High GUD incidence in the early 20th century created a particularly permissive time window for the origin and initial spread of epidemic HIV strains

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Supplementary Text S2: Circumcision prevalences in Central and West Africa

This supplementary information presents the data used to construct Figures 2, 3, and 4 (included in the main article), and Supplementary Table S3. It is to be read in conjunction with Dataset S1. In the latter, we present tables of ethnic composition of cities, at several time points. For each ethnic group, and at a given time, we assign a circumcision class, and we estimate circumcision frequency in urban adult males, based on our extensive survey of the ethnographic literature, and thus we compute estimates of circumcision class distribution, and of circumcision frequency for each city/time point.

As described in more detail in Materials and Methods, in the section Circumcision prevalence survey, we collected primary ethnographic articles and books to complement the main ethnographic references [1–3], and modern Demographic Health Surveys (DHS) [4]. Our survey extended the coverage of circumcision information to 87% of the ethnic groups, in relation to the 48% coverage provided by the Ethnographic Atlas [1,2] (Supplementary Table S2). The reference
numbering used in this supplementary text corresponds to its own reference list.

The supplementary information we provide here is divided into the following sections:

1. Temporal trends in circumcision practices and other background information

2. Definition of circumcision classes (relevant to Figure 3 of the main article)

3. Estimation of circumcision frequencies (relevant to Figure 4 of the main article)

4. Ethnically partitioned census tables (relevant to Figures 3 and 4)

5. Additional demographic information

6. Hunting of apes and monkeys (relevant to Suppl. Table S3)
1. Temporal trends in circumcision practices and other background information

Our survey shows that, in both Central and West Africa, the majority of ethnic groups practiced circumcision before colonialism (see Dataset S1). However, the groups not practicing it were numerous. In Central Africa at around 1880, they consisted of: 1) Most groups of northern Cameroon [2,5–7]; 2) Groups living in the Cameroonian area centered around Bafia [7,8]; 3) Almost all groups belonging to the Adamawa-Ubangi language family (this includes almost all groups of the Oubangui-Chari/Central African Republic (CAR) and many groups from the northern parts of Belgian Congo/Democratic Republic of Congo (DRC)) [6,7,9,10]; 4) Most groups of the Orientale province of DRC [7,11–13]; 5) Many groups of the Équateur province of DRC [6,7,14,15]; 6) Most groups of the extreme south of DRC; 7) Almost all groups in Rwanda and Burundi, and nearby DRC areas [2,5,7,11]. In addition, many coastal groups had less common circumcision because of long standing European Christian influence [7,9,16–20]. The high proportion of men coming from the Équateur and Orientale provinces of DRC in Kinshasa in early 20th century (see tables DRC-2, DRC-4, and DRC-5 in Dataset S1) explains the lower circumcision levels in this city compared to Brazzaville and Libreville (Figures 3 and 4 of the main article; Dataset S1).

In West Africa at around 1880, groups not practicing circumcision consisted of: 1) Most groups from the Kru language family in Côte d’Ivoire [7,21,22]; 2) All groups from the Akan language family, and most groups from the northeast of the same country [2,5,6,23–25]; 3) The Kru and Grebo of southwest Liberia [26–28]. In addition, in Guinea-Bissau, several important northern groups performed circumcision in adulthood only, even up to 40 years old [29–32], which generally lowered the circumcision frequency of adults. These patterns explain the singularly low circumcision rates of Ivorian cities (Abidjan and Bouaké) and Bissau in relation to the other West African cities in early 20th century (Figures 3 and 4 of the main article; Dataset S1).

The profound and rapid ethnic mixing promoted by colonialism produced a powerful trend of imitation, with circumcision being adopted by groups previously not practicing it, and generalizing in groups where it was not generalized previously. These changes concentrated in the period 1880–1920 [6,8,9,11–14,33,34]. The end result was nearly universal circumcision in all countries which cities we included in our study (Dataset S1; Figures 3 and 4 of the main article; Supplementary Table S1) [4,35,36]. In countries where
circumcision was rare (e.g., Rwanda, Burundi, and Zambia) it remained so [2,4,5,7].

Christianity produced a decline in circumcision practice only before the start of organized colonialism (circa 1885), and for groups with longstanding contact with Europeans. Because of this, many coastal groups had abandoned it partially or totally by that time [7,9,16–19], and the slave-descended groups that emerged in islands, such as Cabo Verde [37], and São Tomé e Príncipe [38], and in the Caribbean and the Americas [37], abandoned it up to the present day. However, when colonialism started in the continent, Christian missionaries did not discourage circumcision ([39]; personal communication from Tamara Giles-Vernick (Univ of Minnesota and Institut Pasteur, France)). They were more interested in suppressing the initiations and rituals that, for many peoples, accompanied circumcision at puberty [39–42]. These initiations were also complex and costly, and became less affordable under colonial rule. This, associated with the safety of the circumcision operation in health facilities, produced the gradual abandonment of the initiations, and the moving of the operation to immediately after birth or early childhood [4,6,40–45]. This suggests that convergence to the national norm, and moving the operation to childhood, were the main trends at work in 20th century.

Rebuffat (1927) writes that, when circumcision was performed in adolescence or young adulthood, it often led to scars, which increased susceptibility to syphilis [46]. Modern surveys of ritual circumcision in adolescence and young adulthood confirm that keloid scarring, laceration, swelling, and other complications are common [47]. We do not know to which extent these effects could increase susceptibility to HIV, so we did not attempt to model these effects in our simulations.

In a minority of ethnographic sources, the physical procedures of circumcision are described and, in some cases, the description could suggest that the foreskin was only partially removed; this was observed also in recent surveys of ritual circumcision [47]. However, the descriptions are far from conclusive, are made only for a few ethnic groups, and we could never ascertain how a partial circumcision would affect susceptibility to HIV, so we did not attempt to model this effect in our simulations.

2. Definition of circumcision classes

We classified the male populations of the studied cities in classes according to their likelihood of having uncircumcised adult males. For
groups known as practicing it generally, or not practicing it, at a given moment (e.g., a time point in Figures 3 and 4 of the main article) the definition of classes is straightforward. However, for groups known to have adopted circumcision before a given time point, it is unclear what proportion of men were already circumcised at that time point since, after initial adoptions by some subgroups/villages, many years or decades elapsed until full adoption by the whole ethnic group. In these cases, the time elapsed between the first adoptions and a given moment (e.g., a time point in Figures 3 and 4) can be used to define classes reflecting circumcision probability.

Therefore we were interested in the reported times of the first adoptions by ethnic groups. For many groups which adopted circumcision, the ethnographers provide an approximate date of adoption [6,9,11,12,48]. For many additional groups, the ethnographers state, and describe evidence, that adoption had been recent prior to their visit to the tribe studied [8,9,11–13,23,33,34,49–52]. Several authors refer to the temporal order of adoptions of contiguous ethnic groups (or subgroups within a main ethnic group), and describe with some detail “waves” of adoption of circumcision spreading across regions [8,9,11–14,48–50,53–55]. Based on this information, we estimated the dates of adoption of circumcision by groups displayed in Dataset S1.

We assigned to each ethnic group, at a given time, a “circumcision class” that is entirely based on the information provided by the ethnographic sources, and is not dependent on our estimates of circumcision frequencies. The classes are used in Figure 3 of the main article; the related calculations are implemented in Dataset S1. Table TS2-1 shows their definition.
<table>
<thead>
<tr>
<th>Class</th>
<th>Colorcode in Fig. 3</th>
<th>Explanation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Dark blue</td>
<td>Circumcision is either generalized up to puberty, or its adoption/generalization/move to childhood by the group started more than 45 years before the time of the data point</td>
</tr>
<tr>
<td>2</td>
<td>Blue</td>
<td>Circumcision was, less than 45 years before the time of the data point, done in late adolescence/young adulthood by many men</td>
</tr>
<tr>
<td>3</td>
<td>Green</td>
<td>Adoption/generalization of circumcision by the group started between 30 and 45 years before the time of the data point</td>
</tr>
<tr>
<td>4</td>
<td>Magenta</td>
<td>Adoption/generalization of circumcision by the group started between 15 and 30 years before the time of the data point</td>
</tr>
<tr>
<td>5</td>
<td>Orange</td>
<td>Adoption/generalization of circumcision by the group started less than 15 years before the time of the data point</td>
</tr>
<tr>
<td>6</td>
<td>Red</td>
<td>Circumcision is absent in the group at the time of the data point</td>
</tr>
<tr>
<td>7</td>
<td>Gray</td>
<td>Other situations (e.g., the country of origin and not the ethnic group, is provided, and circumcision is not general in that country)</td>
</tr>
</tbody>
</table>

Table TS2-1. The circumcision classes used in Figure 3 of the main article.

### 3. Estimation of circumcision frequencies

To construct Figure 4 of the main article, we generated lower and upper estimates of circumcision frequency in urban male adults (age > 20) of each ethnic group, as follows:

i) 0–5% if not practiced.

ii) 97–99% if circumcision is culturally mandatory and performed at or before puberty. This high frequency is supported by the following data: 1) for the groups we put in this category (see Dataset S1) ethnographic sources state that circumcision, even when no initiation was involved, was often necessary for engagement in full adult life, including marriage; the uncircumcised would be mocked, and rejected by women; 2) in the DHS surveys [4] of the countries we studied where ethnicity of the cohorts was recorded, the circumcision frequencies in adults were all above 97.9% (Supplementary Table S1) [4]; 3) in our ethnographic survey, we found two studies which measured circumcision frequency in early or mid 20th century, and they were 100% in adults, in a cohort of Mandjia from Fort Crampel (CAR) in 1900 [10], and 99.6% in adults, in a cohort of Manjaco from Guinea-Bissau in 1960 [56].
iii) 75–85% if commonly performed in late adolescence/early adulthood (in this case, many young men would not have undergone circumcision by the time they were recruited to the cities and other labor settings [40,46,57,58]).

iv) for groups which adopted circumcision in late 19th century or afterwards, and the literature provides an approximate timing of the adoption, we estimated it at 0–20% at that time, and raising linearly to attain 97–99% forty five years later. This is broadly supported for several ethnic groups, for which we could track quantitatively the increase of circumcision prevalence after adoption. For example, the Kru of Liberia were said to be invariably non-circumcised by 1929 [28], and the DHS for Liberia reveals that 98.3% of Liberians born between 1967 and 1976 were already circumcised [4], which implies a very high proportion for the Kru at that time. The Ngbandi from northern DRC adopted circumcision around 1915 [6], and by the early 1970s they were universally circumcised (personal communication from Christiaan Van Goethem (experienced doctor who worked in the DRC)). The Ebrié and other Lagunaire peoples of Côte d’Ivoire were mostly non-circumcised in the 1960s (personal communication from Marc Augé (École d’Hautes Études en Sciences Sociales, France)), and their circumcision levels rose to 96% in 2006 [4]. The examples above set up upper limits for the time elapsed from adoption and universality of about 4–6 decades. The Zande of Faradje, in northeast DRC, were adopting circumcision in 1907 [11], and by 1921 many Zande subgroups had not adopted it yet [7,13]. Several authors reporting on the period between 1920 and 1949 (reviewed in [14]) state that many Ngbandi subgroups were not yet circumcised, and the Ngbandi started to practice circumcision in 1915 [6]. These examples set up lower limits of 2–3 decades for the time between adoption and universality. Therefore we choose as estimate 45 years. We note that the wide initial range of our estimates of circumcision at the adoption time (0–20%) partly incorporates the uncertainty that often exists over this time, and the rate at which it became generalized.

v) if the literature states unequivocally that circumcision is practiced but is far from general, or if there are unresolved conflicting statements by several authors, we estimated it as 40–60% up to the time of this observation, and raising linearly after that, to attain 97–99% thirty years later; in such groups, circumcision was already culturally favored, and the simplicity of the operation performed in childhood in health clinics promoted its universality, as modern DHS surveys [4] demonstrate; also, the cultural pressure to imitate circumcision practice of other groups intensified in the period 1880–1920 [6,7,9,11–14,23,49,53–55,59]).
vi) if the literature states that circumcision was practiced but the influence of Europeans and Christianity in the group had started many generations before the 20th century, we estimated it as 65–85% up to about 1920; many sources give examples of groups in this situation that have abandoned circumcision at least partly [9,16–20,37,38]; after 1920 it raises linearly to attain 97–99% thirty years later; in such groups, circumcision was already culturally favored, and the simplicity of the operation performed in childhood in health clinics promoted its universality, as modern DHS surveys [4] demonstrate; also, the cultural pressure to imitate circumcision practice of other groups intensified in the period 1880–1920 [6,7,9,11–14,23,49,53–55,59]).

Where we lacked information on either the circumcision status of a group, the age at which it is performed, or its generality, we assumed the commonest pattern observed in the neighboring groups.

We implemented this algorithm in Dataset S1. The parameters described in points i)–v) above can be changed in its first sheet, and the spreadsheet recalculates all estimates, updating Figures 3 and 4 automatically.

4. Ethnically partitioned census tables

Table TS2-2 below lists the ethnically partitioned censuses of the studied cities and supporting references. Each line of this table corresponds to a full table included in the companion file Dataset S1, by their order of appearance in the latter. Each table produces both a distribution of men by circumcision classes (used in Figure 3 of the main article), and a circumcision rate estimate (used in Figure 4 of the main article).

For Kinshasa only, the tables we collected more often mentioned the district of origin (within the Belgian Congo) of the inhabitants, rather than their ethnicity. Then, we determined the ethnic composition of each district, by juxtaposing ethnic maps [14,60,61] to an administrative map of the relevant period [62]; the demographic weights of ethnic groups in districts were considered proportional to their respective areas (see Table DRC-2 inside Dataset S1).

<table>
<thead>
<tr>
<th>City</th>
<th>Year</th>
<th>Sources on ethnic/regional origin of inhabitants</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kinshasa (D.R. Congo)</td>
<td>1958</td>
<td>Spitaels (1959), p.6 [63]</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1927</td>
<td>AIMO (1927) [64]</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1919</td>
<td>AIMO (1927) [64]</td>
<td>a)</td>
</tr>
<tr>
<td></td>
<td>1912</td>
<td>Douchet &amp; Dubois (1911–12) [65]</td>
<td></td>
</tr>
<tr>
<td>City</td>
<td>Year(s) and Sources</td>
<td></td>
<td></td>
</tr>
<tr>
<td>-----------------------------</td>
<td>------------------------------------------------------------------------------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1932 Subdiv Autonome de Brazzaville (1932) [67]</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1919 Subdiv Autonome de Brazzaville (1932) [67] a)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1949 Lebeuf (1954), p.25 [33]</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1931 Lebeuf (1954), p.25 [33]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Libreville (Gabon)</td>
<td>1953 Lasserre (1958), p.206 [69]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Douala (Cameroon)</td>
<td>1965 Mainet (1985), p.81 [70]</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1935 Service de Santé (1935) [71]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yaoundé (Cameroon)</td>
<td>1957 Roubaud (1994), p.9 [73]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bissau (Guinea-Bissau)</td>
<td>1950 Carreira (1962), p.282 [74]; Junta de Investigação do Ultramar (1950) [75]</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1940 Província da Guiné (1940) [76]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conakry (Guinea)</td>
<td>1950 Goerg (1990), p.96 [77]</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1921 Goerg (1990) [77]; Goerg (2006) [78] b)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Freetown (Sierra Leone)</td>
<td>1963 Harvey (1971), p.98 [79]</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1953 Banton (1956), p.355 [80]</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>1931 Banton (1956), p.355 [80]</td>
<td></td>
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</tr>
<tr>
<td></td>
<td>1921 Banton (1956), p.355 [80]</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1911 Banton (1956), p.355 [80]</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table TS2-2. The ethnically partitioned censuses we used in our study, by the order they appear in Dataset S1, and supporting references.

Notes: a) For these years, no ethnically partitioned censuses were available; we assumed the same ethnic group proportions of the nearest census to the future; b) For these years, we obtained numbers for some ethnic groups from different sources, and we estimated the numbers for the remaining ethnic groups based on either: i) their proportions in the nearest census to the future; ii) statements about their numbers in nearby years from various sources; c) In this case we estimated the numbers based on both the nearest census to the future, and statements on immigration patterns of the city. In several of these cases, we built several scenarios for the ethnic group numbers for which we lacked precise information (see Dataset S1).
5. Additional demographic information

In addition to obtaining ethnically partitioned censuses of cities, we obtained data on their population trends (Figure 2 of the main article), sex ratios, proportion of adults, and other relevant demographic variables, which were important for our simulations. The sources consulted to obtain demographic information are listed in Table TS2-3. They partly overlap with the sources listed in Table TS2-2.

<table>
<thead>
<tr>
<th>City</th>
<th>Refs. of sources on demography</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kinshasa</td>
<td>63–64, 89–96</td>
</tr>
<tr>
<td>Brazzaville</td>
<td>66, 67, 96–98</td>
</tr>
<tr>
<td>Bangui</td>
<td>33, 68, 96, 99–101</td>
</tr>
<tr>
<td>Libreville</td>
<td>69, 96</td>
</tr>
<tr>
<td>Douala</td>
<td>70–72, 96</td>
</tr>
<tr>
<td>Yaoundé</td>
<td>73, 96, 102, 103</td>
</tr>
<tr>
<td>Bissau</td>
<td>74–76, 96</td>
</tr>
<tr>
<td>Conakry</td>
<td>77, 78, 96</td>
</tr>
<tr>
<td>Freetown</td>
<td>79, 80, 96</td>
</tr>
<tr>
<td>Monrovia</td>
<td>26, 81, 96</td>
</tr>
<tr>
<td>Abidjan</td>
<td>82–87, 96, 104–106</td>
</tr>
<tr>
<td>Bouaké</td>
<td>83, 88, 96, 105, 106</td>
</tr>
</tbody>
</table>

Table TS2-3. The cities under study, and the references of sources consulted for demographic information.

6. Hunting of apes and monkeys

We gathered information about practices of ape/monkey hunting from the same ethnographic sources used for the circumcision study, and we constructed Supplementary Table S3. We recorded all statements (mostly from before 1960) that explicitly referred to hunting of/feeding on: i) chimpanzees and/or gorillas (for Central Africa); ii) any monkeys (for West Africa). For some ethnic groups/populations, killing of the relevant animals was practiced without consuming their meat (e.g., the Aka Pygmies killed apes only to supply bushmeat to others [107–110]; the Tutsi and Hutu did it only to protect crops [16,111]; the Ngando killed bonobos rarely, only to obtain skins and bones [112]). Ape bushmeat consumption was inexistent/very rare among: peoples living in grasslands or non-forested highlands (Shi-
Havu, Tutsi, Hutu, Bamileke) because of rich agriculture and/or abundant livestock [16,111–115]; coastal peoples with longstanding contacts with Europeans (e.g., the Mpongwe [116,117]); Aka, Baka, and Twa Pygmies [107–110,115]; peoples heavily relying on fishing (e.g., the Pomo, Bomali, and Kaka living near Ouesso [118]). However, the vast majority of peoples living in chimpanzee and gorilla ranges killed and consumed these animals (Supplementary Table S3).

The remaining sources listed in the reference list [119–196] are additional ethnographic and other sources referred in Supplementary Table S3 and/or in the tables of Dataset S1.

References


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