Title: Oral Health in Late Pleistocene and Holocene North West Africa

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Highlights:

1. Late Pleistocene populations from Northwest Africa exhibit high caries rates
2. Similarity in poor oral health in Iberomaurusian and Capsian populations
3. Cultural and biological continuity between the Iberomaurusian and Capsian periods.

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Abstract

Archaeological sites in North West Africa have yielded a rich record of human occupation, including well dated human burials from the Late Pleistocene Iberomaurusian and early Holocene Capsian periods. The transition broadly coincides with climatic amelioration at the end of the Holocene enabling expansion into slighter dryer inland areas. Here we investigate possible changes in oral health and subsistence behaviours during the transition between the Iberomaurusian (n=109 individuals) and the Capsian (n=19 individuals), based on the study of dental remains.

Frequencies in oral pathologies (caries, abscesses, periodontal disease and antemortem tooth loss) were studied to assess possible differences between the late Pleistocene and early Holocene. The Late Pleistocene Iberomaurusians were characterised by high caries frequencies (60% of observed teeth). The Capsians displayed very similar patterns in oral pathologies but a slightly lower percentage of carious teeth (49%).

The similarity in oral health in Iberomaurusian and Capsian populations is consistent with similarities in diet and oral hygiene. The implication of cultural and biological continuity between the Iberomaurusian and Capsian periods is supported by indicators, such as exploitation of wild plants and snails, tooth evulsion and craniofacial and dental morphology.

1. Introduction

1.1 Oral Health

The impact of the adoption of food production as a subsistence pattern on overall health has been the emphasis of a considerable amount of research (Hugot 1968, Turner 1979, Cook 1984, Ruff *et al.* 1984, Bridges 1989, Deacon 1992, Larsen 1995, Jackes *et al.* 1997, Bar-Yosef 1998, Tayles *et al.* 2000, Schollmeyer and Turner 2004, Eshed *et al.* 2006, Starling and Stock 2007, Temple and Larsen 2007, Lukacs 2008, Pinhasi *et al.* 2008, Watson 2008, Kuijt 2009, Pomeroy and Zakrzewski 2009, Eshed *et al.* 2010). This research has been based on the premise that a shift from diverse food resources as part of a hunting and gathering diet to a more restricted agricultural diet consisting predominantly of complex carbohydrates will result in negative health outcomes (Cook 1984, Larsen 1995, Eshed *et al.* 2006, Starling and Stock 2007, Temple and Larsen 2007, Watson 2008, Eshed *et al.* 2010). Increased sedentism in permanent or semi-permanent housing, poor sanitation and the presence of animals as domesticates and pests would have affected the presence and spread of pathogens. Oral pathologies are strongly correlated to subsistence patterns, and have been used by numerous researchers to assess diet, food preparation, and, indirectly, quality of life of past populations (Larsen et al. 1991). Teeth are sensitive to fluctuations in diet, pathogenic load, physiological stress, oral hygiene, food preparation, non-dietary use of the teeth, and fluoride intake (Hillson 1996; Larsen 2015). The frequencies of oral pathologies within an osteological sample can provide information about the diet and lifeways of past peoples. Most of these pathological conditions result in the destruction of dental tissues and alveolar bone of both the mandible and maxilla. Changes in oral health and dental wear associated with the transition from a hunter gatherer economy to food production have been documented in the Levant (Eshed et al., 2006), South East Asia (Tayles et al., 2000) Europe (Bennike, 1985; Lubell et al., 1994; Meiklejohn et al., 1998), Japan (Joichi et al., 1996; Oyamada et al., 2004; Temple and Larsen, 2007) and North America (Larsen, 1983; Schollmeyer and Turner, 2004).

Caries, or dental cavities, is the progressive demineralization of dental tissues due to increased acidity resulting from the production of organic acids during fermentation of carbohydrates by bacteria in dental plaque (Hillson 2008). The optimal oral environment for these cariogenic bacteria is achieved by a regular intake of soft, sticky, and sweet foods, in combination with poor oral hygiene (Hillson 1996). The increased reliance on carbohydrate-rich foods, such as wheat and maize, since onset of food production has resulted in an oral environment in which these bacteria can thrive (Hillson 2008; Hillson 1996; Temple 2015). The increased caries frequencies observed during the Neolithic has been linked to the regular consumption of fermentable carbohydrates from cultivated plant foods, such as wheat and other grains. A number of studies on both archaeological and historical samples have demonstrated a relationship between high caries rates and the onset of food production. In general, hunter-gatherers show lower caries rates than those with mixed economy or horticulture (Lanfranco and Eggers 2010). Populations with a greater reliance on carbohydrates, and specifically refined carbohydrates have higher caries rates (Lanfranco and Eggers 2010).

In the Levant, caries frequencies increased slightly from 6.4% in Natufian hunter-gatherers (10,500-8300 BC, non-calibrated) to 6.7% with the onset of the Neolithic (8300-5500 BC) (Eshed et al. 2006). In the Americas an increase in caries rates following the transition from horticulture to farming was observed in a number of populations (Cucina et al. 2011; Lanfranco and Eggers 2010; Schollmeyer and Turner 2004). Conversely the introduction of rice as a cultivated staple is not always associated with an increase in caries prevalence, reflecting differences in the cariogenicity of carbohydrate staples (Tayles 2009; Tayles et al. 2000). At the same time, the importance of carbohydrate-rich wild plant foods by pre-agricultural populations may have been underestimated. Humphrey and colleagues (2014) demonstrated that carbohydrate-rich wild plants such as acorns were widely exploited during the

Late Pleistocene in the Maghreb region. Wild acorns were also commonly consumed by Californian Native Americans and in some groups linked to high caries rates (Turner and Machado 1983).

A series of other dento-alveolar parameters can be recorded to assess oral health in skeletal samples including alveolar resorption caused by periodontal disease, abscesses and antemortem tooth loss. Periodontal disease involves infection the tissues surrounding the tooth and can be either acute or chronic. Acute infections tend to heal and leave few signs after healing. Chronic infections of the gum may result in retraction of the gum line and resorption of the alveolar bone causing exposure of the tooth root above the alveolar margin (Hillson 2001; Nelson 2015). The infection of the alveolar tissue near the apex of the tooth root may result in the accumulation of pus, and is referred to as an abscess. Osteoclastic activity will form a fistula (cavity) inside the bone which may open up to the surface to release pressure through the oral cavity. When there is a clear opening to the fistula in the alveolar bone of a skeleton it is possible to identify this as an abscess (Hillson 2001; Nelson 2015). Any of these infections may lead to antemortem tooth loss. Antemortem tooth loss is identified as a tooth that is missing from the dentition and has a remodelled tooth socket. There are a number of reasons why teeth can be missing including accidental loss, and extensive wear, which results in loosening of the tooth due to continued emergence. In some cases, tooth extraction must be considered a possible cause. Teeth may be extracted to avoid pain and discomfort from an infection, but in late Pleistocene and early Holocene Maghreb teeth were often deliberately removed for cultural reasons. The deliberate removal of healthy teeth is referred to as evulsion or ablation. The majority of individuals from the sites considered here show the deliberate removal of two or more incisors (De Groote and Humphrey 2015; De Groote and Humphrey, 2017; Humphrey and Bocaege 2008). The widespread frequency of the practice of evulsion across the region indicates that the absence of anterior teeth in these samples is likely due to cultural tradition, rather than an oral pathology.

1.2 Archaeological context

Research on the transition from the Late Pleistocene (Iberomaurusian) to early Holocene (Capsian) in the Maghreb has focused on changes in lithic assemblages (Linstädter 2008; Linstädter 2011; Lubell et al. 1994; Lubell et al. 1984) and variation in skeletal and dental morphology (Irish 2000; Lubell et al. 1994; Lubell et al. 1984; Sheppard and Lubell 1991) but the transition has not been considered in relation to human diet and health. The study of oral health can provide an additional insight into the nature of this transition since the type and prevalence of oral pathologies are directly influenced by dietary intake and food processing (Hillson 2001; Hillson 1996; Larsen et al. 1991; Lukacs 2008).

Recent research highlighted a very high prevalence of caries in Late Pleistocene hunter –gatherers from the Iberomaurusian site of Grotte des Pigeons, Taforalt, Morocco (Humphrey et al. 2014). More than fifty-one percent of all observed adult teeth had at least one carious lesion. Charred macrobotanical remains from occupational deposits revealed evidence for the use of numerous wild plant foods with a preference for large-sized and potentially stored seeds (Morales, this volume). The most abundant macrobotanical remains found in the site were the fragments of acorn (*Quercus ilex*), pine nuts (*Pinus pinaster*) and juniper (*Juniperus phoeniceae*). Frequent consumption of wild plant foods such as acorns that are rich in fermentable carbohydrates would have contributed to the poor oral health observed in the dental series from Taforalt (Humphrey et al. 2014). This study will expand upon the previously published results by ascertaining whether the patterns of oral pathology (prevalence and distributions of carious lesions, antemortem tooth loss, abscesses, and alveolar resorption) observed at Taforalt were typical for the Iberomaurusian period in the Maghreb. Secondly, we investigate whether the transition from the Late Pleistocene Iberomaurusian to the early Holocene Capsian brought with it a change in oral health and subsistence behaviours.

The Iberomaurusian is a Late Pleistocene Later Stone Age industry dominated by small backed blades and backed points (Barton et al. 2013). The term is also used for the people who made this industry. Recent re-analyses of the lithic technology and a comprehensive re-dating programme and evaluation of existing dates, have dated the earliest occurrence of the Iberomaurusian industry at ~25 ka cal BP and most recent occurrence at ~11.5ka cal BP (Hogue and

Barton 2016). Within the Iberomaurusian stone tool industry two subdivisions can be identified with the older one recognised by Ouchtata retouched blades, and a more recent one dominated by microlithic backed bladelets (Barich and Garcea 2008; Barton et al. 2013). Microlithic components were present at Grotte des Pigeons, Taforalt by 15,500 – 15,000 cal BP (Barton et al. 2013; Hogue and Barton 2016).

At Grotte des Pigeons, Taforalt, (hereafter referred to as Taforalt) the dominant presence of microlithic components occurred shortly before an abrupt sedimentary transition. The overlying Grey Series deposits are characterised by the rapid accumulation of an ashy midden, containing vast quantities of ash, burnt bone, snail shells and lithic debitage, indicating an intensification of human activity around ~15 ka cal BP (Barton et al. 2013). The ash-rich deposits also preserve abundant evidence for harvesting and consumption of wild plant foods such as acorns, pine nuts and juniper berries, which supplemented the animal protein recovered from medium-sized mammals and molluscs (Humphrey et al. 2014; Taylor et al. 2011). The presence of charred rhizomes from Alfa grass/esparto (*Stipa tenacissima*) in the levels investigated is indirect evidence that the Iberomaurusians were producing baskets and other woven pieces of equipment that could have been used to collect wild food items (Morales, this volume). Grindstones have also been recovered from the burial deposits (Humphrey et al. 2014; Roche 1963). Similar changes in sedimentation, suggesting intensification of human occupation during the Iberomaurusian, occur at other sites in Morocco, including Ifri n'Ammar and Ifi El-Baroud (Linstädter et al. 2012).

The Capsian is an early Holocene stone tool industry found primarily at sites in the Eastern Maghreb (modern day Tunisia and Algeria) between ~ 11.5 and 7.0 ka cal BP (Linstädter 2008). The term also refers the people who occupied those sites. The Capsian lithic industry is based on the production of bladelets but distinguished from the Iberomaurusian by the inclusion of small geometric microliths (Lubell 2001). Two typologically distinct industries have been identified: The Typical and the Upper Capsian (Jackes and Lubell 2008; Lubell 2001; Lubell et al. 1976; Lubell et al. 1984; Merzoug 2014; Rahmani 2004). Both have a tool assemblage consisting of backed blades, scrapers and burins, as well as some bone tools. The subdivisions were initially interpreted as consecutive, but are now generally recognised as contemporaneous (Linstädter 2008; Rahmani 2004). The Upper Capsian is characterised by increased variability in raw materials and more efficient use of prepared tools (using a pressure detachment technique (Mulazzani et al.)), and may reflect the movement of Capsian people into more remote regions where high quality raw materials were less abundant (Linstädter 2008; Rahmani 2004). Capsian open air sites, often referred to as *escargotières*, are characterised by mounds of accumulated ash, flint tools, burnt bone and stone and vast quantities of land snail shells. Evidence for harvesting of wild food resources including land snails and plants and hunting of wild animals points to a hunter-gatherer lifestyle (Morales, this volume, Aouadi et al. 2014).

2. Materials and Methods

2.1 Materials

The skeletal and dental sample that was used for this study was assembled from a number of Iberomaurusian and Capsian sites (Figure 1). The number of individuals, number of analysed teeth and sample breakdown into age categories is presented in Table 1.

>> Figure 1 and Table 1

The Iberomaurusian sample comes from three well-dated Late Pleistocene sites in Morocco and Algeria. Historic and recent excavations at Grotte des Pigeons in Taforalt in Morocco revealed numerous partially articulated human skeletons and disarticulated skeletal parts from primary, secondary and disturbed burials in a spatially demarcated area towards the back of the cave (Balout 1954; Ferembach 1962; Humphrey et al. 2012; Mariotti et al. 2009;

Mariotti et al. 2014). Direct dates on human bone from the recent phase of excavations have yielded age estimations between 15,077 cal BP and 13,892 cal BP (Humphrey et al. 2014), but burials may have continued throughout the Iberomaurusian period. The most recent Iberomaurusian deposits at Grotte des Pigeons are dated to around 12,600 cal BP (Barton et al. 2013). The second Iberomaurusian sample is from the rock shelter of Afalou Bou Rhummel in Algeria (hereafter referred to as Afalou) (Arambourg et al. 1934; Hachi 1996). The samples studied here were recovered during excavations between 1928 and 1929 (Arambourg et al.1934). The majority of individuals were found disarticulated and incomplete in Level 1. More recently partially disarticulated human skeletons representing approximately eight individuals were found in a separate burial chamber and these yielded dates of 13,120 +/- 370 BP (Alger 0008), 12,400 +/- 240 BP (Ly 3228) and 12,020 +/- 170 BP (Gif 6532) (Hachi 1996). A single individual from Dar-es-Soltan was also included with a date of 13,400 +/- 700 YA (OSL4-X2402) (Schwenninger et al. 2010).

The Capsian sample is smaller than the Iberomaurusian sample and comprises individuals from nineTypical and Upper Capsian sites in Eastern Algeria and Tunisia (Table 1). Site 12 (Ain Berriche) is an escargotière in Algeria with a Capsian industry (7753-8539 cal BP (Jackes and Lubell 2014)). Six adult and two juvenile skeletons were excavated from the Minnesota trench during excavations led by Jenks in 1930 (Haverkort and Lubell 1999). One of the adult skeletons was considered intrusive at the time of excavation and this has recently been confirmed by radiocarbon dating (Jackes et al 2015). Two other adult skeletons yielded calibrated radiocarbon dates between 9000 and 8700 cal BP (Jackes et al 2015). Dentitions from three of the adult skeletons and an additional fragment were included in this study. Ain Dokkhara is an escargotière in Algeria with an Upper Capsian industry. Excavations in 1949 revealed a well preserved skeleton of a young male in deposits that has been indirectly dated at 6580+/- 100 BC, based on a radiocarbon date on land snails from the same horizon (Chamla 1973).The skeleton of an adult male aged between 40 and 50 years was found during excavations at Ain Meterchem an escargotière in Tunisia in 1948. Some authors have considered this to be an intrusive burial dating to the same Neolithic stage as other bead decorated burials (Camps 1974, but Chamla 1978), but Vallois and Felice (1979) have made a strong case that the skeleton belongs to the Capsian. Disarticulated human bones from several individuals were uncovered during excavations at Grotte des Hyènes between 1925 and 1926, including one relatively complete skull that had undergone evulsion of all eight incisors (Royer 1926, Arambourg et al. 1934, Balout 1954) and upper or lower jaws from several other individuals. A fragmentary female skull was found at Koudiat-el-Kherrouba, an escargotière in Algeria during excavations in 1933 (Arambourg et al. 1934, Balout 1954). Some authors have suggested that the context may be Neolithic (Briggs 1955) but the skull shows evidence of evulsion of all eight incisors which is typical for the Capsian period (Humphrey and Bocaege 2008). Several skulls were found at Khanguet el Mouhaâd, an escargotière in Algeria, but only one of these, is a young adult female found in 194, is considered to be in a secure Upper Capsian context (Briggs 1953). Mechta el Arbi is an escargotière in Algeria with an Upper Capsian industry. A large number of human remains were recovered in a series of excavations between 1907 and 1927 (Balout 1954) including four individuals included in this study. Human bones found at Mesloug, an escargotière in Algeria, in 1928 (Balout 1954) included a partial mandible with evulsion of the lower central incisors that was included in this study. Despite some uncertainty over its cultural association, a partial skull from Redeyef, a rock shelter in Tunisia first reported in 1912 (Balout 1954) was included in this study.

Preservation was variable across the sample, with some individuals represented by complete skeletons and others only by fragmentary dental remains. Fragmentary dentitions were evaluated for caries prevalence and distribution to maximise sample size. The sample was divided into four age categories (see below). It was not possible to make comparisons between males and females because there were too few reliably sexed dentitions. No statistical analyses were undertaken between time periods due to the small and uneven sample sizes.

2.2 Methods

2.2.1 Age estimation

Pubic symphysis morphology, auricular surface morphology, ectocranial suture closure, and sternal rib end changes were used to assign individual skeletons into one of three age categories: young adult (18-25), middle adult (25-55) and old adult (55+) (Buikstra & Ubelaker, 1994). Those dentitions unable to be assigned an age category were grouped into an undetermined age category. Juveniles were excluded from the study. For samples without associated skeletal material, age estimation was carried out using dental wear stages.

2.2.2 Dento-alveolar parameters

A series of dento-alveolar parameters were recorded by the same observer (IDG): caries, antemortem tooth loss (AMTL), postmortem tooth loss (PMTL), abscesses, alveolar bone resorption, and tooth wear. All teeth were examined with good lighting and a magnification of 4x and 10x. The frequency of each pathology is reported as a proportion of its observable parameter (e.g. number of sockets). The number of observations for each of these observable parameters depends on the presence and preservation of teeth and alveoli and which pathology is considered.

- The *observable sockets* are the combination of all teeth and alveoli observed in the sample.
- The *valid observed sockets* are the observable sockets minus sockets affected by post-mortem tooth loss.
- The *observed teeth* are the observable sockets minus sockets affected by post-mortem and ante-mortem tooth loss.

Alveolar resorption

Alveolar bone resorption was recorded as present if at least a 2mm distance was measured between the crest of the alveolar bone and the cemento-enamel junction on any surface of the tooth crown (mesial, distal, lingual or buccal) (Hillson, 1996). Root exposure is reported as a proportion of observed teeth.

Postmortem tooth loss (PMTL)

Postmortem tooth loss was defined as an empty socket showing no sign of alveolar remodelling (Nelson 2015; Ortner and Putschar 1981). PMTL is reported as the proportion of observable sockets.

Caries

For these analyses a carious lesion was only considered present when there was clear penetration and tissue breakdown of the enamel (Hillson 2001). The number of lesions and locations was scored for each observed tooth. For overall caries frequency, only one surface (occlusal, mesial, distal, lingual or buccal) of the tooth had to be affected for caries to be considered present on the tooth. Caries are expressed as the proportion of observed teeth.

Caries categories were expressed as the proportion of carious teeth.

- Gross caries was determined present when a lesion affected more than one tooth surface and the surface of origin of the caries could no longer be determined.
- Crown caries refer to the presence of caries on one of more of these locations on the crown: (a) occlusal molar fissures, (b) occlusal attrition caries in the dentine, (c) buccal surface, (d) lingual surface, (e) mesial surface, (f) distal surface, (g) pit caries, and (h) rim chipping caries.
- Root caries refer to the presence of at least one carious lesion on one or more of these locations on the root: (a) buccal surface, (b) lingual surface, (c) mesial surface, (d) distal surface.

Antemortem tooth loss (AMTL)

Antemortem tooth loss was defined as an empty socket showing any sign of alveolar remodelling (Nelson 2015; Ortner and Putschar 1981). Because of the high prevalence of evulsion of the anterior teeth in these populations, we report AMTL only as post-canine AMTL. AMTL is reported as the proportion of valid observed post-cranial sockets.

Abscesses

The distinction between abscesses, granulomas and cysts is difficult to make in an archaeological assemblage without x-ray observations (Hillson 1996; Nelson 2015). Therefore all periapical cavities are grouped here under the term abscess. Abscesses were recorded by direct observation only and defined as a periapical cavity with relatively smooth walls. Because of the lack of X-ray observations for these cavities their prevalence will be underestimated. We focused on periapical bone loss that was visible by the naked eye only. Abscesses were recorded as present when there was a clear cavity in the alveolar bone and reported as the proportion of observable sockets.

Alveolar bone resorption (root exposure)

Periodontal disease often results in bone resorption and root exposure. It was recorded as present if at least a 2mm distance was measured between the crest of the alveolar bone and the cemento-enamel junction on any tooth surface (mesial, distal, lingual or buccal). Root exposure is reported as the proportion of observed teeth exhibiting alveolar bone resorption.

3. Results

In total 128 individual dentitions from the Iberomaurusian (N=109) and Capsian (N=19) were represented by at least one tooth or alveoli (Table 2 and 3). The number of observable tooth sockets for the Iberomaurusian was 1991 and for the Capsian 404. A summary of the number of individuals and observed sockets and teeth is presented in Table 2 and Table 3 together with frequencies of PMTL for the postcanine dentition. PMTL affected 334 (17%) of Iberomaurusian and 47 (12%) of Capsian observable sockets. Due to the near-universal practice of tooth evulsion in this sample AMTL is only presented for the post-canine dentition. The total number of post-canine sockets observed with AMTL was 112 (9% of valid observable sockets) for the Iberomaurusian (35% of individuals) and 34 (14% of valid observable sockets) for the Capsian (50% of individuals). The total number of surviving observable teeth was 1417 for the Iberomaurusian and 271 for the Capsian.

>> Table 2

>> Table 3

Comparisons between the 951 observable sockets from Taforalt and 1024 observable sockets from Afalou (Table 4) demonstrates that the high caries frequencies observed for Grotte des Pigeon (51%, n=345/681 observed teeth) reported by Humphrey et al. (2014) are actually surpassed by Afalou (69%, n=498/727 observed teeth). Caries rates for the all age groups from Afalou were higher than at Taforalt (50% compared to 33% of observed teeth respectively for young adults, 73% compared to 55% for middle adults and 80% vs 53% for old adults). These results suggest that high caries frequencies may have been characteristic of the time-period represented by these samples.

>> Table 4

The caries frequencies for the Iberomaurusians and Capsians are reported in Table 2 and 3. Both samples presented very high caries frequencies with 60% (n=844/1417) of observed teeth affected in the Iberomaurusian and 49% (133/271) of observed teeth affected in the Capsian. In total, 97% of the 109 Iberomaurusian dentitions and 74% of 19 Capsian dentitions presented at least one carious lesion. Crown caries were the most frequent with more than

30% of observed teeth affected in both time periods. The frequency of root caries was similar during the Iberomaurusian (38% of observed teeth) and Capsian (35% of observed teeth).

Sample sizes for the Capsian are small so comparison across the age categories may be affected by sample bias. Nevertheless it is evident that caries affected young and old adults and that even gross caries were observed amongst all age groups (Table 2). In the Iberomaurusian sample the presence of gross caries followed the expected pattern, increasing between age groups. Post-canine ante-mortem tooth loss followed the same pattern suggesting that caries was an underlying cause.

The prevalence of non-carious oral pathologies is presented in Table 2. Alveolar resorption was present 51% of observed Iberomaurusian teeth and was common even amongst young adults. A similar proportion of Capsian teeth (58%) were affected and, as in the Iberomaurusian, all age categories were affected. Abscesses were present in 37% of Iberomaurusian dentitions and 63% of Capsian dentitions, representing 4% and 7% of observable sockets respectively.

3. Discussion

This research sought to determine whether there are differences in oral pathology between the Iberomaurusian and the Capsian periods and whether the high caries frequencies previously reported for the dental series from Grotte des Pigeons at Taforalt are unique to this site, or whether they are representative of that time period. Comparisons of the dental series from Taforalt and Afalou (Algeria), shows that caries rates are slightly higher at Afalou than at Taforalt. Comparisons between the Iberomaurusian and Capsian samples show that caries rates were slightly lower in the Capsian (59.6% (IB) vs 49.1% (CAP)), but were still very high compared to published caries frequencies for other hunter-gatherers populations (Figure 2) (Lanfranco and Eggers 2010).

>> Figure 2

Reported caries frequencies will be inflated in these samples due to the absence of anterior teeth caused by the widespread practice of evulsion during the Iberomaurusian and Capsian (Humphrey and Bocaege 2008, De Groote and Humphrey 2017). Clinical research has demonstrated that mandibular central incisors are the least likely to be carious, followed by canines and premolars, while molars were the most likely affected by caries (Demirci et al 2010). This observation must be kept in mind when comparing these results to those reported for populations that do not practice evulsion.

Caries causes are multifactorial and complex. The composition and the proportion of carbohydrates consumed by the individual plays a major role. Other factors that contribute to differences in oral health between populations are tooth crown morphology, fluoride content of the local groundwater, and the composition of oral microbiota, oral hygiene and transmission of cariogenic bacteria within the population. Variation in tooth morphology, in particular the number and patterning of cusps and degree of crenulation, can have a major impact on caries susceptibility (Hillson 2001). Detailed analysis of dental morphology has shown that Iberomaurusian and Capsian populations exhibit similar and simple tooth morphology (Irish 2000) such that the effect of tooth morphology on caries development is likely to be equivalent across all samples. Fluoride content in the groundwater in the Maghreb is unlikely to have varied over time, but may show local variation. Studies show there is an excess of fluoride in the groundwater, which has resulted in fluorosis being an endemic disease in this region (Brunt et al. 2004; Fantong et al. 2010) but there was no evidence of fluorosis in the Iberomaurusian and Capsian dentitions.

Poor oral hygiene can lead to a more rapid progression of tooth decay. A lack of tooth cleaning to remove the built-up plaque would have contributed to the detrimental effect of these sticky carbohydrates). Tayles et al (2000) concluded that frequent snacking was the cause of higher caries rates in females compared to males despite consuming the same diet (Tayles et al. 2000). Regular snacking on carbohydrate rich plants or derived foods such as breads and porridges, may have contributed to the extremely high number of oral pathologies in this group.

Caries does not exist without the presence and transmission of oral caries-causing microbiota such as *Streptococcus mutans*. Adler and colleagues (Adler et al. 2013) analysed oral bacteria in dental calculus from archaeological assemblages and concluded that the prevalence and virulence of cariogenic oral bacteria increased during the Neolithic. The evidence presented here for high caries frequencies in hunter-gatherer Late Pleistocene and early Holocene populations from the Maghreb suggests that the origin of highly virulent microbiota predated the Neolithic in North West Africa. Close contact between individuals would have facilitated both horizontal and vertical transmission of cariogenic bacteria (Humphrey et al. 2014). These results warrant the revision of the origins of caries as an epidemic.

The similarity in oral health between Iberomaurusian and Capsian populations implies similarities in subsistence behaviour and oral hygiene and indicates the presence of cariogenic bacterial in the oral microbiota. These similarities are consistent with cultural and biological continuity between the Iberomaurusian and Capsian periods. Charred macro-botanical remains recently found in sites from both periods indicate that carbohydrate-rich plants were extensively processed for human subsistence, and thus confirm that consumption of those could account for the high caries attested (Humphrey et al 2014; Morales, this volume). Acorns, pine nuts, juniper berries, wild pistachios, wild legumes and others, up to 20 different taxa, appear abundantly in layers dated after ~15 ka cal BP. Preservation conditions of the vegetal remains suggest that heat processing and storage could be carried out, increasing the energetic value of plant foods. The presence of wild plants is also recorded in Neolithic deposits from those sites, indicating that, despite the appearance of farming, wild plants kept a very important role in the diet of this period (Mulazzani et al 2016; Morales, this volume). Evidence for systematic exploitation of land molluscs at late Late Pleistocene and early Holocene sites in both Eastern and Western Maghreb is a further indication of cultural similarity in diet between the Iberomaurusian and Capsian. Iberomaurusian deposits at Taforalt show evidence for harvesting of five species of edible snails (Taylor et al. 2011). Shells of terrestrial gastropods are also recorded in epipaleolithic and Neolithic levels at numerous other cave sites in North East Morocco (Hutterer et al 2014). Exploitation of edible land mollusc has long been considered characteristic of the Capsian period, to the extent that Capsian open-air sites are often known as "escargotieres", in reference to vast quantities of snail shells recovered from these sites (Aouadi et al. 2014; Hutterer et al. 2014; Lubell 2004a; Lubell 2004b).

Cultural indicators also support similarities between the Iberomaurusian and Capsian. The technocomplex of both periods is closely related, involving the use of single platform cores for bladelet production (Sheppard and Lubell 1991). The practice of tooth evulsion, or the deliberate removal of healthy teeth, is also characteristic of both periods. During the Iberomaurusian period, most individuals practiced evulsion of both upper central incisors. In the Capsian, this practice became more extreme and in some cases all anterior teeth were removed (De Groote and Humphrey 2015; De Groote and Humphrey 2017; Humphrey and Bocaege 2008). Recent studies of dental morphology are also consistent with a degree of long-term biological similarity in the Maghreb (Irish 2000). Iberomaurusian dentitions already exhibit many of the morphological features present in the North African Dental Trait Complex and share these features with all more recent populations from North West Africa (Irish 2000).

4. Conclusion

This paper set out to investigate whether the transition from the Late Pleistocene Iberomaurusian to the early Holocene Capsian from the Maghreb region brought with it a change in oral health and subsistence behaviours. The results showed high oral pathologies in both populations exceeding those observed in many food producing populations, although those in the Capsian were somewhat lower than those of the Iberomaurusian. The increased reliance on carbohydrates with the onset of food production and their detrimental effect on oral health are well documented in both archaeological and historical samples but both phenomena appear to have predated food production in the Maghreb. The contribution of wild plant foods contributed to Iberomaurusian and Capsian diets is explored elsewhere in this volume (Morales, this volume). The results also suggest that the origin of highly virulent microbiota predated the onset of the Neolithic in North West Africa.

To conclude, the subsistence pattern of the Late Pleistocene Iberomaurusians of North West Africa incorporated a significant component of wild plant foods which was associated with high frequencies of oral pathologies. Early Holocene Capsian populations exhibit similarities in oral pathologies. Other cultural indicators, such as a closely related technocomplex, the exploitation of molluscs and the widespread practice of dental evulsion, suggest further parallels between the time periods.

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List of Figures and Tables in the Manuscript

Figure 1. Map showing site locations included in the sample.

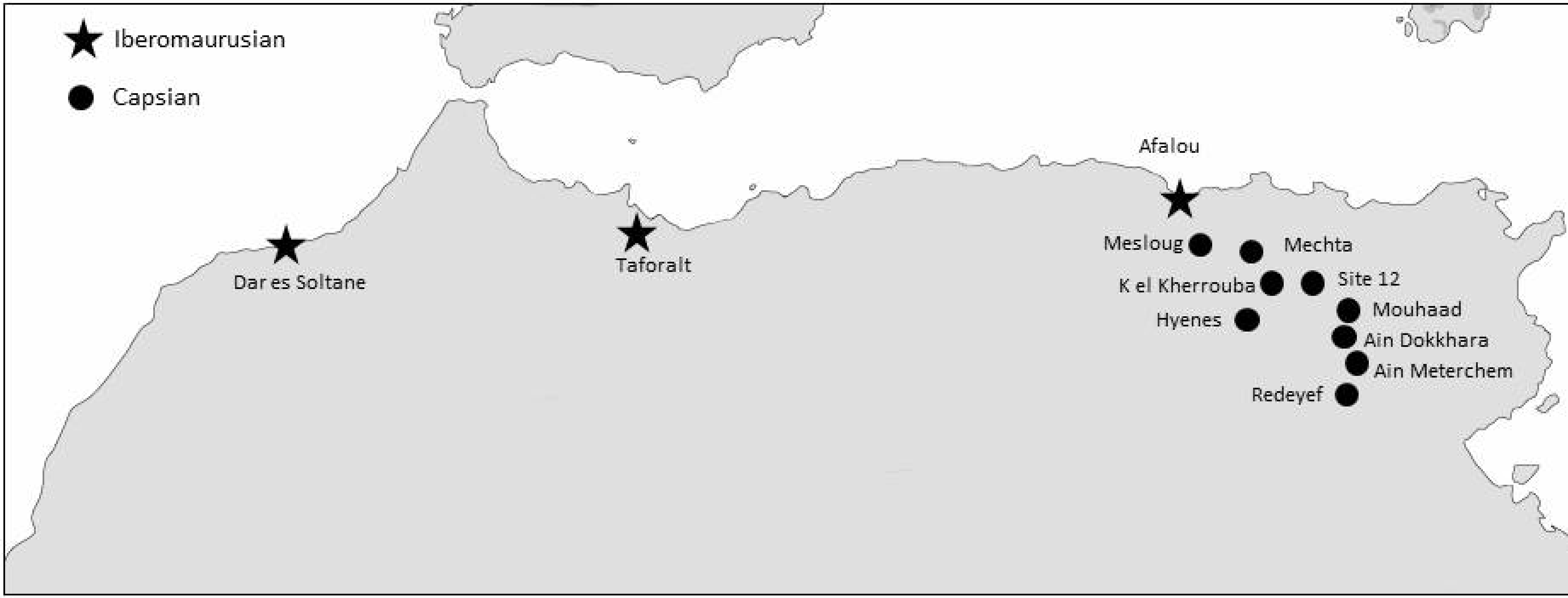
Figure 2. Frequency of carious lesions (per total number of teeth in past populations) grouped according to subsistence pattern: Hunting and Gathering; Mixed Economy including horticulture, agriculture + hunting, gathering or fishing); and agriculture (food producing) compared to the Iberomaurusians and Capsians (Adapted from Lanfranco and Eggers 2010).

Table 1. Sample composition.

Table 2. Frequencies of oral pathologies by tooth sockets and observed teeth.

Table 3. Frequencies of oral pathologies by individual.

Table 4. Sample size and caries frequencies in two Iberomaurusian samples: Taforalt and Afalou.



Iberomaurusian
Capsian
Afalou
Dar es Soltane
Taforalt
Mesloug
Mechta
K el Kherrouba
Site 12
Hyenes
Mouhaad
Ain Dokkhara
Ain Meterchem
Redeyef

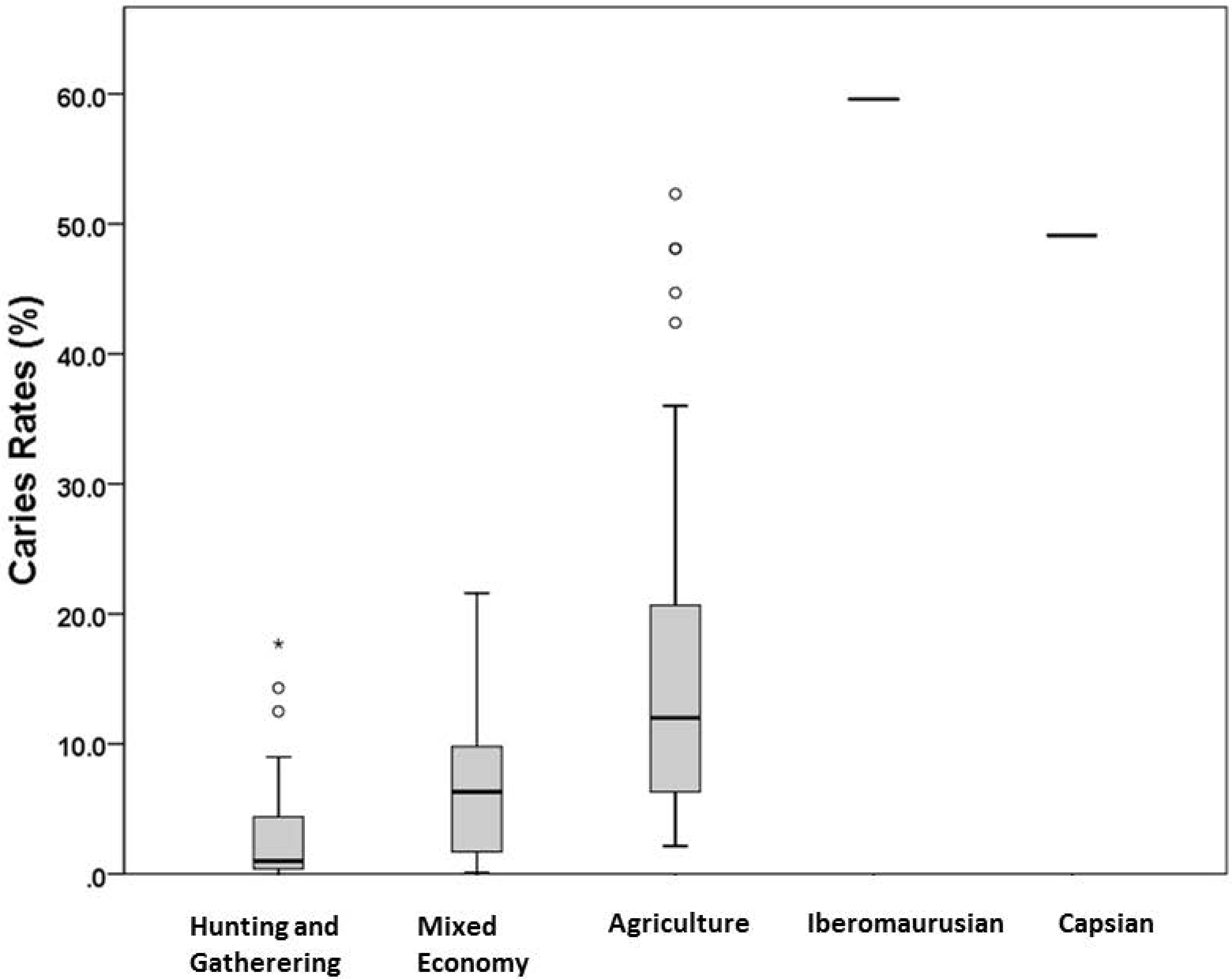

Caries Rates (%)
60.0
50.0
40.0
30.0
20.0
10.0
.0
Hunting and Gatherering
Mixed Economy
Agriculture
Iberomaurusian
Capsian

Table 1: Sample composition

Iberomaurusian

Age category

Young Adult

- Afalou 1
- Afalou 20
- Afalou 22
- Afalou 23
- Afalou 24
- Afalou 29
- Afalou 31
- Afalou 38
- Afalou 48
- Taforalt Ind 5
- Taforalt VIII-1
- Taforalt XVII-C1-C3
- Taforalt XVII-C3 (max)
- Taforalt XX-1
- Taforalt XXV C4 + SXXV

Adult

- Afalou 11
- Afalou 12
- Afalou 13
- Afalou 14
- Afalou 15
- Afalou 17
- Afalou 2
- Afalou 25
- Afalou 28
- Afalou 3
- Afalou 30
- Afalou 32
- Afalou 36
- Afalou 39
- Afalou 43
- Afalou 45
- Afalou 46
- Afalou 47
- Afalou 5
- Afalou 9
- Taforalt Ind 13
- Taforalt Ind 14
- Taforalt Ind 3
- Taforalt Ib
- Taforalt trephanated
- Taforalt VIII-2
- Taforalt XI-1
- Taforalt XII-1
- Taforalt XII-C4
- Taforalt XV-C4C5
- Taforalt XVIII-1
- Taforalt XX-C1
- Taforalt XXII-1
- Taforalt XXIV-1
- Taforalt XXV-C3.1 + C3
- Taforalt XXVII-1

Iberomaurusian continued

Age category

Old Adult

- Afalou 10
- Afalou 27
- Afalou 40
- Afalou 49
- Taforalt IX-1
- Taforalt XV-C2
- Taforalt XXV-C1

Undetermined (UD)

- Afalou 1935 Md 6 R
- Afalou 1936 - 6 "0"
- Afalou 1936 c
- Afalou 34
- Afalou 42
- Afalou 7
- Afalou 8 s.m.
- Afalou A5ho
- Afalou As
- Afalou B4
- Afalou C Md8
- Afalou D6 Ma Fem
- Afalou F Md10
- Afalou I 1935-6
- Afalou Max 1935-6a
- Afalou Max 1935b
- Afalou max 1936-d
- Afalou Maxilla 35
- Afalou Md 2-3
- Afalou Md4b
- Afalou Md5
- Afalou Mx4
- Dar Es Soltan I
- Taforalt Ind 1
- Taforalt Ind 10
- Taf iso mand
- Taforalt I 1952
- Taforalt I- no number (a)
- Taforalt I- no number (b)
- Taforalt innomine
- Taforalt IX-B
- Taforalt VIII ?
- Taforalt XI-B-C2
- Taforalt XII-?
- Taforalt XIV-1
- Taforalt XIX
- Taforalt XIX-C1
- Taforalt XIX-C2
- Taforalt XV-C5
- Taforalt XV-C5max
- Taforalt XVI C1 NOPD mand
- Taforalt XVI C1 NOPD max
- Taforalt XVI-C2
- Taforalt XVII-C2

Iberomaurusian continued

Age category

Undetermined continued (UD)

- Taforalt XX
- Taforalt XXI-1
- Taforalt XXIV-2
- Taforalt XXV-C3-2+C3
- Taforalt XXVI
- Taforalt XXVII-C1
- Taforalt-no number

Capsian

Age category

Young Adult

- Ain Dokkhara 1

Adult

- Khanguet al Mouhaad IV
- Ain Meterchem 1
- Site 12 3A1
- Site 12 3A-2
- Site12 3A-5

Old Adult

- Hyenes 4-255 mand
- Mechta type male

Undetermined (UD)

- Hyenes 4-254 skull
- Hyenes 4-255
- Hyenes D
- Hyenes G
- Koudiat-el-Kherrouba
- Mechta 4
- Mechta 5
- Mechta max mand part
- Mesloug
- Redeyef A
- Site 12 Mand frag

Table 2: Frequencies of oral pathologies by tooth sockets and observed teeth.

	No. Of observable sockets	No. Of observable PC sockets *		No. sockets with PMTL*		No. of valid observable Sockets*		No. of PC sockets with AMTL~		No. of observed teeth*		No. teeth with caries^		No. teeth with gross caries$		No. teeth with crown caries$		No. teeth with root caries$		No. of teeth with resorption^		No. of sockets with abscess*	
Iberomaurusian	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%	n	%
YA	350	222	63.4	49	14.0	301.0	86.0	7	3.2	273	78.0	115	42.1	4	3.5	64	55.7	14	12.2	136	49.8	6	1.7
MA	752	468	62.2	89	11.8	663	88.2	49	10.5	557	74.1	364	65.4	14	3.8	104	28.6	33	31.7	320	57.5	32	4.3
OA	176	113	64.2	17	9.7	159	90.3	24	21.2	124	70.5	84	67.7	10	11.9	11	13.1	6	54.5	55	44.4	21	11.9
UA	713	455	63.8	179	25.1	534	74.9	32	7.0	463	64.9	281	60.7	13	4.6	93	33.1	49	0.0	216	46.7	28	3.9
Total	1991	1258	63.2	334	16.8	1657	83.2	112	8.9	1417	71.2	844	59.6	41	4.9	272	32.2	102	37.5	727	51.3	87	4.4
Capsian																							
YA	32	20	62.5	1	3.1	31	96.9	0	0.0	31	96.9	22	71.0	0	0.0	7	31.8	0	0.0	32	103.2	1	3.1
MA	142	88	62.0	6	4.2	136	95.8	13	14.8	103	72.5	39	37.9	3	7.7	15	38.5	9	60.0	56	54.4	14	9.9
OA	35	23	65.7	6	17.1	29	82.9	4	17.4	21	60.0	11	52.4	1	9.1	7	63.6	3	42.9	17	81.0	2	5.7
UA	195	119	61.0	34	17.4	161	82.6	17	14.3	116	59.5	61	52.6	0	0.0	14	23.0	3	21.4	53	45.7	13	6.7
Total	404	250	61.9	47	11.6	357	88.4	34	13.6	271	67.1	133	49.1	4	3.0	43	32.3	15	34.9	158	58.3	30	7.4

Young adults (YA), middle adults (MA), old adults (OA), Undetermined age (UA)
* % of no. of observable sockets
# % of no. of valid observed sockets (=observed sockets - PMTL)
~ % of no. observable PC sockets
^ % of no. of observed teeth
$ % of no. of teeth with caries

Table 3: Frequencies of oral pathologies by individual.

	No. of ind.	No. of ind. with PC sites §		No. of ind. with PMTL §		No. of ind. with PC AMTL sites §		No. of ind. with resorption §		No. of ind. with abscess §		No. of ind. with caries §		No. of ind. with gross caries #	
Iberomaurusian	n	n	%	n	%	n	%	n	%	n	%	n	%	n	%
YA	15	15	100.0	10	66.7	4	31.0	12	80.0	6	40.0	14	93.3	2	14.3
MA	36	36	100.0	20	55.6	16	44.0	34	94.4	15	41.7	36	100.0	9	25.0
OA	7	7	100.0	5	71.4	6	86.0	6	85.7	5	71.4	7	100.0	2	28.6
UA	51	51	100.0	44	86.3	44	86.0	41	80.4	14	27.5	49	96.1	10	20.4
Total	109	109	100.0	78	71.6	38	35.0	93	85.3	40	36.7	106	97.2	23	21.7
Capsian															
YA	1	1	100.0	1	100.0	0	0.0	1	100.0	1	100.0	1	100.0	0	0.0
MA	5	5	100.0	4	80.0	4	80.0	3	60.0	4	80.0	4	80.0	2	50.0
OA	2	2	100.0	2	100.0	1	50.0	2	100.0	1	50.0	1	50.0	1	100.0
UA	11	11	100.0	9	81.8	5	45.5	7	63.6	6	54.5	8	72.7	0	0.0
Total	19	19	100.0	16	84.2	10	52.6	13	68.4	12	63.2	14	73.7	3	21.4

§ % of no. of individuals

% of ind with teeth with caries

Table 4: Sample size and caries frequencies in two Iberomaurusian samples: Taforalt and Afalou.

	No. Of observable sockets	No. sockets with PMTL	No. sockets with AMTL	No. of observed teeth	No. teeth with caries^	
Afalou	n	n	n	n	n	%
YA	183	24	18	141	71	50.4
MA	465	53	83	329	239	72.6
OA	90	8	13	69	55	79.7
UA	286	68	30	188	133	70.7
Total	1024	153	144	727	498	68.5
Taforalt						
YA	167	25	10	132	44	33.3
MA	287	36	23	228	125	54.8
OA	86	9	22	55	29	52.7
UA	411	105	40	266	147	55.3
Total	951	175	95	681	345	50.7

Young adults (YA), middle adults (MA), old adults (OA), Undetermined age (UA)

^ % of no. of observed teeth (observed teeth = observable sockets - AMTL - PMTL)