reveal the strongest relationship between combined M1 and M2 dental wear with TMJ-OA severity (r_s =.842), followed by M1 wear, age, and betel nut staining (Table 5.6). The weakest relationship appears between betel staining and TMJ-OA (r_s =.231), with moderate relationships observed between betel staining and age (r_s =.592), as well as between tooth wear and age (r_s =.613 and .568 for M1 and combined M1 and M2).

Table 5.6. Results of Spearman's rank order correlations.

	TMJ-OA Severity	Betel Staining	M1 Wear	Combined M1 and M2 Wear	Age
TMJ-OA Severity	1.000				
Betel Staining	0.231	1.000			
M1 Wear	0.780	0.553	1.000		
Combined M1 and M2 Wear	0.842	0.526	0.869	1.000	
Age	0.500	0.592	0.613	0.568	1.000

Discussion

A strikingly large number of adults (35/50, or 70% of joint surfaces examined in this study) exhibit some form of bony response indicative of impact on the TMJ. However, the overall frequency of lesions diagnostic of TMJ-OA is within the range of what has been observed in other archaeological studies (Hodges 1991, Richards and Brown 1981). The Chelechol ra Orrak assemblage reflects a relatively young population, with the majority of adults assigned to the Young Adult (20-35) category, suggesting that these responses begin relatively early. The two males that displayed florid cases of TMJ-OA were assigned to the Young (Burial 12) and Middle (Isolated cranium #100) Adult categories. However, among the two oldest individuals in this sample (Burials 14 and 27) assigned to the Old Adult (50+) category, only one displayed lesions diagnostic of TMJ-OA. Therefore, it does not appear that TMJ-OA increases with age despite the fact that a significant correlation between TMJ-OA and age was observed. Similarly, only a moderate correlation was observed between age and degree of betel staining. This is likely due to several factors, including variation in the individual frequency of regular betel chewing, and potentially the loss of posterior teeth over time, which could lead to the reduction and eventual cessation of betel chewing. Burial 14, a partially edentulous

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female placed into the Old Adult category who exhibits antemortem loss of molars and betel staining on the remaining anterior teeth, is one such example of these confounding factors.

Age does appear to be a factor in the onset of betel chewing practice. While not included in the samples scored here, a number of juvenile individuals possessing deciduous and mixed dentitions are present in the Chelechol ra Orrak assemblage. None of these individuals possess evidence for betel staining. Among individuals with fully adult dentitions, only one (Burial 16) has been found with no evidence of staining. Although the time needed for betel staining to appear has not been formally investigated and likely varies due to a number of factors, including preparation of the betel quid and dental hygiene practices, it appears that juveniles do not chew betel, nor did the abovementioned adult individual. While there is no known rite of passage associated with the onset of betel chewing, the distribution across the Chelechol ra Orrak assemblage suggests that the behavior initiated in the late teenage years or older, similar to the pattern found today. In the case of Burial 16, there are no apparent osteological factors or aspects of the burial context to suggest that this individual was unique; instead this may be due to personal preference.

There also appears to be a greater number of males affected by TMJ-OA than females, which is contrary to findings in clinical studies, but similar to observations among prehistoric Fijians, where sex differences in TMJ-OA frequency were attributed to gendered behavior, specifically the processing of fibrous plants, including kava (Magnusson et al. 2008, Warren and Fried 2001, Visser 1994). Historic records detailing the processing and consumption of kava also describe these activities as being undertaken "overwhelmingly by males" (Visser 1994: 313). Nearly every adult individual at Chelechol ra Orrak demonstrates evidence of betel chewing regardless of sex, with the exception of Burial 16 described above. This suggests that sex-related differences in frequency of TMJ-OA are due to activities other than chewing betel that involve the dentition or TMJ. A preliminary analysis of paleodiet based on light stable isotopes at Chelechol ra Orrak suggests possible minor differences in access to dietary resources, whereby females may have consumed less marine protein from lower trophic level resources and had a more varied diet overall (Stone et al. 2019, or see Chapter IV).

Alternatively, these differences may instead be capturing individual dietary variation due to personal preference. Dietary differences may contribute to sex-based differences in TMJ involvement as well, but due to the small number of individuals for whom sex could be estimated, these suggestions are merely exploratory and must be reconsidered at a later date.

Clinical research focused on variation in joint surface morphology as a potential etiological factor for TMJ-related disorders has shown mixed and often contradictory results (Cruz et al. 2017, Hirata et al. 2007, Kurita et al. 2000, Rabelo et al. 2017, Yamada et al. 2004, Yasa and Akgul 2017). Similarly, TMJ-OA appears to affect joint surfaces of each morphological category of the mandibular condyle and articular eminence in this study, suggesting that morphology does not result in TMJ-OA susceptibility. There is a high frequency of flat-shaped articular eminences displaying lesions diagnostic of TMJ-OA (50%), but this may be a result of the small sample size. However, these results could suggest that flatter or shallower articular eminences contributes to TMJ-OA development. This is contrary to clinical studies where articular eminences with steeper slopes were more often associated with TMJ-related issues (Hirata et al. 2007, Kurita et al. 2000, Rabelo et al. 2017, Shahidi et al. 2013). Interestingly, there is a noticeable difference between the number of mandibular condyles and temporals affected; a pattern that was also noted in a study involving skeletal remains of prehistoric hunter-gatherers from southern Patagonia, suggesting that the articular eminence may exhibit bony responses earlier than the corresponding mandibular condyle (Suby and Giberto 2019).

Of the remaining etiological factors potentially associated with TMJ-OA, tooth wear is the most strongly correlated, and while the degree of betel staining is positively correlated, the relationship is much weaker. Together these support the suggestion that activities other than, or alongside, betel chewing played a role in TMJ-OA development at Chelechol ra Orrak. Activities creating patterns of tooth wear observed in our sample include using the dentition as a tool for processing fibrous plants, or the inclusion of abrasive material in the diet. In coastal areas, the presence of sand in marine foods like shellfish is a common source of dental abrasion and may be a factor contributing to the tooth wear observed here (e.g., Littleton and Frohlich 1993). Additionally, older age is

correlated with higher rates of tooth wear, which may serve as another indirect factor contributing to TMJ-OA. Previous paleopathological research has explored the role of AMTL in the development of TMJ-OA (Hodges 1991, Lovell 2014). At Chelechol ra Orrak, the occurrence of AMTL is low, with only four of the 17 individuals in the dental subset used for this study affected. Of these individuals, two (Burials 12 and 14) display lesions diagnostic of TMJ-OA. Burial 12 is missing a single tooth (maxillary left canine), while Burial 14 is edentulous in the posterior dentition. Therefore, it appears that AMTL may be one factor alongside tooth wear contributing to shifts in occlusion that indirectly affect the joint (Griffin et al. 1979). However, given the low frequency of individuals exhibiting AMTL in the posterior dentition at Chelechol ra Orrak, this possibility will require further exploration with a larger sample.

Conclusion

This chapter provides important insight into the potential etiology of TMJ-OA in prehistoric populations by focusing on a highly specialized parafunctional activity, betel chewing. Over the course of millennia, the behavior has grown to become common practice throughout the Pacific Islands and Southeast Asia. Today, as many as 600 million people consume betel nut. Understanding the potential relationship between this behavior and the development of TMJ-OA could impact treatment of TMJ-related disorders (Gupta and Warnakulasuriya 2002). Results show that tooth wear has the strongest correlation with TMJ-OA, and while chewing betel nut might be an indirect contribution to this relationship, it is not the sole etiological factor contributing to the high TMJ-OA frequency observed in this assemblage.

CHAPTER VI

CONCLUSION

The initial settlement of Remote Oceania represents one of the most rapid and widespread dispersal events in human history. Despite this being the last major geographical region to be colonized by humans, information regarding the timing, trajectory, and origins of settlement in many respects remains unclear (Bedford and Spriggs 2019, Carson 2013, Kirch 2010, Matisoo-Smith 2015). The majority of archaeological and bioarchaeological work conducted in the region has focused on the dispersal of Lapita groups from the Bismarck Archipelago across much of Remote Oceania, but western Micronesia, which appears to have been settled by contemporary yet separate groups, has been noticeably absent from broader regional discussions of Remote Oceanic settlement history (Clark 2004, Clark et al. 2017, Fitzpatrick 2018, Lum and Cann 1998, Lum et al. 2002). In order to generate a comprehensive picture of the lifeways of early inhabitants, including adaptations to these small and remote landmasses, a transdisciplinary understanding of the initial colonization of Remote Oceania that includes these apparent non-Lapita dispersals is critical.

The Chelechol ra Orrak site in the northern Rock Islands of Palau contains one of the largest human skeletal assemblages in Remote Oceania and is one of two mortuary sites in the region that dates to ~3000 BP, and the only one located in Micronesia (Fitzpatrick 2002, 2003a, 2003b, Nelson and Fitzpatrick 2006, Nelson et al. 2015). Therefore, analysis of the Chelechol ra Orrak skeletal assemblage is ideal for filling in gaps regarding the population origins and adaptations of early Remote Oceanic inhabitants. In this dissertation, I use a bioarchaeological approach that integrates aDNA, stable isotopes, and osteological analyses at Chelechol ra Orrak to address questions related to the initial human settlement and subsequent adaptation of small island environments in Palau, and more broadly, Remote Oceania. I also include results from archaeological fieldwork at Ucheliungs, a second Rock Islands site that is contemporary with Chelechol ra Orrak, to assess claims of insular dwarfism following initial settlement (Berger et al. 2008). Although some of the results presented in this work are preliminary, this dissertation is the first research to apply stable isotope and aDNA methods to human

skeletal remains in Palau; as such, it makes a significant contribution to our understanding of the initial colonization of Palau and provides a foundation upon which ongoing and future work at both Chelechol ra Orrak and Ucheliungs will continue to build.

The results of aDNA from Chelechol ra Orrak presented in Chapter II have provided complete or partial mitochondrial genomes for four individuals in addition to 11 new radiocarbon dates directly from articulated burials. Four distinct maternal lineages are represented in these individuals, who date from 2700-1815 cal. BP, with the majority dating to an earlier portion of that timespan, from 2700-2365 cal. BP. The distribution of radiocarbon dates across the burial assemblage suggests the possibility of coarse spatio-temporal clustering across the site, but a wider distribution of dates across the excavation area is needed to assess this possibility. The genetic results are characteristic of Austronesian-speaking ISEA groups, supporting previous linguistic and archaeological evidence, while a lack of Papuan-associated haplogroups suggests a lack of support for population origins in New Guinea (Callaghan and Fitzpatrick 2008, Lum and Cann 2000, Pietrusewsky 1990). Additionally, the lack of shared haplogroups with Lapita individuals suggests that multiple separate population dispersals from ISEA to Remote Oceania took place ca. 3300-3000 BP. Although the mtDNA presented in Chapter II is informative, results only reflect maternal inheritance. Future research will assess the feasibility of whole-genome work, and work to expand the number of available mitochondrial genomes as aDNA methods continue to improve. Additionally, the genetic data will be complemented by results of a biodistance study utilizing three-dimensional geometric morphometrics of crania from Chelechol ra Orrak that is in progress.

Based on archaeological excavation at Ucheliungs, I generated archaeological, zooarchaeological, and bioarchaeological data to disprove suggestions of insular dwarfism. Previous work at the site claimed that Ucheliungs was used exclusively for mortuary activity, and the small, isolated nature of landmasses within the Rock Islands region led to small body size among individuals interred at this site and others. My results instead indicate that Ucheliungs was more diverse and utilized for both mortuary activity and small-scale temporary habitation for a longer time period than initially thought. The presence of a diverse and abundant marine invertebrate assemblage and artifacts

transported from other islands suggest that isolation and an impoverished resource base, both critical factors for the process of insular dwarfism, would not have affected inhabitants of Ucheliungs. Additionally, radiocarbon dates from this site provided further evidence for the presence of Palauans in the Rock Islands just prior to and after 3000 BP. Future work involving taxonomic identification of a bone implement may shed light on early ISEA-Micronesian connections, while expansion of excavations beyond a single test unit will provide a more comprehensive picture of site use.

The results of stable isotope analysis on human bone from Chelechol ra Orrak, Koror Quarry, and Peleliu presented in Chapter IV are providing a first look at paleodiet in Palau from a bioarchaeological perspective. Generally, elevated $\delta^{13}C_{co}$ and $\delta^{15}N$ values are consistent with a marine-based diet supplemented by a variety of terrestrial plants. Compared to baseline data from other islands, early Palauans consumed marine shellfish and other taxa from reef and inshore environments, which is consistent with what has been observed in the faunal record at other Rock Island sites and is reflected in the dental health of burials from Chelechol ra Orrak (Carucci 1992, Fitzpatrick 2003c, Fitzpatrick et al. 2011, Masse 1989, Nelson et al. 2015, Ono and Clark 2012). Elevated $\delta^{13}C_{ap}$ values for bone apatite suggest some ^{13}C-enriched source of carbohydrate, which may be due to consumption of marine plants, such as kelp or seaweed, or perhaps sugarcane. Protein consumption appears largely similar to Lapita populations, suggesting that both groups relied upon endemic resources following initial settlement, with the addition of some terrestrial translocated fauna found at Lapita sites. The addition of future baseline dietary resources from samples will allow for further refinement of these results, while new analyses involving strontium and lead isotopes from tooth enamel will provide information on the mobility of these individuals, and where people resided prior to burial at Chelechol ra Orrak. By identifying trajectories of early Palauan mobility throughout the archipelago, we may also be able to further understand how groups utilized different island types and ecosystems for subsistence.

Lastly, an examination of temporomandibular joint osteoarthritis (TMJ-OA) at Chelechol ra Orrak found that osteoarthritis affected a large number (40.1%) of adults, with bony responses to impact on the TMJ beginning relatively early. While the focus of this research was on the potential relationship between TMJ-OA and habitual chewing of

betel nut, a number of potential etiological factors were investigated, including tooth wear, antemortem tooth loss, joint surface morphology, and demography. Despite evidence for widespread habitual chewing of betel nut, only moderate correlations between TMJ-OA and dental staining indicative of betel nut chewing were found. The strongest associations were found between tooth wear and TMJ-OA, suggesting that indirect effects of parafunctional dental activity are a factor in TMJ-OA frequency. While betel nut may be one such example, it is more likely one of a suite of activities that contribute to tooth wear, including processing fibrous plants or the presence of abrasive materials in the diet. Because patterns of occlusion could play a role in TMJ development, future work focused on dental conditions resulting in occlusal variation, including third molar agenesis, antemortem loss of the posterior dentition, malocclusion, or variation in tooth wear by side, may help clarify etiological factors associated with use of the dentition and the development of TMJ-OA.

Taken together, this research not only contributes new lines of evidence to complement existing archaeological and linguistic data related to the colonization of western Micronesia and Palau, but it also begins to characterize the lifeways of early inhabitants of the archipelago, who successfully adapted to a wide array of island types and ecosystems. Additionally, it illustrates the importance of looking beyond Lapita when describing initial settlement of Remote Oceania. As excavations continue at both Chelechol ra Orrak and Ucheliungs, I hope to build upon these data to better characterize and refine our knowledge of regional- and archipelagic-scale mobility and small island adaptation.

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