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Archives of Oral Biology

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Hyperdontia across sub-Saharan Africa: Prevalence, patterning, and implications

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ARTICLE INFO

Keywords: Supplemental teeth Supernumerary teeth Inter-regional variation Temporal variation Sex differences Africa

ABSTRACT

Objective: Hyperdontia data in modern and premodern sub-Saharan Africans are presented by region—West, Central, East, and South, and sex. Beyond describing the anomaly, comparisons are made with other world populations and future work is promoted. These findings may be useful to both dental clinicians and anthropologists.

Methods: Hyperdontia presence and patterning were recorded in 51 samples of skeletal dentitions and hardstone casts (n=1916). Its infrequency prompted regional pooling after grouping by time. Only adults were included to record later forming fourth molars reportedly common in Africans. Quantitative analyses, including 95% confidence intervals, were conducted to characterize spatiotemporally sub-Saharan peoples.

Results: Forty-four of 1429 modern individuals (3.08%) exhibit hyperdontia (CI 2.24–4.13%). Regional variation is significant, particularly West-Central vs. East-South, between 6.8% and 1.5%. Four of 487 premodern individuals, 0.82%, have hyperdontia (0.22–2.10%), with minimal regional differences. Males are most affected, as reported by other researchers. Other similarities with non-African research are evident regarding isomere, antimere, and form, with one key exception—a proclivity for the posterior over anterior maxilla.

Conclusions: 3.08% is toward the upper end of published world ranges, including an oft-cited 0.1–3.6+%. However, the regional variation argues against a single prevalence to describe collectively the subcontinental inhabitants. This variation parallels past west to east and south migrations like other biocultural indicators. Thus, beyond a health concern to clinicians or interesting anomaly to anthropologists, hyperdontia may be useful in other studies. There are no equivalent premodern ranges for comparison. Similarity in patterning overall to previous findings suggests a shared, potentially ancient genetic component in expression.

1. Introduction

Hyperdontia, a.k.a. supernumerary teeth in most clinical works, refers to teeth in excess of the standard human dental formula (Arandi et al., 2020; Garvey et al., 1999; Kwon & Jiang, 2018; Lam, 2017; Wang & Fan, 2011). It is rare, accounting for 1.0–3.0% of dental anomalies (Bello et al., 2019), but can be striking in expression. Multiple teeth may form—although singletons are most common, which may be erupted or impacted, and run the gamut from conical- or tuberculate-shaped to fully formed third incisors, premolars, and fourth molars (Aldred et al., 2013; Bello et al., 2019; Garvey et al., 1999; Giudice et al., 2008; Lam, 2017; Mossaz et al., 2014; Pindborg, 1970; Suljkanovic et al., 2021; Wang & Fan, 2011), at least in the permanent dentition as covered here.

It is said to chiefly involve the maxilla, especially the premaxilla, with one article listing the rate at 98% (Aldred et al., 2013); this tendency is often linked to a conical mesiodens between the upper central incisors (Arandi et al., 2020; Ata-Ali et al., 2014; Garvey et al., 1999; Giudice et al., 2008; Kwon & Jiang, 2018; Lam, 2017; Mossaz et al., 2014; Pindborg, 1970; Suljkanovic et al., 2021; Wang & Fan, 2011), though not all concur (Anibor et al., 2015; Bello et al., 2019; Eshgian et al., 2021; Harris & Clark, 2008). As these and other articles describe, hyperdontia can occur in both arches, all dental fields including canines (Mossaz et al., 2014), and is mostly asymmetrical with no reports of side dominance. Overall prevalence and, to some extent, intra-oral patterning vary by population (see below) and by sex, with male to female ratios of 1.2:1.0–4.5:1.0 (Aldred et al., 2013; Anibor et al., 2015;

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Arandi et al., 2020; Brook, 1984; Eshgian et al., 2021; Garvey et al., 1999; Giudice et al., 2008; Hyun et al., 2008; Kwon & Jiang, 2018; Mossaz et al., 2014; Pindborg, 1970; Prasada Ravo and Chidzonga, 2001; Suljkanovic et al., 2021; Wang & Fan, 2011).

Though long studied (e.g., Tomes, 1873; Bolk, 1914) the developmental process remains obscure. Some have doubts concerning when such teeth form (Khalaf et al., 2018), though the proliferation stage of odontogenesis is likely (Aldred et al., 2013). The aetiology is also debated, with three key theories proposed (reviewed in Arandi et al., 2020; Garvey et al., 1999; Eshgian et al., 2021; Mallineni, 2014; Mossaz et al., 2014; Pindborg, 1970; Wang & Fan, 2011); of these, the most accepted implicates hyperactivity of the dental lamina where, through indefinite means, excess lamina develops to form additional tooth buds (Arandi et al., 2020; Lam, 2017). Despite this uncertainty an important genetic component is indicated. Yet, once again, the degree and candidate gene(s) responsible are not known (Arandi et al., 2020; Brook, 1984; Garvey et al., 1999; Harris & Clark, 2008; Takahashi et al., 2017; Wang & Fan, 2011), at least in cases not linked to systemic diseases or syndromes as studied here (overviews in Aldred et al., 2013; Bello et al., 2019; Bloch-Zupan et al., 2012; Giudice et al., 2008; Kwon & Jiang, 2018; Mallineni, 2014; Pindborg, 1970; Ramakrishna & Rajashekarappa, 2013; Subasioglu et al., 2015; Van der Merwe & Stevn, 2009; Wang & Fan, 2011).

If the number of articles by field reviewed for this report is any indication, it appears that hyperdontia is of greater clinical concern than anthropological. Clinicians view such teeth as a health issue in need of intervention to avoid impaction, displacement, and root resorption of the normal complement (Garvey et al., 1999; Giudice et al., 2008; Mossaz et al., 2014). With exceptions (Rosenzweig and Garbarski, 1965; Suk, 1919; Van der Merwe & Steyn, 2009), anthropologists have focused on prehistoric specimens, seeing hyperdontia as worthy of description, but mostly in conjunction with recording other dental anomalies and pathologies (Gibbon & Grimoud, 2012; Goldstein, 1948; Hooton, 1930; Leigh, 1937; Ruffer, 1920). In any event, articles from both fields largely comprise (a) case studies (Giudice et al., 2008; Phillips et al., 2021; Prasada Ravo & Chidzonga, 2001; Ramakrishna & Rajashekarappa, 2013; Randell, 1925; Suljkanovic et al., 2021; Suzuki et al., 1995; Tomczyk et al., 2020) or, at most, (b) analysis of a sample, some of considerable size (Hyun et al., 2008; Rosenzweig & Garbarski, 1965), but from a single region (Adeyemi et al., 2012; Anibor et al., 2015; Arandi et al., 2020; Bello et al., 2019; Brook, 1984; Eshgian et al., 2021; Gibbon & Grimoud, 2012; Goldstein, 1948; Harris & Clark, 2008; Hooton, 1930; Ize-Iyamu et al., 2016; Leigh, 1937; Ruffer, 1920; Van der Merwe & Steyn, 2009). In most of the latter non-anthropological cases, samples consisted of dental patients visiting their local clinics. Broader research to promote inter-regional and global comparisons is wanting.

At present, literature reviews and their findings in case/intraregional studies are the best comparative sources. Interestingly, many provide markedly similar figures to represent prevalence among world populations, in a range from 0.1 to 3.6 + % (e.g., (Aldred et al., 2013; Bello et al., 2019; Mossaz et al., 2014; Peker et al., 2009; Pindborg, 1970; Van der Merwe & Steyn, 2009). These figures may be traceable to recurrent primary and secondary citations of the same six clinical studies (Lacoste et al., 1962; Lind, 1959; Niswander & Sujaku, 1963; Parry & Iyer, 1961; Rosenzweig & Garbaski, 1965; Stafne, 1932) from Israel (0.1%), the U.S. (1.0%), India (2.5%), France (2.8%), Japan (3.4%), and Sweden (3.6%) (overview in Pindborg, 1970). Some reviews do provide alternate ranges, for example, (a) Mallineni (2014) lists 0.4-6.0%, with the latter percentage in African Americans (from Harris and Clark, 2008), (b) the Arandi et al. (2020) study of 1970 Palestinians (0.86%) mentions 0.04-2.4% based in part on clinical research in Italy (0.9%), Turkey (1.0%), Saudi Arabia (1.0%), Syria (1.2%), and Iran (2.4%), and (c) Lam (2017) presents 1.0-4.0%, while suggesting Asians and Native Americans are more affected, though without supporting evidence.

The current report provides data from sub-Saharan Africans, whose frequencies are largely absent in reviews [though see Mallineni, 2014

mention of a South African sample (from Van der Merwe & Steyn, 2009)]. This is not to say that the subcontinent is completely overlooked, which is often the case with dental anomalies (e.g., Irish, 2020). Indeed, one of the earliest projects to systematically record hyperdontia on a large scale occurred in South Africa, via oral exams of 1008 Zulu subadults (Suk, 1919). Since then research continued, though, as above, only in the form of case and intra-regional studies (Adeyemi et al., 2012; De Villiers, 1968; Randell, 1925; Shaw, 1931; Van der Merwe & Steyn, 2009; Watters, 1962; Gibbon & Grimoud, 2012; Anibor et al., 2015; Ize-Iyamu et al., 2016; Bello et al., 2019).

Here, the whole of the subcontinent is covered. Prevalence and information about the diverse forms hyperdontia can take among modern samples are presented by region—West, Central, East, and South Africa, and between the sexes. A temporal component is also introduced by analysing premodern (archaeological) samples from the same four regions to help explore changes in prevalence and pattern. Not only is spatiotemporal characterization of the peoples from this vast geographic area provided, but comparisons with populations in other world regions can be promoted. Further, these findings may be useful to understand better hyperdontia relative to the specific emphases of clinicians and anthropologists. This includes the present report where, together with other dental indicators, hyperdontia data seemingly reflect early population movements.

2. Materials and methods

The absence, presence, and forms of hyperdontia were recorded routinely in conjunction with a separate project, which entailed estimating population affinities among sub-Saharan Africans (Irish & Guatelli-Steinberg, 2003; Irish, 1993, 1997, 1998, 2010, 2013, 2016a, 2016b; Irish et al., 2018, 2014a, 2014b) from nonmetric traits in the Arizona State University Dental Anthropology System (ASUDAS) (Scott & Irish, 2017; Turner et al., 1991). With a high genetic component in expression, these traits serve as suitable proxies for DNA to assess population relatedness (Irish et al., 2020). Up to 52 samples consisting of 2742 individuals with known ethnicity and/or site origin from 19 countries were included in these affinity analyses. In the present report classification of hyperdontia form follows Tomes (1873), a common approach in dental anthropology where 'supplemental' refers to teeth identifiable to tooth class, and 'supernumerary' indicates atypical forms like tuberculate and conical/peg that are smaller than normal. As stated, clinicians often use 'supernumerary' to describe all teeth in excess of the normal complement, which may lead to confusion in other fields. It is also important to mention that like ASUDAS traits, hyperdontia data were recorded visually—without the benefit of radiographs used in most clinical and a few anthropological studies (e.g., Gibbon & Grimoud, 2012). So, while partially impacted or small supernumerary and supplemental teeth are more likely visible in skeletal dentitions than living individuals, fully impacted teeth such as a mesiodens may not be detected without radiographs. Further, to maximize sample size, specimens with one extant quadrant in each maxilla and mandible matched to sample were included. Thus, prevalence results may be regarded as minimum values.

Before proceeding one premodern sample from Tanzania, comprised only of loose teeth and no supporting structures, was dropped to leave 51 samples (Fig. 1). Of these, only data from adults are included to yield 1916 individuals for analysis. Ageing was based on the presence of the third molar, i.e., 'dentally adult,' based on its near lack of agenesis in sub-Saharan Africans (Irish, 1993, 1997, 2013), along with basilar suture fusion. This strategy is modified from Harris and Clark (Harris & Clark, 2008), who used radiographs of European- and African American dental patients \geq 12 years old "to ensure that all teeth that were going to form, notably third molars, were forming." Here, the study of adults ensured recording of potential late forming fourth molars, which were reported to affect African and African-derived populations to a much greater degree (Eshgian et al., 2021; Harris & Clark, 2008; personal

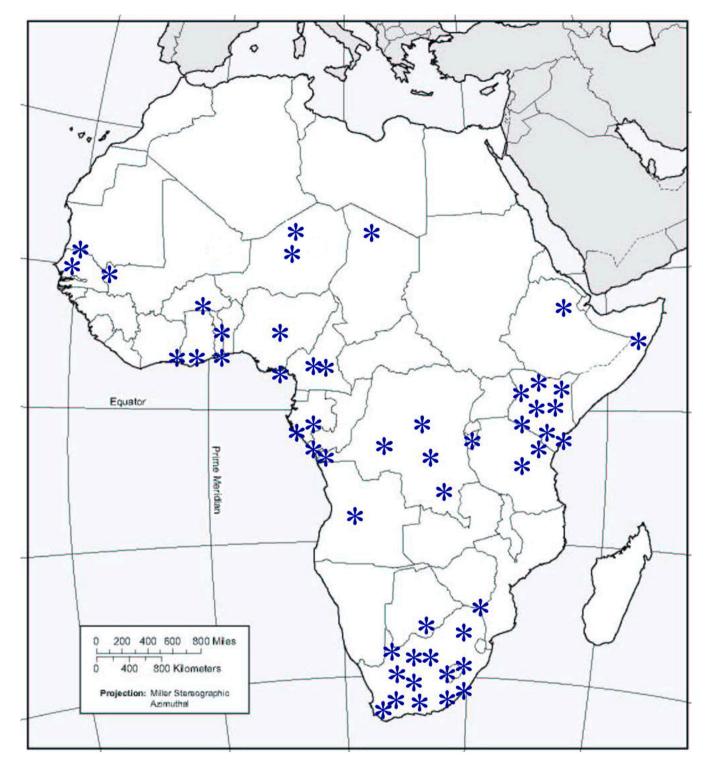


Fig. 1. General distribution of the 51 sub-Saharan African samples used in the present study. See text and Supplementary data (Table S1) for details. Africa map courtesy of Arizona Geographic Alliance, Department of Geography, Arizona State University, Terry Dorschied.

observation by author). Sex determination was based on curation records and/or diagnostic skeletal features (Buikstra & Ubelaker, 1994), to provide categories of "male" or "male?" consisting of 995 individuals, "female" or "female?" with 613 individuals, and 308 of indeterminate sex.

The 51 samples were then subdivided into two categories based on dating. The first, 'modern," here considered 19th to 20th centuries, consists of 36 samples from the affinity studies, plus three 'new' miscellaneous samples of unassociated individuals from various locales

in western, eastern, and southern Africa, totalling 1429 dentitions (Supplementary data, Table S1). Second, the 'premodern' category contains 12 samples with 487 dentitions. Of the latter, 482 date between 10,800 BCE and ca. AD 1500; the remaining five, from South Africa dating as recently as AD 1780, do not meet the definition of modern as defined above so, simply, were designated as premodern to enhance the sample size. These dates come from curation records or sources in Irish (1993, 1997, 2013, 2016b) and Irish et al. (2014a, 2014b). Refer to the tables in the Results section for details on samples and affected

individuals, including ID number, individual sex, countries of origin, cultural affiliations, dating, and curatorial information.

The rarity of hyperdontia prompted pooling of samples assigned to the two temporal periods (after Irish, 2020) to determine modern and premodern prevalence by the four sub-Saharan geographic regions noted above, rather than 36 and 15 percents, respectively, of mostly 0.00%. This rarity, along with sample sizes relative to the vast subcontinental area also encouraged application of a Poisson model to yield 95% confidence intervals (CI), within which the true population prevalence is likely contained (e.g., Rothman et al., 2008). Finally, chi-square tests of independence, using Yate's correction as needed, were calculated to test if frequencies differed significantly between regions and by sex in samples of sufficient size (see below).

3. Results

3.1. The modern samples

Forty-four of the total 1429 modern sub-Saharan individuals, or 3.08%, exhibit at least one supernumerary or supplemental tooth, with a 95% Poisson CI of 2.24–4.13% (Table 1). Inter-regional variation is evident, with 14 of 302 individuals in the West, 4.64% (CI 2.53–7.78%); 11 of 120 in the Central, 6.78% (CI 4.58–16.40%); seven of 266 in the East, 2.63% (CI 1.06–5.42%); and a prevalence of 1.49% based on 12 of 741 in the South (CI 0.84–2.83). Of these, differences between West and South ($\chi^2=8.03$; 1 df; p=0.005), Central and East ($\chi^2=7.94$; 1 df; p=0.005), and Central and South ($\chi^2=19.005$) are significant.

Regarding sex differences, males (n=871) exhibit more hyperdontia than females (n=451) overall, at 3.44% and 2.44%, respectively, for a ratio of 1.41:1. Regionally, variation is again evident (Table 1), with corresponding M:F ratios for West, Central, East, and South of 1.66:1, 1.73:1, 2.60:1, and 0.75:1. However, none of these intra-regional differences are significant at the 0.05 alpha level.

Of the 44 individuals with hyperdontia, 30 were categorized as male, 11 as female, and three of unknown sex; combined, 33 of these 44 have one additional tooth and 11 have two or more, for a total of 61 teeth (see Table 2; some examples in Fig. 2). The most striking expression was recorded in a Zulu male from South Africa (ID SAm3) with seven additional premolars; five of these are in the mandible (Fig. 2e), the most common site for multiple eruption (Scheiner & Sampson, 1997). Otherwise, the maxilla is favoured with 48 teeth vs. 13 in the mandible. Of the maxillary teeth, 39, or 81.25%, are within the posterior dentition. Asymmetry predominates, with antimere pairing in only 11 individuals. When asymmetrical, side occurrence is equivalent with the right accounting for 16 and the left 17 cases, plus one medial mesiodens

(WAm9).

With reference to supplemental vs. supernumerary expression, 32 of the 61 extra teeth are of the former type, and 29 of the latter. Sixteen supplemental teeth are on the left side and 16 on the right vs. 15 supernumerary teeth on the left and 13 on the right (plus the mesiodens). Twenty-six supplemental teeth are in the maxilla and six in the mandible vs. 22 supernumerary teeth in the maxilla and seven in the mandible. Supplemental teeth consist of six upper incisors, nine upper premolars, 11 upper molars, five lower premolars, and one lower molar. The supernumerary teeth include two upper incisors, six upper premolars, 15 upper molars, five lower premolars, and one lower molar. Lastly, concerning sex differences, the 11 females with hyperdontia (Table 2) express six supplemental and six supernumerary teeth. For the 30 males, equivalent expression is again indicated with 24 supplemental and 22 supernumerary teeth.

3.2. The premodern samples

Four of the 487 premodern individuals, 0.82%, exhibit hyperdontia, with a 95% CI of 0.22-2.10% (Table 3). The smaller samples, particularly West Africa, and few affected individuals dissuade making any overarching statements about inter-regional variation. One of 13 West individuals (WAp1) expresses a supplemental premolar, for a frequency of 7.69% with, of course, a sizeable CI (0.20-42.86). The remaining samples are more indicative, geographic scale notwithstanding, with 1 of 96 individuals in Central Africa, 1.04% (CI 0.03-5.80%); two of 139 in East Africa, 1.44% (CI 0.17-5.20%); and 0.00% in 239 South Africans. None of these differences are significant. Two males, one female, and one of unknown sex comprise the affected individuals. Intra-sample prevalence by sex in the three larger samples ranges from 0.00% in the South to 7.69% in the East (Table 3); however, these small subsamples are not conducive to additional descriptive or inferential analyses. Similarly, the few data in Table 4 are sufficient to characterize expression without needing explanation or summary.

4. Discussion

4.1. Modern prevalence

The 3.08% of individuals with hyperdontia among all 1429 modern sub-Saharan Africans is near or just above the upper end of most published global prevalence ranges listed in the Introduction (Arandi et al., 2020; Lam, 2017; Pindborg, 1970). The exception is Mallineni (2014) 0.4–6.0% where, as noted and of potential relevance here, the highest value is from a sample of African Americans (in Harris and Clark, 2008). Thus, the pooled sub-Saharan data fit within what many consider to be

Table 1

Modern regional sub-Saharan African samples and sex-based sub-samples, with numbers of individuals observed (n), those with hyperdontia (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, Gambia, Ghana, Ivory Coast, Liberia, Nigeria,	19th-20th centuries	Male	157	9	5.73	
	Senegal, Togo		Female	116	4	3.45	
			Unknown	29	1	3.45	
			Total	302	14	4.64	2.53-7.78
Central	Chad, Congo, Democratic Republic of the Congo, Gabon, Rwanda	19th-20th centuries	Male	64	8	8.06	
			Female	43	2	4.65	
			Unknown	13	1	7.69	
			Total	120	11	6.78	4.58-16.40
East	Ethiopia, Kenya, Somalia, Tanzania	19th-20th centuries	Male	170	6	3.53	
			Female	88	1	1.36	
			Unknown	8	0	0.00	
			Total	266	7	2.63	1.06-5.42
South	Botswana, South Africa	19th-20th centuries	Male	480	7	1.46	
			Female	204	4	1.96	
			Unknown	57	1	1.75	
			Total	741	12	1.49	0.84-2.83
			Grand Total	1429	44	3.08	2.24-4.13

 $\begin{tabular}{ll} Table 2 \\ Modern sub-Saharan African individuals exhibiting hyperdontia. \end{tabular}$

Individual	Sex	Individual Sex Cultural Affiliation Country	Country	Date	Institution*	Catalogue No.	Supplemental Teeth	Supernumerary Teeth	' Teeth	Total
West Africa										
WAm1	Z	Yoruba	Benin	19th Century	MH	17011 1900 12		UM Left, UM Right	ight	2
WAm2	F?	Yoruba	Benin	19th Century	MH	33914 E-295	UP Left, UP Right			2
WAm3	M	Ewe?	Benin	19th Century	AMNH	VL3449	UP Left			1
WAm4	ç.	Boki	Cameroon	19th Century	AMNH	VL4208	UP Left			1
WAm5	H	Ashanti	Ghana	19th Century	AMNH	VL116	UM Right			1
WAm6	Z	Ashanti	Ghana	19th Century	AMNH	VL592		UM Left		1
WAm7	Z	Ashanti	Ghana	19th Century	AMNH	VL594	UM Left, UM Right			2
WAm8	Z	Ashanti?	Ghana	19th Century	AMNH	VL368	UM Right	UM Left		2
WAm9	щ	Unknown	Ghana	19th Century	AMNH	VL577		UI Medial		1
WAm10	M	Ibo	Nigeria	19th Century	NHML	AF23/111	UM Left, UM Right			2
WAm11	M?	Efik?	Nigeria	19th Century	AMNH	VL405		UP Right		1
WAm12	M	Efik?	Nigeria	19th Century	AMNH	VL1292	UI Left, UI Right			2
WAm13	M	Balanta	Senegal	20th Century	MH	4965		UP Left		1
WAm14	H	Ewe	Togo	19th Century	AMNH	VL1474		UP Left		1
							Total	12	8	20
Central Africa										
CAm1	Z	Toubou	Chad	20th Century	MH	18812		UM Right		1
CAm2	M	Toubou	Chad	20th Century	MH	12360	UI Left, UI Right	•		2
CAm3	M	Bateke	Congo	19th Century	MH	20501		UM Left		1
CAm4	Щ	Chokwe?	Dem Repub Congo	19th Century	RBINS	AF50 228		UM Right		1
CAm5	M?	Unknown	Dem Repub Congo	19th Century	RBINS	AF74 10	UM Left	•		1
CAm6	ć	Unknown	Dem Repub Congo	19th Century	RBINS	AF75 17		LM Right		
CAm7	. ≽	Adoima?	Gabon	20th Century	MH	19256		III Right, IIP Left, IIP Right	off. UP Right	ı en
CAm8	Ι	Fano	Gabon	19–20th Century	MH	22261	IIM Left		, , , , , , , , , , , , , , , , , , ,	- c
CAm9	Σ	Fang	Gabon	19–20th Century	MH	22269	UM Left, UM Right			. 2
CAm10	Σ	Nkomi?	Gabon	19th Century	NHML	1864 G.7.32	UI Right			1
CAm11	Σ	Nkomi?	Gabon	19th Century	NHMI	64 G.7.44		I.M Left		-
;	:						Total	7	8	15
East Africa										
EAm1	M	Haya	Kenya	19-20th Century	CAMDL	AF23.0.4 AF308		UM Left		1
EAm2	×	Haya	Kenya	19-20th Century	CAMDL	AF23.0.23 AF329		UM Right		1
EAm3	M	Kikuyu?	Kenya	20th Century	NMNH	257589		UM Left		1
EAm4	Z	Swahili?	Kenya	19th Century	MH	8246		UP Right		1
EAm5	ц	Darod	Somalia	20th Century	CAMDL	AF15.0.52		LP Right		1
EAm6	Z	Ikoma?	Tanzania	19th Century	AMNH	VL1596	LM Right			1
EAm7	Z	Gogo?	Tanzania	19th Century	AMNH	VL396	UP Left			1
							Total	2	5	7
South Africa										
SAm1	F?	San	Botswana	20th Century	ASU	A327		UM Right		1
SAm2	Z	Tswana	South Africa	20th Century	WITS	A3793	UP Left			1
SAm3	Z	Zulu	South Africa	20th Century	WITS	A3961	UP Left, UP Right; LP Left (x2), LP Right	LP Left, LP Right	ht	7
SAm4	Z	Zulu	South Africa	20th Century	WITS	A1373		UM Left		1
SAm5	۲.	Zulu	South Africa	20th Century	WITS	A1429	UI Right			1
SAm6	M	Zulu	South Africa	20th Century	WITS	A1971		LP Right		1
SAm7	Н	Venda	South Africa	20th Century	WITS	A1653		UM Left		1
SAm8	Z	Venda	South Africa	20th Century	WITS	A1820		UM Left		1
SAm9	M	Xhosa	South Africa	20th Century	WITS	A2288	LP Left			1
SAm10	щ	Swazi	South Africa	20th Century	WITS	A3977	UP Right			1
SAm11	M	Pedi	South Africa	20th Century	WITS	A1205	LP Right	LP Left		2
SAm12	H	Unknown "Bantu"	South Africa	20th Century	WITS	A4008	UM Right			1
							Total	11	80	19
							Grand Total	32	29	61

AMNH=American Museum of Natural History, ASU=Arizona State University, CAMDL=Cambridge University Duckworth Laboratory, MH=Musée de l'Homme, NHML=Natural History Museum London, NMNH=National Museum of Natural History, RBINS= Royal Belgian Institute of Natural Sciences, WITS=University of the Witwatersrand Dart Collection.

the most representative range of hyperdontia worldwide, 0.1-3.6+% (e.g., Aldred et al., 2013; Bello et al., 2019; Mossaz et al., 2014; Peker et al., 2009; Pindborg, 1970; Van der Merwe & Steyn, 2009).

However, the 3.08% masks inter-regional differences, some of which are significant, seen across the subcontinent—notably West (4.64%) and Central (6.78%) vs. East (2.63%) and South (1.49%). So compared with global ranges, the rates from West and Central Africa are among the highest worldwide (though see below). Of interest, this variation parallels the directional change previously recorded in frequencies of highly genetic ASUDAS nonmetric traits that, as noted, serve as proxies for DNA (Irish et al., 2020). Of course, the number of individuals observed for hyperdontia relative to the geographic scale must be considered, particularly the vast Central region (n = 120, CI 4.58–16.40; Table 1); however, samples from there and West Africa were also found to exhibit more complex crown and root morphology than those from East and South (Irish, 1993, 1997, 2013). These include high frequencies of 6-cusped lower first molars and 5-cusped lower second molars, along with many from the "Afridont dental pattern" (Irish, 2013:288), including upper first molars having a Carabelli's expression, 3-rooted upper second molars, fully erupted third molars, lower first premolars with a Tomes' root, lower first molar cusp 7, and lower second molars with two separate roots (Irish, 1993, 1997, 2013). Their overall decrease in frequencies, along with an increase in others, from West to Central to East to South was attributed to evidence for a remnant dental cline that marked population movement during the so-called 'Bantu' expansion (Irish, 1993, 2013). Specifically, 4000-3000 years ago proto-'Bantu' slash-and-burn agriculturalists began moving out of West Africa in search of more cultivatable lands, with some migrations continuing through the mid-19th century into South Africa. Along the way they contacted the original inhabitants of these regions. Eventually, Bantu-speaking peoples came to populate most of the subcontinent (Barker, 2009; Collet, 1982; July, 1992; Soper, 1982).

Differences in hyperdontia prevalence are also patent across sub-Saharan Africa in comparing results from earlier studies. However, not all support the current findings. Actual inter-population variation is probable, but method may be a contributing factor as well, e.g., whether living individuals or crania were studied and if either were x-rayed. Again, partially impacted or small teeth are more likely visible in crania than in living individuals, but fully impacted teeth may not be detected in either without radiographs. Of specific relevance to the present study, a midline diastema occurs in 10.5% of sub-Saharan Africans (Irish, 2013), and one of several causes can be an impacted mesiodens (Hussain et al., 2013). Another factor that may underrepresent true prevalence is that most clinical hyperdontia samples comprise subadults, to miss any later forming fourth molars; as noted, the latter have been observed with some regularity in individuals of African ancestry (Eshgian et al., 2021; Harris and Clark, 2008; personal observation by author). On the other hand, some patients may have been at clinics specifically for treatment of anomalies, including hyperdontia, to then inflate prevalence.

With these caveats in mind, two West African clinical studies in Nigeria reported high rates of 9.0% (Adeyemi et al., 2012) in 100 radiographs, and 12.7% though 1004 intra-oral exams (Anibor et al., 2015). Others are low, (a) 1.5% of 984 children (Ize-Iyamu et al., 2016), (b) 1.74% of 57 individuals with "mixed Nigerian" heritage (Bello et al., 2019:e934), and (c) 2.5-3.0% in > 3000 adult males on the Guinea Coast (Watters, 1962). The former two studies used radiographs, and the latter visual exams. There are no previous Central or East African results for modern populations, but in the South the abovementioned intra-oral study of Zulu found just 0.3% to have hyperdontia (Suk, 1919), and similarly 0.4% via visual recording of 745 'Bantu' crania and 648 mandibles (De Villiers, 1968). Not only are these two figures extremely low, but a recent study reported a seemingly uncharacteristic high rate (per Irish, 1993; Irish, 1997; Irish, 2013) of 14% for a contrary anomaly, hypodontia (Esan & Schepartz, 2017). On the other hand, two further South African studies based on visual observation revealed high hyperdontia rates of 4.8% in > 130 'Bantu' skeletal dentitions (Shaw,

1931), and 6.7% in the crania of 89 19th century migrant workers (Van der Merwe & Steyn, 2009).

So, while some support the current findings of more hyperdontia toward the West (Adeyemi et al., 2012; Anibor et al., 2015) and less in the South (De Villiers, 1968; Suk, 1919), other studies do not. However, all serve to demonstrate that notable variation exists among the populations, methodological differences notwithstanding. The implication is that for any large world region, whether comparing hyperdontia between populations or calculating a range of prevalence, the use of average values should be avoided, e.g., 3.08% here, 1.0% in the U.S. (Stafne, 1932). At a minimum, confidence intervals, including 2.24-4.13% for the sub-Saharan Africans, should be calculated to yield more representative results. It is equally problematic to generalize from a regional sample. For example, it cannot be assumed that the 3.6% rate in 1717 Swedish children (Lind, 1959) is representative of greater Europe, any more than it is the true maximum of the 0.1-3.6% worldwide range. Intra- and inter regional analyses of numerous samples can more accurately assess prevalence and patterning of the anomaly on a global scale.

4.2. Modern pattern and form

With a few exceptions, the patterning and forms of hyperdontia in the modern sub-Saharan samples parallel generalizations made in prior studies, to suggest some uniformity around the world. Uniformity also supports, indirectly, a shared genetic component in expression.

First, the overall male to female ratio of 1.41:1 fits findings of male bias (Aldred et al., 2013; Arandi et al., 2020; Brook, 1984; Eshgian et al., 2021; Garvey et al., 1999; Giudice et al., 2008; Hyun et al., 2008; Kwon & Jiang, 2018; Pindborg, 1970; Suljkanovic et al., 2021; Wang & Fan, 2011). Brook (1984) suggested it is linked to tooth size; in his sample of English children, males, with larger teeth, were more likely to have hyperdontia, whereas females, with smaller teeth, were more disposed to hypodontia (also Carter & Worthington, 2015). Regionally, though none are significant, the differences between extremes of 2.60:1 in East and 0.75:1 in South Africa again make a case against averaging rates. One Nigerian ratio is 1:1 (Bello et al., 2019), but the present South African female partiality is uncommon. The reason(s) are indeterminate here, but it is likely not a function of sample size, which is the largest of all regions (compare Table 2). Second, in agreement with most (e.g., Arandi et al., 2020; Ata-Ali et al., 2014; Garvey et al., 1999; Giudice et al., 2008; Kwon & Jiang, 2018; Lam, 2017; Mossaz et al., 2014; Pindborg, 1970; Suljkanovic et al., 2021; Wang & Fan, 2011), the maxilla is more affected, with 48 extra teeth, than the mandible with just 13. But contra the predilection for the premaxilla (Aldred et al., 2013), > 81% of these teeth come from the posterior maxilla (Table 2). As stated by Harris and Clark (Harris and Clark, 2008), this contradiction is likely related to a clinical emphasis on European derived individuals. In accord with these authors, increasing awareness of variation in understudied populations encourages a more inclusive understanding of hyperdontia by anthropologists and clinicians, e.g., alternate treatment based on patient ancestry. Third, back in agreement with previous studies, asymmetry is evident in 33 of the 44 (75.0%) affected individuals. As well, there is no notable antimere dominance; the right side accounts for 16 and the left 17 cases.

Finally, any differences between supplemental and supernumerary teeth in presence and intra-oral location are not common topics in previous research. However, as quantified in Table 2 and summarized in the Results, it is evident that the likelihood of a supplemental tooth forming vs. a supernumerary is largely equivalent; there is no clear predisposition for one over the other. Sex does not appear to be a factor. Of the 30 males with a total 46 extra teeth, 24 are supplemental and 22 are supernumerary. Of the 11 females with a total of 12 extra teeth, the respective counts are six and six. Comparability is also evident by antimere, isomere, and tooth class in which the extra teeth formed (again see Table 2).

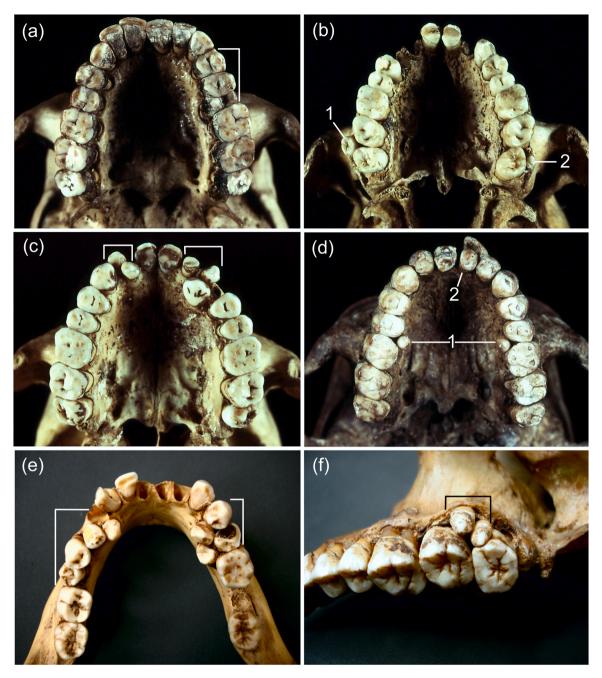


Fig. 2. Examples of hyperdontia evident in sub-Saharan African dentitions from the study. (a) Supplemental upper left premolar in modern, probable Ewe male from Benin in West Africa (ID WAm3; refer to Table 2). (b) Supplemental (1) upper right molar and supernumerary upper left molar (2) in modern, probable Ashanti male from Ghana, West Africa (ID WAm8). (c) Supernumerary upper right and left lateral incisors in a modern, probable Efik male from Nigeria, West Africa (ID WAm12). (d) upper right and left supernumerary premolars (1) and (based on root and crown size) probable supernumerary upper left central incisor (2) that displaced normal upper left central incisor seen in image, in modern probable Adouma male from Gabon, Central Africa (ID Cam7). (e) Two supplemental and one supernumerary lower left premolars (one missing post-mortem), and one supplemental and one supernumerary lower right premolars in modern Zulu male from South Africa (ID SAm3). (f) Supernumerary upper left molar (also note paramolar tubercle fused to upper left third molar) in a modern Venda male from South Africa (ID SAm8).

4.3. Premodern prevalence, pattern, and form

The 487 premodern individuals have an appreciably lower hyperdontia rate of 0.82% (CI 0.22–2.10%; see Table 3). One previous Central Africa study (Gibbon & Grimoud, 2012) did report 4.17%, but that was based on one supernumerary incisor in a small sample of 24 Iron Age crania from the Democratic Republic of the Congo. Disregarding the very small sample from West Africa in the present study (n=13;7.69%; CI 0.20–42.86), little can be said about those from the Central, East, and South other than that the anomaly appears to have been rarer there in

the past, with a range of 0.00–1.44% and no significant differences between regions. Some individuals are relatively recent (e.g., AD 1350–1780; Table 3), but most lived before the 'Bantu' expansion. Of the four with hyperdontia, one was dated to ca. AD 1180, another to ca. 700–500 BCE, and the remaining two to ca. 9000–4000 BCE (Table 4). It appears that the latter two Late Stone Age individuals from Kenya (EAp1, EAp2) represent the oldest examples of hyperdontia known in humans—not only in Africa, but worldwide (c.f., Gibbon & Grimoud, 2012; Goldstein, 1948; Hooton, 1930; Leigh, 1937; Ruffer, 1920; Phillips et al., 2021; Suzuki et al., 1995; Tomczyk et al., 2020).

Table 3
Premodern regional sub-Saharan African samples and sex-based sub-samples, with numbers of individuals observed (n), those with hyperdontia (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 BCE-AD 1390	Male	1	0	0.00	
			Female	2	0	0.00	
			Unknown	10	1	10.00	
			Total	13	1	7.69	0.20-42.86
Central	Democratic Republic of the Congo, Niger	7700 BCE-AD 1400	Male	21	0	0.00	
			Female	35	1	2.86	
			Unknown	40	0	0.00	
			Total	96	1	1.04	0.026-5.80
East	Kenya	8100 BCE-AD 1350	Male	26	2	7.69	
			Female	33	0	0.00	
			Unknown	80	0	0.00	
			Total	139	2	1.44	0.17-5.20
South	South Africa	10 880 BCE-AD 1780	Male	76	0	0.00	
			Female	92	0	0.00	
			Unknown	11	0	0.00	
			Total	239	0	0.00	NA
			Grand Total	487	4	0.82	0.22 - 2.10

Table 4Premodern sub-Saharan African individuals exhibiting hyperdontia.

Individual	Sex	Culture/Site Affiliation	Country	Date	Institution *	Catalogue No.	Supplemental Teeth	Supernumerary Teeth		Total
West Africa										
WAp1	?	Iron Age/ Mouhoun Bend	Burkina Faso	ca. 700–500 BCE	EM	15, KS74 E.8 2000	UP Right			1
							Total	1	0	1
Central Africa										
CAp1	F	Kisalian/Sanga	Dem Repub	ca. AD 1180	ULB	SGA74 T172		UI Left		1
			Congo				m . 1	•		
East Africa							Total	0	1	1
East Africa EAp1	M	Late Stone Age/	Kenya	ca. 9000–4000	NMK	KNM-LT	UM Right			1
EAPI	IVI	Lothagam	Keliya	BCE	INIVIK	27710	OW RIGHT			1
EAp2	M	Late Stone Age/	Kenya	ca. 9000-4000	NMK	KNM-LB-162	UM Left			1
		Loboi		BCE?			m-+-1	0	•	
South Africa							Total	2	0	2
South Africa							Total	0	0	0
							Grand Total	3	1	4

^{*} EM=Emory University, NMK=National Museum of Kenya, ULB=Université Libre de Bruxelles.

Though anecdotal, the relative rarity in these premodern samples may imply 'Bantu' migrants 'transported' a higher prevalence of hyperdontia as they proceeded out from West Africa across the subcontinent; the frequency then decreased when moving from Central to East to South as they encountered the indigenous regional populations. In support, Bantu-speaking migrants, beyond having morphologically complex teeth, were suggested to have brought with them another dental-related characteristic, albeit cultural, in the practice of incisor chipping/filing and ablation (Irish, 2017; Van Reenen, 1978). The oldest documented sub-Saharan ablation is from Cameroon in West Africa, dated 7000-3000 BCE (Irish, 2017); the oldest chipping/filing is from Burkina Faso at 700-500 BCE (Maes et al., 2004). The next oldest modification, ca. AD 679 to AD 1335, is in Central Africa, i.e., the Democratic Republic of the Congo (de Maret, 1992); it predates subsequent examples once distributed along the probable migration route(s) into East and South Africa. By early historic times populations from all four regions practiced modification; of relevance is chipping/filing, which evidences spatiotemporal evolution in form from simple mesial and distal incisor reduction in West Africa, to elaborate variations like deep mesial filing and a 'swallowtail' shape in the East and beyond (Irish, 2017). However, no such modifications are reported in indigenous pre-'Bantu.' Thus, with the possible exception of East African ablation for medical purposes, it appears the practice spread across sub-Saharan Africa during the migration event(s) (Irish, 2017; Van Reenen, 1978).

Finally, the premodern data are too few to realistically contribute much information about variation in patterning and form relative to other world populations. That said, with one exception, they do not contradict the generalizations made about sex, isomere, or other biases in expression of hyperdontia. In agreement, of the four affected individuals with one extra tooth each—three supplemental and one supernumerary, (a) the M:F ratio is literally 2:1 (not including one individual of unknown sex); (b) there is no side preference, with two teeth in the right and two in the left antimere; and (c) all four of these teeth erupted in the maxilla. However, like the modern sub-Saharan Africans three of these four teeth are from the posterior maxilla rather than premaxilla (Tables 3 and 4).

5. Conclusion

In sum, this report contributes new information about hyperdontia in sub-Saharan Africans at both collective and regional levels. Though not absent in the clinical and anthropological literature, data from this geographic area are wanting in the calculation of global prevalence

ranges and, as mentioned, population comparisons at this broad level. It is clear that future studies will benefit by the ongoing addition of data on multiple regional levels to understand better the anomaly. That said, based on the data at hand hyperdontia does exhibit enough uniformity worldwide concerning sex, isomere, antimere, and tooth form to imply a shared, potentially ancient genetic component in expression. However, despite its rarity, enough variation in prevalence and patterning is known, e.g., area of maxilla affected, to ascertain spatiotemporal differences among populations—at least within Africa and particularly in conjunction with other biological and cultural characteristics. Thus, beyond an interesting anomaly or negative health issue, hyperdontia may be useful for other reasons, e.g., further comprehension of population variation and biological affinities, which can in turn influence clinical treatment of patients from underrepresented groups.

CRediT authorship contribution statement

Joel D. Irish: Conceptualization, Investigation, Writing – original draft, Methodology, Writing – review & editing, Photography.

Declaration of Competing Interest

The author reports no declarations of interest.

Acknowledgements

The author thanks everybody for their help at the: American Museum of Natural History, Arizona State University, Florisbad Quaternary Research Station, Institut royal des Sciences naturelles de Belgique, Museé de l'Homme, National Museums of Kenya, Natural History Museum, National Museum of Natural History, Université Libre de Bruxelles, University of Cambridge, University of Cape Town, and University of the Witwatersrand. Funded through the US National Science Foundation (BNS-9013942, BNS-0104731, BCS-0840674).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.archoralbio.2022.105463.

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