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Agenesis of the permanent teeth in sub-Saharan Africans: Prevalence, patterns, interpretations

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ABSTRACT

Objective: Dental agenesis data in modern and premodern sub-Saharan Africans are presented by region, West, Central, East, and South, and by sex. Beyond characterizing the anomaly, comparisons are made with other populations and future work is encouraged. The findings should be of use to dental clinicians and anthropologists.

Methods: Agenesis of the UI2, LI1, UP2, LP2, UM3, and LM3 was recorded in 52 discrete samples of mainly skeletal dentitions ($n = 2162$) from across the subcontinent. After dividing into temporal categories, regional pooling was effected for adequate sample sizes across the vast geographic area. Only adults were included to record M3 status. Analyses included 95% confidence intervals and chi-square comparisons by region and sex.

Results: Of 1668 modern individuals 2.3% have UI2-LP2 agenesis (CI 1.6–3.1%). Regional and sex differences are non-significant, though females are most affected. For M3s it is 7.0% (5.7–8.4%), with the Central region sample differing significantly from the East and South. Females again have greater prevalence, with the difference in the West significant. UI2-LP2 agenesis affects 0.6% of 494 premodern individuals (0.1–1.8%), while M3 agenesis is 8.5% (6.1–11.5%). None of these differences are significant.

Conclusions: Rates are toward the low end of global ranges, including 0.0–12.6% for UI2-LP2 from case reports, and 5.3–56.0% for M3 agenesis. With exceptions, generally insignificant inter-region differences imply that rates reasonably represent sub-Saharan peoples overall. Results will be of interest to anthropologists, but those related to risk factors, patterning, and prevalence may assist clinicians in tailoring treatment, while informing patients how this anomaly differs by population ancestry.

1. Introduction

Regardless of the concentration, articles concerning congenitally absent permanent teeth are almost universal in declaring them as the most common dental anomaly (Affan & Serour, 2014; Akram et al., 2011; AlShahrani et al., 2013; Amini et al., 2012; Duke et al., 2023; Farcaşiu et al., 2022; Heuck Henricksson et al., 2019; Kerekes-Máthé et al., 2023; Rakhshan, 2015; Vastardis, 2000). This refers to non-syndromic cases, the subject of the present study, not those associated with syndromes that inhibit tooth development [Down syndrome, cleft palate, among others (AlShahrani et al., 2013; Duke et al., 2023; Kabli et al., 2022; Kerekes-Máthé et al., 2023; Sadaqah & Tair, 2015)]. As Rakhshan states (2015:1), this commonness attracts considerable attention, most notably in the "clinical, basic science and public health fields, such as orthodontics, paediatric dentistry, prosthodontics, periodontics, maxillofacial surgery, anatomy, anthropology and even the insurance industry." That is, beyond scientific interest in cause, effect, and spatiotemporal variation, more immediate physical, emotional, and financial burdens on the affected individuals prompt continual new clinical strategies in patient support and restoration methods (Affan & Serour, 2014; Akram et al., 2011; Amini et al., 2012; Duke et al., 2023; Ford & Ashley, 2023; Kerekes-Máthé et al., 2023; Ng'ang'a & Ng'ang'a, 2001; Rakhshan, 2015). As a result, the number of publications is considerable. Entering 'hypodontia' into Google Scholar returns > 1100 hits for last year alone, ~12,000 in the past decade, and > 21,000 total. 'Dental agenesis' is more common, > 2000, ~17,000, and > 32,000. Similar counts occur with allied terms and alternate search engines.

Yet in all these searches it appears that only nine publications present original data from sub-Saharan Africa. Indeed, in a global meta-analysis Carter and Worthington (2015:890) "cautioned that this continent

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[Africa] was severely under sampled." Four of these nine are based on living individuals within the sub-continent (Adeniji, 1993; Affan & Serour, 2014; Hassan et al., 2014; Ng'ang'a & Ng'ang'a, 2001; Temilola et al., 2014), three are from crania (Chagula, 1960; Esan & Schepartz, 2017; Hellman, 1928), and another is unspecified (Sofaer, 1975). Related, albeit more tangential data come from a study of sub-Saharan African UK immigrants (Lavelle & Moore, 1973) and several about African Americans (Blayney & Hill, 1967; Garner & Yu, 1978; Harris & Clark, 2008; Harris, 2009; Muller et al., 1970; Salinas & Jorgenson, 1974). Additional articles listing African-related information simply cite previous work for comparative purposes (Akram et al., 2011; Carter & Worthington, 2015; Khalaf et al., 2014; Polder et al., 2004). As such, the main aim of this paper, among others below, is to address this lack of sub-Saharan attention by presenting new data.

As indicated, multiple terms describe dental congenital absence depending on the field of study, but it largely concerns the total number of missing teeth, especially in clinical research. Thus, while hypodontia may, for example, be a catchall indicator for any number of developmentally missing teeth (Akram et al., 2011; Duke et al., 2023; Farcaşiu et al., 2022; Heuck Henricksson et al., 2019; Kabli et al., 2022), it more specifically denotes less than six. Further, it and other terms, including those describing more absences (oligodontia, anodontia, mild, moderate, or severe hypodontia), ordinarily exclude third molars (Akram et al., 2011; AlShahrani et al., 2013; Duke et al., 2023; Khalaf et al., 2014; Ng'ang'a & Ng'ang'a, 2001; Sadaqah & Tair, 2015). So, without getting side-tracked by terminology (see above references for specifics), the more generic 'dental agenesis' is used here to denote the lack of one or more teeth (Duke et al., 2023), including third molars; as well, this term is said to best account for the latent developmental defects responsible for the anomaly (after Polder et al., 2004; Vastardis, 2000).

Regarding background, including the aetiology, prevalence, patterning, risk factors, implications, and treatment, among others, a significant amount of information is detailed elsewhere by dental experts in each area (including present references). Excellent articles with 'primer'-like contents also exist for a quick yet comprehensive review (e.g., Rakhshan, 2015; Vastardis, 2000). Thus, only areas relevant for present purpose are discussed below to any extent beyond mention.

Any permanent tooth may be agenetic (Farcaşiu et al., 2022; Harris & Clark, 2008; Ng'ang'a & Ng'ang'a, 2001; Polder et al., 2004; Sajjad et al., 2016). However, excluding the upper (UM3) and lower (LM3) third molars, prevalence rates typically include only the other common teeth: upper lateral incisors (UI2), lower central incisors (LI1), and upper (UP2) and lower (LP2) second premolars (Affan & Serour, 2014; Amini et al., 2012; Duke et al., 2023; Khalaf et al., 2014; Lavelle & Moore, 1973; Sadaqah & Tair, 2015). Such rates, as presented to characterize the global population, vary markedly by study (Akram et al., 2011; Amini et al., 2012; Duke et al., 2023; Khalaf et al., 2014; Ng'ang'a & Ng'ang'a, 2001; Pindborg, 1970; Polder et al., 2004; Sadaqah & Tair, 2015; Vastardis, 2000). A likely factor is the addition of new, more diverse data since Pindborg (1970) provided a range of 2.6–9.6% based on just six studies. The ranges of prevalence from the above articles include 1.6–9.6%; 2.3–11.3%, 2.5–6.5%, 2.6–11.3%, ~3.3–11.7%, and 4.4–13.4%. To account for this variation, the extreme values across studies may provide a more representative range of 1.6–13.4%. Overall the prevalence worldwide is stated as ~6.4% (Pace-Balzan et al., 2023; Khalaf et al., 2014). A review of case reports cited for these figures reveals 1.6% is from a clinical study of White patients. The 13.4% is simply listed as 'African' (in Khalaf et al., 2014; Sajjad et al., 2016), but is clearly not representative of the continent; it comes from a single study in North Africa, i.e., Tunisia, of a group said to be affected by considerable consanguinity (Maatouk et al., 2008).

Findings from additional case reports on UI2, LI2, UP2, and LP2 agenesis, including sub-Saharan Africa, suggest an even more likely global range is 0.0–12.6%, excluding some extreme outliers (e.g., Afify & Zawawi, 2012). To illustrate, 0.0% was recorded in > 1000 patients from Ile-Ife, Nigeria (Temilola et al., 2014), 0.4% from Lagos, Nigeria (Adeniji, 1993), 2.7% and 5.1% in southern Sudan (Affan & Serour, 2014; Hassan et al., 2014), 5.2% in Iran (Amini et al., 2012), 6.1% in Saudi Arabia (Sajjad et al., 2016), 6.3% in Kenya (Ng'ang'a & Ng'ang'a, 2001), 11.2% in Korea (Chung et al., 2008), and 12.6% in Germany (Behr et al., 2011). Hassan et al. (2014) provide additional details. Some premodern data have also been collected, mainly just involving incisors, but they are individual case reports (Lieverse et al., 2014) or cannot confirm whether all missing teeth were agenetic (Nelsen et al., 2001; Lee, 2017).

Third molar agenesis, though the most common of all, ~10.0–35.0% (Pindborg, 1970) with an overall prevalence of ~20.0% (Vastardis, 2000), receives less attention in the dental literature. This is particularly evident in clinical and public health fields, for largely practical reasons. Unlike M3 presence (erupted, impacted, or otherwise), which can often necessitate extraction, their absence is not considered a major health concern by many practitioners (though see overview of potential issues in Vastardis, 2000). Thus, the main field of interest is biological anthropology, notably dental anthropology.

Anthropological research includes recording presence/absence of the UM3 and LM3, plus the UI2, LI1, UP2, and LP2, in the Arizona State University Dental Anthropology System (ASUDAS) to estimate individual (Scott et al., 2018) and population ancestry (Scott & Irish, 2017). Like other ASUDAS traits (see Irish et al., 2020) dental agenesis has a strong genetic component, where the mode of inheritance and genes responsible are often established (AlShahrani et al., 2013; Duke et al., 2023; Harris & Clark, 2008; Kabli et al., 2022; Kerekes-Máthé et al., 2023; Sadaqah & Tair, 2015; Shimizu et al., 2013; Vastardis, 2000). Others are focused on diachronic variation. Heuck Henriksson et al. (2019) found a change of 27.7% to 17.2% between medieval and modern Norwegians. This contrasts with most other findings, e.g., Yamada et al. (2004) reported an increase in Japan from 4.1% > 2000 years ago (Jomon era) to 29.4% in the 17th century. In the long term, a significant increase in M3 agenesis was observed from the first documented case > 26,000 years ago at Dolní Věstonice to present (overall 14.3% rate in 139 Late Pleistocene dentitions) (Lacy, 2021). And still others simply list the prevalence. It can be unclear when some of the following are based on individual or tooth counts, but premodern examples include 8.7–14.6% in the Canary Islands (Bermudez de Castro, 1989), 16.3% vs. 7.2% in Neolithic and Byzantine Anatolia (Özbek & Erdal, 2003; Arıhan & Türkekul, 2021), and 42.7% in post-medieval Chichester, Britain (Caldwell, 2021). Modern findings include 0.0% in West African individuals (Hellman, 1928), 1.9% in Kenyans (Chagula, 1960), 7.3–9.2% in South African males (Esan & Schepartz, 2017), and 14.0% in White and 19.0% African Americans (Harris, 2009). The global range is 5.3–56% and 22.6% overall (Carter & Worthington, 2015). Lastly, on rare occasion all teeth including the third molars may be combined, e.g., ~1.0% in unspecified Africans (Sofaer, 1975), 6.9% for White British and 28.2% African UK immigrants (Lavelle & Moore, 1973), and 27.0% in White and 11% in African Americans (Harris & Clark, 2008).

Variation also occurs within populations. With exception (e.g., Sisman et al., 2007; Tallón-Walton et al., 2010), a female bias in UI2, LI2, UP2, and LP2 agenesis relative to males is noted, though the difference is often not significant (Amini et al., 2012; Harris, 2009; Harris & Clark, 2008; Heuck Henriksson et al., 2019; Pindborg, 1970; Sajjad et al., 2016). Some publications cite the same global F:M ratio of 3:2, aka 1.5:1 (Duke et al., 2023; Rakhshan, 2015; Sadaqah & Tair, 2015), or something similar, ~1.4:1 (Polder et al., 2004). Others present lower global ratios, e.g., 1.2:1 (Khalaf et al., 2014), and individual case reports around the world (review in Amini et al., 2012) vary from 2:1 to a contrary ~0.7:1 ratio. Of relevance, the latter is from the above-mentioned Kenyan study (Ng'ang'a & Ng'ang'a, 2001). In a second sub-Saharan case report an approximate 1:1 ratio was recorded in Nigerians (Temilola et al., 2014). With M3 agenesis it is ~1.4:1 in both medieval and modern Norwegians (Heuck Henriksson et al., 2019), ~1.4:1 in White and ~1.5:1 in African Americans (Harris, 2009), and

across a range of global populations females are 14% more likely to be affected (Carter & Worthington, 2015).

Finally, other variation is routinely reported, including the prevalence and patterning of which teeth, antimere, and isomere are affected—overall, by population and, again, by sex. Details are provided in the preceding references, so to conclude this section only a few highlights are presented. For example, the M3 may be most agenetic, but depending on the population the second most likely is either the LP2 (Khalaf et al., 2014; Ng'ang'a & Ng'ang'a, 2001; Polder et al., 2004; Sajjad et al., 2016), or UI2 (Affan & Serour, 2014; Sofaer, 1975). In some the maxilla is most affected (Amini et al., 2012), in others it is the mandible (Affan & Serour, 2014; Heuck Henriksson et al., 2019), and a few are equal (Ng'ang'a & Ng'ang'a, 2001; Polder et al., 2004; Sajjad et al., 2016). For many, bilateral expression is evident, but it is often dependent on the teeth involved (c.f., Harris, 2009; Pindborg, 1970; Polder et al., 2004; Kerekes-Máthé et al., 2023). And not only prevalence, but variation in patterning can differ between the sexes, e.g., White American females show significantly more agenesis in the mandible than do males (Harris & Clark, 2008). Some of these differences are noticeable but, like the prevalence between females and males, are often not significant.

With this review as a backdrop the aforementioned objective is to address the lack of information on sub-Saharan agenesis. Data in > 2000 dentitions across the subcontinent are presented in formats applicable to both clinicians and anthropologists. For the former, a knowledge of risk factors, patterning, and prevalence in this and other underrepresented groups may help tailor the treatment and outcomes, while affording associated patients a better understanding of the anomaly (Carter & Worthington, 2015; Rakhshan, 2015). Results of interest to anthropologists about spatiotemporal variation might also be useful to clinicians in diagnosis and treatment, through an expanded baseline of how agenesis changed through time and is influenced not only by genetics, environment, and skeletal morphology, but by culture(s) (Forna, 2019). Like a prior sub-Saharan study by the author on hyperdontia (Irish, 2022), which included the same dentitions here, data are divided geographically into regional samples, i.e., West, Central, East, and South Africa, as well as between the sexes. A temporal element is also integrated, with data from premodern archaeological remains to discern change, if any. Given this content, a couple research questions may be addressed along the way. First, will the global trend for an increase in agenesis from premodern to modern times be evident here as well? And second, hyperdontia is common among sub-Saharan Africans relative to other global populations (Irish, 2022), so does it follow that its antithesis, agenesis, is less common?

2. Materials and methods

The presence or absence of UI2, LI1, UP2, LP2, UM3, and LM3 was

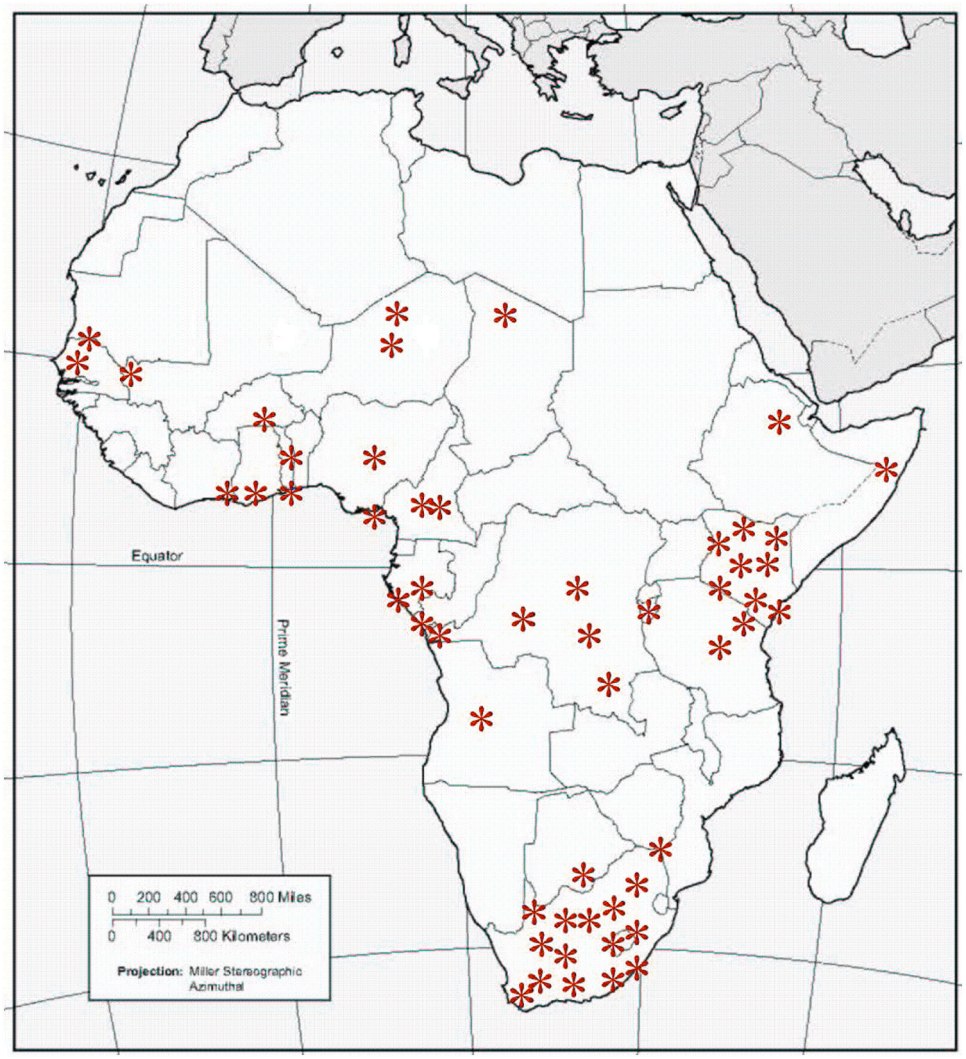

Fig. 1. General distribution of the 52 sub-Saharan African samples used in the present study. See text and Supplementary data (Table S1) for details. Africa map from Arizona Geographic Alliance, Arizona State University, Terry Dorschied.

recorded previously for research about late Pleistocene through recent sub-Saharan dentitions with the ASUDAS to estimate biological affinities (Irish, 1997, 2013, 2016, Irish et al., 2014; etc.). Individuals of various ages totalling ~3000 were included, contingent on the presence of at least one permanent tooth. However, like the hyperdontia study (Irish, 2022) only adults are included, as based on curation records, fusion of the basilar suture, and M3 presence—which allowed its agenesis recording. To maximize sample sizes, individuals with a minimum of one quadrant in both the maxilla and mandible, matched to sample, were included. This provided 2162 dentitions in 52 discrete samples, based on provenience, ethnic, and/or linguistic identity (detailed in above references), from 20 sub-Saharan countries (Fig. 1; Supplementary data, Table S1). Fifty of these 52 samples consist of skeletal dentitions, and two comprise crania and a few hardstone casts. Individual sex was determined using diagnostic skeletal traits (Buikstra & Ubelaker, 1994) or curation records for categories of "male" or "male?" with 1132 individuals, "female" or "female?" with 706 individuals, and 324 with indeterminate sex.

Retained deciduous teeth are obvious indicators in recording agenesis. Otherwise, an important caveat in this study is that the data collection was not or, indeed, could not be done with the aid of radiography. This could affect true prevalence, as an impacted tooth could be recorded erroneously as agenetic. Fortunately, partially impacted teeth remain visible in skeletal remains, although a fully impacted tooth might be missed. Antemortem loss, including intentional incisor evulsion once common (Irish, 2017) and still practiced by some sub-Saharan groups (Friedling, 2017; Asefa, 2022), may also be an issue. However, to a well trained observer it can be identified by evidence of: 1) a remnant alveolus or alveolar remodelling, 2) occlusal wear on what would be the isomere of the missing tooth, and 3) wear and signs of caries on the interproximal surface of the adjacent tooth. In any event, when in doubt agenesis was just not recorded. Thus, while these rates could be considered minimum values, they should at least provide useful approximations.

The 52 samples were then split into two temporal categories. The first consists of 37 'modern' samples with 1688 dentitions from the 19th and 20th centuries; 34 have known provenience, and three miscellaneous samples comprise individuals from different locations in western, eastern, and southern Africa, (Table S1). Of these, 1002 are male/male?, 543 are female/female?, and 123 are indeterminate. Second, 12 'premodern' samples account for 494 dentitions. Most, 482, date from 10,800 BCE to ca. AD 1500. A few from South Africa date as recently as the 1700 s, which is too early to be considered modern here; they are listed as premodern to boost numbers for statistical purposes. The dates are from curation records or other sources in Irish (1997, 2013, 2016) and Irish et al. (2014). For uniformity, premodern dates are listed below in BP (before present), approximate to 'years ago' (refer to Table 6 for details). Regarding sex determinations, the male/male? category has 130 individuals, female/female? 163, and 201 are unknown. It should be noted that while the same material from the earlier sub-Saharan hyperdontia study (Irish, 2022) is examined these numbers do not match, because one sample and 242 individuals could be added here that had not been recorded for extra teeth.

Finally, the relative rarity of agenesis prompted pooling (after Irish, 2022) of the 52 total samples into the abovementioned regional samples, i.e., West, Central, East, and South Africa, for both the modern and premodern periods (again see Table S1). Doing so also greatly enhanced sample sizes across this expansive geographic area, while countering the issue of small, potentially nonrepresentative samples said to adversely affect many studies (per Polder et al., 2004). Moreover, a Poisson model was applied to yield 95% confidence intervals (CI), within which the true prevalence should be contained (Rothman et al., 2008). Chi-square tests of independence, using Yate's correction for any expected cells of ≤ 5, were calculated to test if prevalence differed significantly between regions and sexes. Numbers and patterning of agenetic teeth for each affected individual are also tabulated.

3. Results

Prevalence is listed first for those concerned with clinical agenesis (hypodontia), excluding the third molars, and second for third molars only—of interest to anthropologists among others. More specialized output (as above) is largely summarized, but can be interpolated to yield additional detail, as needed, from the data tables by interested readers.

3.1. Modern regional samples

Agenesis of the UI2, LI1, UP2, and/or LP2 (from now on UI2-LP2) was recorded in 38 of the 1668 dentitions, for a prevalence of 2.3% with a 95% CI of 1.6–3.1% (Table 1). Results within each geographic region are: seven of 301 in the West, for 2.3% (CI 0.9–4.8%); five of 235 in Central Africa, 2.1% (CI 0.5–5.0%); 11 of 358 in the East, 3.1% (CI 1.5–5.5%); and 15 of 774 in the South, 1.9% (CI 1.1–3.2%). None of these results differ significantly (χ^2 contingency tables in Table S2). With regard to F:M ratios, it is 1.63:1 overall, 1.79:1 for the West, 1.83:1 for the East, and 2.64:1 for the South. None of these differ significantly (Table S2). Neither ratio nor chi-square can be determined for the Central region given its 0.0% for female agenesis.

The prevalence of UM3 and LM3 (from now on M3) agenesis (Table 2) is based on 31 fewer cases totalling 1637 individuals; this results from incomplete dental arches, among other factors. Of these, 114, or 7.0%, were found to have agenesis of at one least tooth, for a 95% CI of 5.7–8.4%. By region it is: 17 of 295 in West Africa, 5.8% (CI 3.4–9.2%); nine of 230 in Central, 3.9% (CI 1.8–7.4%); 29 of 353 in the East, 8.2% (CI 5.5–11.8%); and 59 of 759 in the South, 7.8% (CI 5.9–10.0%). Comparing interregional rates, Central vs. East ($\chi^2 = 4.23$; 1 df; $p = 0.039$) and Central vs. South ($\chi^2 = 4.11$; 1 df; $p = 0.042$) differ significantly. Regarding sex, a significant difference only exists in the West ($\chi^2 = 6.00$; 1 df; $p = 0.014$). These and other chi-square results are again presented in Table S2. The F:M ratios are 1.14:1 overall, 3.84:1 for West, 2.64:1 Central, 1.11:1 East, and an opposing 0.75:1 for the South.

All modern individuals with agenesis are identified in Table 3 by region and sex, with the sample code, name, and ID number. This sample information is relevant to the ASUDAS studies cited previously, which provide detailed background (also Table S1). Data on which teeth are absent, their total number, isomere, antimere, and whether uni- or bilateral are tabulated. Again, results are, or can be separated by sex, region, and overall to address the different interests of clinical, anthropological, and other researchers.

Some UI2-LP2 variation across regions is evident, but focusing on the subcontinent the 38 affected individuals of 1668 total were recorded to have 51 agenetic teeth. Only one has four missing teeth, while the remaining 37 individuals have one or two. The UI2 is most commonly absent ($n = 18$, 35.3%), followed by the LI1 (17, 33.3%), UP2 (10, 19.6%), and LP2 (6, 11.8%). Twenty-eight of the 51 missing teeth (54.9%) were recorded for the maxilla and 23 (45.1%) for the mandible. Ten of the 38 affected individuals, accounting for 22 agenetic teeth, evidence bilateral agenesis (26.3%); the remaining 28 individuals, with 29 agenetic teeth, have unilateral absence (73.7%). This in turn accounts for 30 absent teeth in the left (58.8%) and 21 in the right antimere (41.2%).

Third molar interregional differences are also observable but, again, 114 of 1637 individuals account for 183 agenetic teeth overall. The UM3 is the most affected with 113 teeth recorded (61.7%), compared to 70 for the LM3 (38.3%). Forty-three individuals with a total of 116 agenetic teeth have bilateral absence of the UM3 and/or LM3 (37.7%). Of these 43, five are missing both UM3 and LM3 bilaterally; four more have bilateral LM3 absence and unilateral UM3 absence. Unilateral absence only is evident in the other 71 individuals (62.3%), with a total 67 agenetic teeth. By antimere, it is 88 missing in the left (48.1%) and 95 (51.9%) in the right.

Table 1
Modern regional sub-Saharan African samples and sex-based sub-samples, with numbers of individuals observed (n), those with dental agenesis of UI2, LI1, UP2 and LP2 only (k), percentages of occurrence (%), and Poisson 95% confidence intervals (CI). See text for details.

Region	Countries of origin	Date	Sex	n	k	%	CI 95%
West	Benin, Cameroon, Ghana, Nigeria, Senegal, Togo	19th-20th centuries	Male	157	3	1.9	
			Female	116	4	3.4	
			Unknown	28	0	0.0	
			Total	**301**	**7**	**2.3**	**0.94-4.79**
Central	Chad, Congo, Democratic Republic of the Congo, Gabon, Rwanda	19th-20th centuries	Male	122	4	3.3	
			Female	93	0	0.0	
			Unknown	20	1	5.0	
			Total	**235**	**5**	**2.1**	**0.54-4.97**
East	Ethiopia, Kenya, Somalia, Tanzania	19th-20th centuries	Male	220	5	2.3	
			Female	120	5	4.2	
			Unknown	18	1	5.6	
			Total	**358**	**11**	**3.1**	**1.53-5.50**
South	Botswana, South Africa	19th-20th centuries	Male	503	7	1.4	
			Female	214	8	3.7	
			Unknown	57	0	0.0	
			Total	**774**	**15**	**1.9**	**1.08-3.20**
			Male	1002	19	1.9	
			Female	543	17	3.1	
			Unknown	123	2	1.6	
			Grand Total	**1668**	**38**	**2.3**	**1.61-3.13**

Table 2
Modern regional sub-Saharan African samples and sex-based sub-samples, with numbers of individuals observed (n), those with agenetic UM3s and/or LM3s only (k), percentages of occurrence (%), and Poisson 95% confidence intervals (CI). See text for details.

Region	Countries of origin	Date	Sex	n	k	%	CI 95%
West	Benin, Cameroon, Ghana, Nigeria, Senegal, Togo	19th-20th centuries	Male	153	4	2.5	
			Female	115	11	9.6	
			Unknown	27	2	7.4	
			Total	**295**	**17**	**5.8**	**3.36-9.23**
Central	Chad, Congo, Democratic Republic of the Congo, Gabon, Rwanda	19th-20th centuries	Male	120	3	2.5	
			Female	91	6	6.6	
			Unknown	19	0	0.0	
			Total	**230**	**9**	**3.9**	**1.79-7.43**
East	Ethiopia, Kenya, Somalia, Tanzania	19th-20th centuries	Male	217	18	8.3	
			Female	120	11	9.2	
			Unknown	16	0	0.0	
			Total	**353**	**29**	**8.2**	**5.50-11.80**
South	Botswana, South Africa	19th-20th centuries	Male	493	41	8.3	
			Female	209	13	6.2	
			Unknown	57	5	8.8	
			Total	**759**	**59**	**7.8**	**5.92-10.03**
			Male	983	66	6.7	
			Female	535	41	7.7	
			Unknown	119	7	5.6	
			Grand Total	**1637**	**114**	**7.0**	**5.74-8.37**

3.2. Premodern regional samples

Agenesis of the UI2-LP2 was recorded in three of the 494 premodern individuals, for a rate of 0.6% and CI of 0.1–1.8% (Table 4). All three are from the East region with a total of 139, or 2.2% (CI 0.4–6.3%). Due to the many zeros for region and by sex, F:M ratios and chi-square comparisons could not be calculated.

The prevalence of M3 agenesis (Table 5) in these 494 dentitions is 42, or 8.5% with a CI of 6.1–11.5%. Regionally it is 0 of 13 in the West; six of 96 in Central, 6.3% (CI 2.3–13.6%); eight of 139 in East, 6.5% (2.5–11.4%); and 28 of 246 in South Africa for 11.4% (7.6–16.5%). Excluding the small West sample, no between-region rates differ significantly. The same goes for sex. All chi-square output is provided in Table S3. The F:M ratios, also discounting the West, are 0.75:1 overall, 0.60:1 Central, 1.57:1 East, and 0.66:1 for South Africa.

Premodern individuals having M3 agenesis are identified in Table 6 by region, date, and sex, plus sample code, name, and ID number. Again this information is relevant to the ASUDAS studies that provide additional background (also Table S1). Data on which teeth are absent, the number, isomere, antimere, and whether uni- or bilateral are listed.

With the noted exception of East Africa, UI2-LP2 agenesis is lacking in the two other regions. The UP2 ($n = 2$, bilateral in female) and LP2 ($n = 2$, bilateral in individual of unknown sex) are most agenetic, followed by the UI2 ($n = 1$) in another female. Three missing teeth were

Table 3
Modern sub-Saharan African individuals with missing teeth identified, as summarized in Tables 1–2. Non-highlighted tooth columns identify incisors and premolars, while those in grey list the third molars, to facilitate alternate tooth counts. See text for details.

Region	Sample Code	Sample Name	Ind ID	Sex	Upper (U) and Lower (L) Tooth with Side Affected: Right (R), Left= (L), Both (B)						Total Absent	Total Absent
					UI2	UP2	UM3	LI1	LP2	LM3	*UI2-LP2*	*M3 only*
West	MSW	Miscellaneous West Africa	39	M				B			2	0
	NIC	Nigeria and Cameroon	10	M			B					2
	SEN	Senegal and Gambia	18	M			L					1
	SEN	Senegal and Gambia	26	M		B					2	0
	TUK	Tukulor from Senegal	14	M						B		2
	YOR	Yoruba from Benin	11	M	L						1	0
	YOR	Yoruba from Benin	23	M			B					2
	IBO	Ibo from Nigeria	36	F	L		B				1	2
	MSW	Miscellaneous West Africa	40	F						B		2
	MSW	Miscellaneous West Africa	41	F					R	R	1	1
	NIC	Nigeria and Cameroon	28	F				L			1	0
	SEN	Senegal and Gambia	9	F						B		2
	SEN	Senegal and Gambia	15	F			R					1
	SEN	Senegal and Gambia	28	F			R					1
	SEN	Senegal and Gambia	38	F			R					1
	SEN	Senegal and Gambia	39	F			R					1
	TUK	Tukulor from Senegal	15	F			R					1
	TUK	Tukulor from Senegal	18	F			B			B		4
	TUK	Tukulor from Senegal	21	F			L					1
	YOR	Yoruba from Benin	3	F	L						1	0
	GHA	Ghana	42	?			L					1
	TUK	Tukulor from Senegal	37	?			L					1
			Total Absent		**3**	**2**	**17**	**3**	**1**	**9**	**9**	**26**
Central	CHA	Chad	7	M		L		R			2	0
	CON	Congo	25	M		R					1	0
	DCB	Democratic Rep Congo Bas	4	M		L					1	0
	FVR	Fernand Vaz River, Gabon	42	M			R					1
	GAB	Gabon	1	M						B		2
	PYG	Democratic Rep Congo Pygmy	30	M	B					B	2	2
	DCB	Democratic Rep Congo Bas	27	F						L		1
	DCH	Democratic Rep Congo Haut	4	F						B		2
	DCH	Democratic Rep Congo Haut	16	F			B					2
	DCR	Democratic Rep Congo/Ruanda	9	F			R					1
	DCR	Democratic Rep Congo/Ruanda	44	F			R					1
	FVR	Fernand Vaz River, Gabon	18	F						B		2
	CON	Congo	22	?	L						1	0
			Total Absent		**3**	**3**	**5**	**1**		**9**	**7**	**14**
East	ETH	Ethiopia	5	M			B					2
	HAY	Haya from Tanzania	24	M			B					2
	HAY	Haya from Tanzania	49	M			B					2
	KEN	Kenya	21	M			R					1
	KEN	Kenya	67	M	B						2	0
	KKU	Kikuyu from Kenya	1	M			R					1
	KKU	Kikuyu from Kenya	6	M			B					2
	KKU	Kikuyu from Kenya	12	M						L		1
	KKU	Kikuyu from Kenya	53	M						R		1
	KKU	Kikuyu from Kenya	56	M			R					1
	KKU	Kikuyu from Kenya	59	M	L						1	0
	MSE	Miscellaneous East Africa	16	M						R		1
	SOM	Somalia	18	M			L			B		3
	SOM	Somalia	30	M						R		1
	SOM	Somalia	31	M			L					1
	SOM	Somalia	37	M						B		2
	SOM	Somalia	39	M						B		2
	SOM	Somalia	55	M		B			B		4	0
	TAN	Tanzania	22	M			B					2
	TAN	Tanzania	30	M	B						2	0
	TAN	Tanzania	41	M	L						1	0
	TEI	Teita from Kenya	1	M			L					1
	TEI	Teita from Kenya	3	M			R			B		3
	TEI	Teita from Kenya	17	M			L					1
	ETH	Ethiopia	22	F			B					2
	ETH	Ethiopia	23	F				L		B	1	2
	HAY	Haya from Tanzania	22	F			L					1
	HAY	Haya from Tanzania	39	F			B					2
	KEN	Kenya	33	F					L		1	0
	KEN	Kenya	34	F	B						2	0

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Table 3 (*continued*)

Region	Sample Code	Sample Name	Ind ID	Sex	Upper (U) and Lower (L) Tooth with Side Affected: Right (R), Left= (L), Both (B)										Total Absent	Total Absent
	KKU	Kikuyu from Kenya	58	F				B								2
	NLT	Nilotic peoples from Kenya	17	F				L								1
	NLT	Nilotic peoples from Kenya	23	F					B						2	0
	SOM	Somalia	27	F				L								1
	TAN	Tanzania	16	F				R						L		2
	TEI	Teita from Kenya	19	F				L								1
	TEI	Teita from Kenya	46	F					B						2	0
	TEI	Teita from Kenya	47	F				R								1
	TEI	Teita from Kenya	48	F				L								1
	ETH	Ethiopia	1	?			B								2	0
			Total Absent		**8**	**4**		**31**	**5**	**3**		**15**			**20**	**46**
South	KAK	Kakamas Khoekhoe from South Africa	5	M										R		1
	KAK	Kakamas Khoekhoe from South Africa	15	M										L		1
	KAK	Kakamas Khoekhoe from South Africa	37	M				B						B		4
	KAR	Kareeboom (Khoekhoe), South Africa	8	M										B		2
	KAR	Kareeboom (Khoekhoe), South Africa	14	M				R								1
	KAR	Kareeboom (Khoekhoe), South Africa	20	M				L								1
	KHO	Khoekhoe from South Africa	33	M				R				R			1	1
	KHO	Khoekhoe from South Africa	34	M				R								1
	KHO	Khoekhoe from South Africa	52	M				B								2
	MSS	Miscellaneous South Africans	6	M										L		1
	MSS	Miscellaneous South Africans	24	M				B								2
	MSS	Miscellaneous South Africans	28	M	L										1	0
	NDB	Ndebele from South Africa	12	M										L		1
	NDB	Ndebele from South Africa	19	M				L								1
	NDB	Ndebele from South Africa	36	M				B						B		4
	NGU	Nguni from South Africa	10	M				R								1
	NGU	Nguni from South Africa	18	M										L		1
	NGU	Nguni from South Africa	20	M										L		1
	NGU	Nguni from South Africa	22	M				L						B		3
	PED	Pedi from South Africa	106	M	R										1	0
	RRI	Riet River (Khoekhoe), South Africa	49	M				B								2
	RRI	Riet River (Khoekhoe), South Africa	70	M										L		1
	SAN	San from Botswana/South Africa	87	M				R								1
	SAN	San from Botswana/South Africa	94	M					L						1	0
	SAN	San from Botswana/South Africa	98	M										R		1
	SOT	Sotho from South Africa	3	M				L								1
	SOT	Sotho from South Africa	17	M				B						B		4
	SOT	Sotho from South Africa	22	M				B								2
	SOT	Sotho from South Africa	29	M										R		1
	SOT	Sotho from South Africa	30	M					L						1	0
	SWZ	Swazi from South Africa	8	M				B								2
	TSW	Tswana from Botswana/South Africa	22	M				R								1
	VEN	Venda from South Africa	1	M				R								1
	VEN	Venda from South Africa	6	M				B								2
	VEN	Venda from South Africa	7	M										B		2
	VEN	Venda from South Africa	24	M				R						L		2
	VEN	Venda from South Africa	26	M				R								1
	VEN	Venda from South Africa	29	M				R								1
	VEN	Venda from South Africa	50	M				L								1
	XOS	Xhosa from South Africa	4	M				L								1
	XOS	Xhosa from South Africa	27	M	L										1	0
	XOS	Xhosa from South Africa	58	M				L								1
	ZUL	Zulu from South Africa	20	M				B								2
	ZUL	Zulu from South Africa	21	M				R								1
	ZUL	Zulu from South Africa	38	M										R		1
	ZUL	Zulu from South Africa	54	M				R								1
	ZUL	Zulu from South Africa	59	M					L						1	0
	KAK	Kakamas Khoekhoe from South Africa	55	F			L								1	0
	KAK	Kakamas Khoekhoe from South Africa	69	F				R						R		2
	KAR	Kareeboom (Khoekhoe), South Africa	25	F				B								2
	MSS	Miscellaneous South Africa	37	F				B								2
	MSS	Miscellaneous South Africa	49	F										B		2
	SAN	San from Botswana/South Africa	18	F					R						1	0
	SAN	San from Botswana/South Africa	25	F										B		2
	SAN	San from Botswana/South Africa	46	F					R						1	0
	SAN	San from Botswana/South Africa	92	F				B								2
	SAN	San from Botswana/South Africa	105	F								R			1	0
	SWZ	Swazi from South Africa	51	F	L										1	0
	TSW	Tswana from Botswana/South Africa	5	F				R								1
	TSW	Tswana from Botswana/South Africa	24	F										B		2
	TSW	Tswana from Botswana/South Africa	28	F				B								2
	TSW	Tswana from Botswana/South Africa	30	F				R						B		3

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Table 3 (*continued*)

Region	Sample Code	Sample Name	Ind ID	Sex	Upper (U) and Lower (L) Tooth with Side Affected: Right (R), Left= (L), Both (B)	Total Absent	Total Absent
	TSW	Tswana from Botswana/South Africa	58	F	L	1	0
	TSW	Tswana from Botswana/South Africa	59	F	R	1	0
	XOS	Xhosa from South Africa	10	F	R		1
	XOS	Xhosa from South Africa	15	F	B		4
	ZUL	Zulu from South Africa	56	F	R	1	0
	ZUL	Zulu from South Africa	61	F	L		1
	KAK	Kakamas Khoekhoe from South Africa	17	?	B		2
	KAK	Kakamas Khoekhoe from South Africa	64	?	L		1
	RRI	Riet River (Khoekhoe), South Africa	34	?	B		2
	RRI	Riet River (Khoekhoe), South Africa	55	?	B		2
	SAN	San from Botswana/South Africa	49	?	B		2
			Total Absent		**4 1 60 8 2 37**	**15**	**97**
					UI2 UP2 UM3 LI1 LP2 LM3	***UI2-LP2***	***M3 only***
			Grand Total		**18 10 113 17 6 70**	**51**	**183**

Table 4
Premodern regional sub-Saharan African samples and sex-based sub-samples, with numbers of individuals observed (n), those with dental agenesis of UI2, LI1, UP2 and LP2 only (k), percentages of occurrence (%), and Poisson 95% confidence intervals (CI). See text for details.

Region	Countries of origin	Date	Sex	n	k	%	CI 95%
West	Burkina Faso, Cameroon	5879 BC-AD 1390	Male	1	0	0.0	
			Female	2	0	0.0	
			Unknown	10	0	0.0	
			Total	**13**	**0**	**0.0**	**NA**
Central	Democratic Republic of the Congo, Niger	7700 BC-AD 1400	Male	21	0	0.0	
			Female	35	0	0.0	
			Unknown	40	0	0.0	
			Total	**96**	**0**	**0.0**	**NA**
East	Kenya	8100 BC-AD 1350	Male	26	0	0.0	
			Female	33	2	6.1	
			Unknown	80	1	1.3	
			Total	**139**	**3**	**2.2**	**0.44-6.31**
South	South Africa	10 880 BC-AD 1780	Male	82	0	0.0	
			Female	93	0	0.0	
			Unknown	71	0	0.0	
			Total	**246**	**0**	**0.0**	**NA**
			Male	130	0	0.0	
			Female	163	2	1.2	
			Unknown	201	1	0.5	
			Grand Total	**494**	**3**	**0.6**	**0.13-1.77**

Table 5
Premodern regional sub-Saharan African samples and sex-based sub-samples, with numbers of individuals observed (n), those with agenetic UM3s and/or LM3s only (k), percentages of occurrence (%), and Poisson 95% confidence intervals (CI). See text for details.

Region	Countries of origin	Date	Sex	n	k	%	CI 95%
West	Burkina Faso, Cameroon	5879 BC-AD 1390	Male	1	0	0.0	
			Female	2	0	0.0	
			Unknown	10	0	0.0	
			Total	**13**	**0**	**0.0**	**NA**
Central	Democratic Republic of the Congo, Niger	7700 BC-AD 1400	Male	21	2	9.5	
			Female	35	2	5.7	
			Unknown	40	2	5.0	
			Total	**96**	**6**	**6.3**	**2.29-13.60**
East	Kenya	8100 BC-AD 1350	Male	26	2	7.7	
			Female	33	4	12.1	
			Unknown	80	2	2.5	
			Total	**139**	**8**	**5.8**	**2.48-11.37**
South	South Africa	10 880 BC-AD 1780	Male	82	12	14.6	
			Female	93	9	9.7	
			Unknown	71	7	9.9	
			Total	**246**	**28**	**11.4**	**7.56-16.45**
			Male	130	16	12.3	
			Female	163	15	9.2	
			Unknown	201	11	5.5	
			Grand Total	**494**	**42**	**8.5**	**6.13-11.49**

recorded in the maxilla and two in the mandible. Two individuals date to the Early Holocene, > 7400 years ago (BP), with one of a Late Holocene age, 3000–1000 BP (Table 6).

For M3 agenesis some interregional differences can be seen, but at the subcontinent level 42 of the 494 individuals have 71 agenetic teeth. The UM3 is missing 35 times (49.3%) relative to 36 for the LM3 (50.7%), meaning that isomere prevalence is equivalent (Table 6). Twenty-one individuals (50.0%), with 50 agenetic teeth, are missing bilaterally the UM3 and/or LM3. Of these 21, two individuals have bilateral absence of the UM3 and LM3. Two have bilateral absence of the UM3, plus unilateral absence of the LM3. Two more have an opposite pattern—bilateral LM3, plus unilateral UM3 absence. Unilateral absence is evident in the other 21 individuals (50.0%) with 21 agenetic teeth. Together, it is 31 missing teeth in the left (43.7%) and 40 (56.3%) in the right antimere. The date range of these individuals is perhaps > 12,000 BP, and definitely > 8000 BP, to ~200 BP (details below).

Table 6
Premodern sub-Saharan African individuals with missing teeth identified, as summarized in Tables 3–4. Non-highlighted tooth columns identify upper and lower incisors and premolars only. Those in grey include the upper and lower third molars to provide alternate tooth counts. See text for details.

Region	Sample Code	Sample Name	Ind ID	Date of Individual[a]	Sex	Upper (U) and Lower (L) Tooth with Side Affected: Right (R), Left= (L), Both (B)						Total Absent	Total Absent
						UI2	UP2	UM3	LI1	LP2	LM3	*UI2-LP2*	*M3 only*
Central	DBI	Democratic Rep Congo Bas Iron Age	3	2150-950 BP	M						R		1
	UPB	Democratic Rep Congo Upemba Valley	39	1650-600 BP	M			R			B		3
	UPB	Democratic Rep Congo Upemba Valley	34	1650-600 BP	F			R					1
	GOT	Mali Gobero Tenerian	28	6800-4500 BP	F			B			R		3
	UPB	Democratic Rep Congo Upemba Valley	1	1650-600 BP	?						R		1
	UPB	Democratic Rep Congo Upemba Valley	8	1650-600 BP	?						R		1
				Total Absent				**4**			**6**	**0**	**10**
East	KHE	Kenya Early Holocene	64	10000-8000 BP	M						R		1
	KHE	Kenya Early Holocene	69	10000-8000 BP	M						B		2
	KHE	Kenya Early Holocene	8	7410 + /- 160 BP	F		B					2	0
	KHL	Kenya Late Holocene	21	~3000 BP	F						L		1
	KHL	Kenya Late Holocene	52	~3000 BP	F						R		1
	KHL	Kenya Late Holocene	61	3000-1000 BP	F			R					1
	KHL	Kenya Late Holocene	66	3000-1000 BP	F	L					B	1	2
	KHE	Kenya Early Holocene	3	9000-8000 BP	?						R		1
	KHE	Kenya Early Holocene	34	8000-6000 BP	?						L		1
	KHE	Kenya Early Holocene	71	10000-8000 BP	?					B		2	0
				Total Absent		**1**	**2**	**1**		**2**	**9**	**5**	**10**
South	MAT	South Africa Matjes River	26	12800-2000 BP	M			B			L		3
	MAT	South Africa Matjes River	29	12800-2000 BP	M			R					1
	MAT	South Africa Matjes River	45	12800-2000 BP	M						B		2
	SHE	South Africa Early Holocene	38	6891 + /- 37 BP	M						R		1
	SHL	South Africa Late Holocene	53	~1400 BP	M			B					2
	SHL	South Africa Late Holocene	68	2195 + /- 80 BP	M						B		2
	SHL	South Africa Late Holocene	83	2100 or 620 BP	M						R		1
	SHL	South Africa Late Holocene	92	207 + /- 25 BP	M			B					2
	SHMe	South Africa Middle Holocene (East)	50	~2200 BP	M			R					1
	SHMw	South Africa Middle Holocene (West)	15	2880 + /- 50 BP	M			B					2
	SHMw	South Africa Middle Holocene (West)	19	2580 + /- 40 BP	M			B			B		4
	SHMw	South Africa Middle Holocene (West)	81	2920 + /- 60 BP	M			B					2
	MAT	South Africa Matjes River	49	12800-2000 BP	F						R		1
	SHE	South Africa Early Holocene	12	9000-4000 BP	F			B					2
	SHE	South Africa Early Holocene	20	4120 + /- 60 BP	F			B					2
	SHL	South Africa Late Holocene	37	1364 + /- 32 BP	F						B		2
	SHMe	South Africa Middle Holocene (East)	1	2590 + /- 60 BP	F			L					1
	SHMe	South Africa Middle Holocene (East)	26	2145 + /- 40 BP	F			L					1
	SHMw	South Africa Middle Holocene (West)	46	2304 + /- 29 BP	F			B			B		4
	SHMw	South Africa Middle Holocene (West)	65	3363 + /- 34 BP	F			B					2
	SHMw	South Africa Middle Holocene (West)	80	2660 + /- 70 BP	F			B					2
	MAT	South Africa Matjes River	50	12800-2000 BP	?						B		2
	SHE	South Africa Early Holocene	42	5680 + /- 70 BP	?						B		2
	SHL	South Africa Late Holocene	63	~1400 BP?	?						L		1
	SHL	South Africa Late Holocene	84	1880-1580 BP	?			L					1
	SHL	South Africa Late Holocene	91	370-207 BP	?			R					1
	SHMe	South Africa Middle Holocene (East)	98	> 2100 BP	?			L					1
	SHMw	South Africa Middle Holocene (West)	77	2560 + /- 50 BP	?			R			B		3
				Total Absent				**30**			**21**	**0**	**51**
						UI2	**UP2**	**UM3**	**LI1**	**LP2**	**LM3**	***UI2-LP2***	***M3 only***
				Grand Total		**1**	**2**	**35**		**2**	**36**	**5**	**71**

[a] BP date indicates the number of years 'before present,' which by radiocarbon dating convention is considered the year AD 1950.

3.3. Modern and premodern comparisons

A major increase in UI2-LP2 agenesis is patent between premodern and modern categories (Tables 1 and 4), but a lack of affected individuals in the former dissuades quantifying the difference. In opposition, with evident interregional variation M3 agenesis overall decreases from 8.9% to 7.0%, though this difference is not significant (Table S4). A reversal in F:M ratios of 0.80:1 to 1.14:1 is also seen, but only the difference between premodern and modern males is significant ($\chi^2 = 5.26$; 1 df; $p = 0.022$; Table S4).

4. Discussion

4.1. Modern regional samples

The 2.3% prevalence of UI2-LP2 agenesis among 1668 individuals is at the low end of most global ranges, and below that of two others (Akram et al., 2011; Amini et al., 2012; Duke et al., 2023; Khalaf et al., 2014; Ng'ang'a & Ng'ang'a, 2001; Pindborg, 1970; Polder et al., 2004; Sadaqah & Tair, 2015; Vastardis, 2000). The lack of x-rays could be a contributing factor, but other than the outlier Tunisian sample (13.4%; Maatouk et al., 2008) used by some authors to represent Africa, none of these studies include sub-Saharan African data to challenge the present result. In reality, 2.3% fits in the proffered 0.0–12.6% global range based on these and other case reports, with several from the African subcontinent. To review, the latter, all of which utilized radiography, include from west to east 0.0% and 0.4% in Nigeria (Adeniji, 1993; Temilola et al., 2014), 2.7% and 5.1% in Sudan (Affan & Serour, 2014; Hassan et al., 2014), and 6.3% in Kenya (Ng'ang'a & Ng'ang'a, 2001). The four regional rates parallel these reports, with 2.3% in West, 2.1% in Central, and 3.1% in East Africa, before falling to 1.9% in the South (Table 1). Because none differ significantly (Table S2) and are not widely divergent from other global results, it is not unreasonable to advocate 2.3% as representative of sub-Saharan Africans for clinical and other comparative research.

The same goes for F:M ratios of UI2-LP2 agenesis. The overall 1.63:1 ratio compares with the global 1.5:1 (Duke et al., 2023; Rakhshan, 2015; Sadaqah & Tair, 2015). Regional variation from 2.64:1 in East Africa to the complete absence in Central region females (Table 1) is also not immeasurably different from other groups, 2:1 to 0.7:1 (Amini et al., 2012). Again, F:M ratios in cited sub-Saharan reports vary as well, trending toward a male bias: 1:1 in Nigeria (Temilola et al., 2014) and 0.7:1 in Kenya (Ng'ang'a & Ng'ang'a, 2001).

For M3 agenesis the total sub-Saharan prevalence of 7.0% is, again, lower than one purported global range of ~10.0–35.0% (Pindborg, 1970) and overall prevalence of ~20.0% (Vastardis, 2000). However, it does fit in the 5.3–56.0% from a global meta-analysis (Carter & Worthington, 2015) and, more importantly, that gleaned from case reports: 0.0% in West Africans (Hellman, 1928), 1.9% in Kenyans (Chagula, 1960), and 7.3–9.2% in South African males (Esan & Schepartz, 2017). Other than the East (8.2%), regional rates (Table 2) are not too dissimilar from these findings, i.e., high in in the South (7.8%) vs. low in the West (5.8%) and particularly the Central (3.9%) regions. The latter does differ significantly from the East and South (Table S2), but 7.0% is arguably not unreasonable as a general estimate for the subcontinent's inhabitants, as above. Similarly, while the West evidences an extreme F:M ratio of 3.84:1 with a significant difference between the sexes (Table S2), and the South has a contrary 0.75:1, the overall female partiality in M3 agenesis compared to males across all regions (1.14:1) is akin to other referenced results (Carter & Worthington, 2015; Harris, 2009; Heuck Henriksson et al., 2019).

Finally, at the individual level M3s are most agenetic (Table 3), as they are globally. The UI2 is second most common, at 35.3% of 51 total agenetic UI1-LP2 teeth (Table 3), like some (Affan & Serour, 2014) including Africa (Sofaer, 1975), but not all; in most the LP2 is the second most affected (Khalaf et al., 2014; Ng'ang'a & Ng'ang'a, 2001; Polder et al., 2004; Sajjad et al., 2016). Also distinctive is the high incidence of LI1 agenesis—33.3% of 51 teeth, followed by the UP2 at 19.6%, and LP2 at just 11.8% (Table 3). That said, no individuals have more than four teeth missing, which fits the clinical definition of hypodontia (Akram et al., 2011; Duke et al., 2023; Farcaşiu et al., 2022; Kabli et al., 2022). The proclivity for the maxilla over mandible in UI2-LP2 agenesis (54.9% vs. 45.1%) and, particularly the M3 (62.3% vs. 38.3%), differs from several studies (Affan & Serour, 2014; Heuck Henriksson et al., 2019), but is not exceptional (Amini et al., 2012). That follows for other pattern deviations, such as sidedness. Here unilateral agenesis is dominant contra many examples for bilaterally (above). Yet antimere involvement is seemingly dependent on the teeth (e.g., Harris, 2009). For UI2-LP2 agenesis the left is favoured (58.8%), but for the M3 it is the right (51.9%).

4.2. Premodern regional samples

As stated, the principal reason for including the premodern data is to explore diachronic change. That said, ostensibly like other premodern peoples (although based on a dearth of publications), agenesis of the UI2-LP2 minimally affects the present dentitions (see Table 4), Thus, with the exception of three individuals from the East region, two of which date > 7400 BP, it appears to be mostly a modern issue (Table 6).

Conversely, M3s are agenetic at a higher rate, 8.5%, than in the modern sub-Saharan Africans. Dismissing the small West sample, the premodern prevalence runs from 6.3% to a maximum of 11.4% in the South (Table 5). Though these differences are not significant, the latter relatively high percentage may be attributable to the sample, which consists entirely of Holocene foragers deemed ancestors of modern Khoesan (Irish et al., 2014). Khoekhoe and San have long been known to differ craniodentally from other sub-Saharan Africans including, contra the latter, minimal prognathism with a concomitant reduction in arch size (Schepers, 1934; Hiernaux, 1975; Nurse et al., 1985). This reduction, whether determined by genetics (as above), the environment, or otherwise, is associated with dental agenesis (review Duke et al., 2023). This might be supported by the high modern rate (7.8%) from the South, which contains a sizable number of Khoekhoe, San, and Khoesan admixed peoples (Table S1).

In any event, by way of comparison the overall M3 agenesis prevalence is greater than in Japan > 2000 BP (4.1%; Yamada et al., 2004) and Byzantine Anatolia (7.2%; Arıhan & Türkekul, 2021), but lower than the Canary Islands (8.7–14.6%; De Castro, 1989), Late Pleistocene Europe (14.3%; Lacy, 2021), Neolithic Anatolia (16.3%; Ozbek & Özbek & Erdal, 2003), medieval Norway (27.7%; Heuck Henriksson et al., 2019), and post-medieval England (42.7%; Caldwell, 2021). Not all of these studies provide directly comparable data; however, the sub-Saharan F:M ratio of 0.75:1 for M3 agenesis is seemingly atypical, in that those reporting differences by sex generally find it more in females, including 1.4:1 interpolated from the Norwegians (Heuck Henriksson et al., 2019).

Finally, dental agenesis is recorded in individuals dating to perhaps as long ago as 10,000 BP in Kenya, up to 12,800 BP in South Africa, but definitely before 8000 BP (Table 6). Older documented cases, at least for M3 agenesis, are known elsewhere including Europe (Lacy, 2021; above) and perhaps Japan, with a potential range of > 2000–12,500 ± BP (Yamada et al., 2004; above), among others. However, until determined otherwise, the female from the East region, i.e., Kenya (KHE 8; 7410 ± 160 BP) putatively provides the oldest evidence of UP2 agenesis, and the individual of indeterminate sex from Kenya (KHE 71; >8000 BP), the oldest for the LP2 (Table 6).

4.3. Temporal change and other considerations

Prior studies indicating greater prevalence of dental agenesis through time are supported by the increase of 0.6% to 2.3% for UI2-LP2 and, likely more representative, 2.2% to 3.1% for East Africa. On the

other hand, while two regional rates do increase (Tables 2 and 5), M3 agenesis decreases slightly between premodern and modern categories. Perhaps agenesis of UI2-LP2 and M3 is not unequivocally connected or, as stated, it may come down to the sample composition. Nevertheless, to address the first research question stated at the outset, i.e., whether the widespread diachronic increase worldwide also occurred within Africa, there is no straightforward answer from the present findings.

In any event, all modern agenesis rates are relatively low; perhaps they result from extra arch space via alveolar prognathism reported at high frequencies in non-Khoesan (Hiernaux, 1975; Nurse et al., 1985), especially for the M3. These rates may also identify a key population difference as established with other highly genetic ASUDAS traits (Irish, 1997, 2013). Similarly distinctive is the patterning of agenesis. The M3 is most affected in both the premodern and modern categories. However, the second most agenetic is not the LP2 like most global populations; in fact, it is least affected (Table 3). Further, the LI1 is the third most agenetic here, but least elsewhere (Khalaf et al., 2014; Ng'ang'a & Ng'ang'a, 2001; Polder et al., 2004; Sajjad et al., 2016). Lastly hyperdontia, which also has an apparent genetic component, may be included in this population distinction. As stated, it is relatively common, 3.1% overall, with a decrease in prevalence across the subcontinent: West (4.6%) and Central (6.8%) vs. East (2.6%) and South (1.5%) (Irish, 2022). This is basically the opposite spatial trend for modern M3 agenesis—in the same West (5.8%) and Central (3.9%) regions vs. East (8.2%) and South (7.8%). Along these lines, none of the 44 modern nor four premodern individuals exhibiting hyperdontia have dental agenesis. So in this instance, there does appear to be a negative association between the two anomalies in answer to the second research question.

Finally, several other diachronic tendencies are evident between the premodern and modern samples for M3 agenesis. First, isomere involvement shifted from approximate equivalence to 62.3% in the maxilla. However, whether this change is of any importance is not clear given the marked variation worldwide, from roughly the same (Ng'ang'a & Ng'ang'a, 2001; Polder et al., 2004; Sajjad et al., 2016), to an inclination for the maxilla (Amini et al., 2012) or the mandible (Affan & Serour, 2014; Heuck Henriksson et al., 2019). Second, bilateral gave way to unilateral partiality at a similar rate to isomere, though left vs. right antimere rates changed little. Again, others have not reported much significance in these trends, and tooth type may be a factor (Harris, 2009; Pindborg, 1970; Polder et al., 2004; Kerekes-Máthé et al., 2023). Lastly, a seemingly atypical reversal in M3 F:M ratios occurred, from 0.80:1 to 1.14:1, but the numerous premodern individuals ($n = 201$) for whom sex is indeterminate may play a role.

5. Conclusion

In sum, this study offers new data concerning UI2, LI1, UP2, LP2, UM3, and LM3 agenesis in sub-Saharan Africa—past and present—by region, sex, and overall. For context, comparisons were made with other world populations, to reveal some notable differences. Of greater import the lack of data is addressed, to help characterize peoples derived from the vast subcontinent and update the range of global prevalence, while promoting future inter-population comparisons. Continuing African research at more specific regional and ethnic levels, using radiography, can provide even better insight as to how and why diachronic change in agenesis occurs, and what form it may take eventually (e.g., increasing UI2-LP2 prevalence) from the influence of genetics, environment, skeletal morphology, other linked conditions, and perhaps culture. Together, these findings will be of general scientific interest, notably to dental anthropologists concerning spatiotemporal variation. Information on risk factors, pattern, and prevalence may assist clinicians in diagnosis, treatment, and outcome, and afford patients of African heritage a better understanding of how this anomaly differs in expression from other populations.

Ethical considerations

These data were collected while the author was affiliated with universities in the US prior to 2012 which, at that time, did not require ethics approval for non-destructive collecting of dental data in human skeletal material or existing hardstone casts from living individuals.

CRediT authorship contribution statement

Joel D. Irish: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The author reports no declarations of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.archoralbio.2024.105961.

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