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The introduction and spread of plague in the Great Lakes region of East Africa, c.1700–1900: a palaeogenetic and social history

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ABSTRACT

This article reconstructs and explains the introduction and spread of plague in the Great Lakes region of East Africa in the pre- and early colonial period (c.1700–1900). It argues that plague arrived and focalised in the region, which was marked by isolation from the outside world, towards the end of the seventeenth century and in unique circumstances of human migration, triggered by climatic anomaly and environmental factors. The most likely route of introduction was along the Nile, from Egypt and Sudan. Subsequent spread waves, each characterised by different spatio-temporal contours, were triggered largely by anthropogenic and demographic factors (including conflicts and human migration), but it was not until the colonial period that the disease left the region and spread farther east to the Swahili Coast and beyond. The article conjoins both textual and non-textual evidence, including recent palaeogenetic work (the study of ancient DNA), to demonstrate the value of an inherently interdisciplinary approach to plague history.

KEYWORDS

East Africa; the Great Lakes; Buganda Kingdom; plague; environment; climatic shocks; trade; migration; palaeogenetics; aDNA

The historiography of plague in general and the Second Plague Pandemic in particular has been characterised, up until recently, by two predominant trends: (1) a disproportionate attention to the Black Death (the first wave of the so-called Second Plague Pandemic), and (2) Eurocentrism.[1] This situation has somewhat changed in the last 10 or so years, with some historians and scientists becoming aware of the global nature of the Second Plague Pandemic and, thus, diverting their attention to different regions outside of Europe.[2] In particular,

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[1]By the 'Second Pandemic', we mean here a series of recurrent plague waves, on both a global and a regional scale, commencing with the Black Death (1338–1353) and continuing into the 1840s.

[2]For instance, M.H. Green, 'Taking "pandemic" seriously: making the Black Death global', *The Medieval Globe*, 1 (2014), 27–62; S. Borsch and T. Sabraa, 'Refugees of the Black Death: quantifying rural migration for plague and other environmental disasters', *Annales de démographie historique*, 134, 2 (2017), 63–93; P. Slavin, 'The birth of the Black Death: biology, climate, environment and the beginnings of the Second Plague Pandemic in early fourteenth-century Asia', *Environmental History*, 28, 2 (2023), 300–34; M.A. Spyrou et al., 'The source of the Black Death in fourteenth-century Central Eurasia', *Nature*, 606, 7915 (2022), 718–24; P. Slavin, 'From the Tian Shan to Crimea: dynamics of plague spread during the early stages of the Black Death, 1338–46', *Journal of the Economic and Social History of the Orient*, 66 (2023), 513–627; P. Slavin, 'Looking for trouble: non-textual indications of plague mortality crises in late Chinggisid world, c.1330–1400' in Y. Isahaya and N. Di Cosmo (eds), *Climate Changes, Plagues and Wars: The crisis of the fourteenth century in the Afro-Eurasian context* (Edinburgh, 2025) (forthcoming).

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scholarly discussions of the origins of the Black Death have increasingly focused on Central Asia, positioning the region at the centre of emerging historiographical approaches. Other regions have received much less attention, and, while there has been *some* awareness of the place of pre-colonial Africa in the history of global plague pandemics – and, in particular, its Sub-Saharan regions – there is still very little literature on this subject.

This article offers the first systematic treatment of early plague history in the Great Lakes region of East Africa, c.1700–1900. It is focused on one overarching research question. When and how was plague introduced into the region and how did it spread across local polities? This question is related to a fascinating historical paradox: the Great Lakes region remained isolated from the outside world until the 1830s and, thus, might be expected to have been spared from plague outbreaks – at least until its 'discovery' by Arab and later European traders and missionaries. Yet historical evidence, backed up by (palaeo)genetic data, indicates that the plague was introduced there some 130 years earlier and, having seeded a local reservoir (an ecological niche in which pathogens are being maintained by wild rodents or in soil) probably in the Kingdom of Buganda on the northern shore of the Lake Victoria, it then persevered there for centuries. This finding is significant, as it challenges the idea that plague spread is associated with an inter-connected world whose regions are bound together by various means of exchange – most notably, trade, migration, travel and warfare.[3]

To understand the emergence and subsequent spread of plague in such an isolated region, we have to consider a combination of environmental and anthropogenic factors – in particular, climatic shifts and human migrations. Although there is no doubt that eco-climatic factors initiate new plague waves, to understand their spatio-temporal trajectory (in terms of geographic pervasiveness and speed), it is essential to consider how human institutions and agency facilitate them.[4] This article follows this dictum and shows that different spatio-temporal phases of plague spread in the Great Lakes region were conditioned by different anthropogenic factors and their structural changes in the pre- and early colonial eras. It utilises a wide array of historical documentary sources, including early codified histories of local polities (and Buganda in particular), chronicles from neighbouring regions (Egypt, Sudan, Ethiopia and Portuguese-controlled Mombasa), early travellers' and missionaries' accounts, colonial state papers and plague investigation reports. This textual evidence is supplemented by oral histories collected by twentieth-century missionaries and anthropologists, archaeological records and recent palaeo-genetic work. Such an inherently interdisciplinary approach is the only way to penetrate the history of one of the world's most isolated regions, which lacks native written narratives until the colonial era.

Structurally, the article begins by reviewing recent historiography and research on ancient DNA (aDNA) relating to early plague in Sub-Saharan Africa, and then traces three phases of its spread in the Great Lakes (c.1700–1917). It next pieces together evidence from wide-ranging textual sources to identify the factors (exogenous and endogenous) that explain the spatio-temporal contours of plague introduction and spread, before combining historical and palaeo-genetic evidence to provide a fully integrated account of how plague, previously unknown in

[3]Green, 'Taking "pandemic" seriously', *op. cit.*, 47–51; R. Yue, H. Lee and C. Wu, 'Trade routes and plague transmission in pre-industrial Europe', *Scientific Reports*, 7 (2017), article 12973; D. Kaniewski and N. Marriner, 'Conflicts and the spread of plagues in pre-industrial Europe', *Humanities and Social Sciences Communication*, 7 (2020), article 162.

[4]As reflected in recent scholarship dealing with the early spread of the Black Death from Central to West Eurasia: Slavin, 'From the Tian Shan to Crimea', *op. cit.*; H. Barker, 'Laying the corpses to rest: grain, embargoes, and *Yersinia pestis* in the Black Sea, 1346–48', *Speculum*, 96, 1 (2021), 97–126.

East Africa, was introduced, established and spread. Two Supplementary Information (SI) tables list outbreaks (c.1700–1910) and putative reservoirs, and an appendix provides a glossary of key palaeogenetic terms.[5]

Plague in Sub-Saharan Africa: recent historical and aDNA work

Renewed historical interest in African plague history has paralleled advances in studying *Yersinia pestis*, the causative agent of plague. In 2010, Achtman's team published the first comprehensive phylogenetic reconstruction of the bacterium's evolution, including 21 genomes (1948–2004) from the Democratic Republic of Congo (DRC), Uganda, Tanzania and Kenya, all placed on so-called Branch 1.ANT.[6] This branch is much older than the aforementioned genomes: Cui et al.'s analysis, based on probability computations, dated its emergence between 1377 and 1650 CE (median date: 1499).[7] Later, Spyrou and colleagues recalibrated the date to between 1485 and 1589 CE.[8] In 2018, Nyirenda et al. genotyped five genomes from the 2015–2016 Zambia outbreak, associating them with lineage 1.ANT and extending its phylogeography farther south.[9] Alongside 1.ANT strains, a contentious 'Angola' isolate, allegedly from a pre-1984 freeze-dried laboratory sample, was placed on the ancient 0.PE3 lineage by Eppinger and colleagues.[10] The Angolan provenance of that isolate is disputed, since 0.PE3 belongs to a lineage that emerged millennia ago and is confined to Central Asia and the Caucasus.[11] Building on this genetic work, historians have examined plague in pre-colonial Sub-Saharan Africa, including through contributions to a 2018 special issue of the journal *Afriques*. Green argued for two introductions of the disease: into north-eastern Africa before the Justinianic Plague (541), and into the Great Lakes during the Second Pandemic, possibly in the late seventeenth century.[12] Green also suggested that *Yersinia pestis* may have focalised in East Africa much earlier, linked to the 0.PE3 branch (and likely unrelated to Angola at all).[13] Chouin has provided a general survey of potential evidence (archaeological and textual) of plague in Africa from the fourteenth century to the nineteenth, while Gallagher and Dueppen analysed abandoned

[5]For SI tables, see the supplemental data.

[6]G. Morelli et al., '*Yersinia pestis* genome sequencing identifies patterns of global phylogenetic diversity', *Nature Genetics*, 42, 12 (2010), 1140–43. The authors estimated, in a very crude manner, the divergence of 1.ANT from the main *Yersinia pestis* tree between 628 and 6914 years before present (at 1141).

[7]Y. Cui et al., 'Historical variations in mutation rate in an epidemic pathogen, *Yersinia pestis*', *Proceedings of the National Academy of Sciences of the United States of America*, 110, 2 (2013), 577–82, here 579.

[8]Spyrou et al. 'Source of the Black Death', *op. cit.*, and SI: Figures 11, 34.

[9]S. Nyirenda et al., 'Molecular epidemiological investigations of plague in eastern province of Zambia', *BMC Microbiology*, 18 (2018), https://doi.org/10.1186/s12866-017-1146-8.

[10]M. Eppinger et al., 'Genome sequence of the deep-rooted *Yersinia pestis* strain Angola reveals new insights into the evolution and pangenome of the plague bacterium', *Journal of Bacteriology*, 192 (2010), 1685–99.

[11]M. Harbeck et al., '*Yersinia pestis* DNA from skeletal remains from the 6th century AD reveals insights into Justinianic Plague', *PLoS Pathogens*, 9 (2013), e1003349, 5.

[12]M.H. Green, 'Preface: the Black Death and Ebola: on the value of comparison', *The Medieval Globe*, 1 (2015), xiv–xv; M.H. Green, 'Putting Africa on the Black Death map: narratives from genetics and history', *Afriques*, 9 (2018), https://journals.openedition.org/afriques/2125. The theory of the Ethiopian origins of the Justinianic Plague, based on vague mentions of late Antique historians, has been accepted by some historians ever since Edward Gibbon – see E. Gibbon, *The History of the Decline and Fall of the Roman Empire*, Vol. VII (Basel, 1788), 365. This is discussed in T.P. Newfield et al. 'Proxies for plague? New approaches in studying the causes and consequences of the First Plague Pandemic' in W. Brandes, H. Reimitz and J. Tannous (eds), *Legal Pluralism and Social Change in Late Antiquity and the Middle Ages: A conference in honour of John Haldon* (Frankfurt, 2024), 89.

[13]Green, 'Putting Africa on the Black Death map', *op. cit.*, 40, note 24.

sites in West Africa, and Derat examined textual evidence of plague in 'late-medieval' Ethiopia.[14] In 2021, Seidensticker et al. suggested plague may have contributed to a population collapse in the Congo rainforest (c.400–600 CE), a hypothesis that sparked immediate disagreement.[15] In contrast, Sussman (2015) questioned the presence of plague in pre-colonial Africa, arguing that it only reached the Swahili Coast and Great Lakes in the late nineteenth century via Gujarati cotton trade.[16]

Despite their merits, these studies remain hypothetical due to limited and inconclusive evidence – textual, archaeological and especially genetic – with only three fully sequenced Sub-Saharan genomes published by 2024. This changed dramatically with the publication by Mas Fiol et al. of 46 fully sequenced East African genomes (plus over 100 from elsewhere in Africa), greatly advancing our understanding of the topic.[17] This analysis of the 46 genomes – from the DRC, Uganda, Tanzania, Kenya and Yemen (1948–2010) – showed that all belong to three sub-branches of the 1.ANT lineage identified by Achtman's team. The branch in question had a long evolutionary history, having diverged from Branch 1B (responsible for the *pestis secunda* of 1356–1366) between 1344 and 1537 (median date: 1431).[18] Subsequently, the most recent common ancestor (MRCA) of the oldest known sub-branch – 1.ANT3 – emerged at some point between 1471 and 1712 (median date: 1591). The emergence of 1.ANT3 was followed by a parallel rise of two additional sub-branches – 1.ANT1 and 1.ANT2, at some point between 1616 and 1823 (median date: 1728). All three sub-branches underwent a process of diversification, whereby new sub-lineages diverged from each main sub-branch, during the nineteenth century. Sub-branch 1.ANT1 was the first to undergo the diversification event between 1736 and 1897 (median date: 1826), followed by 1.ANT2 (between 1771 and 1918; median date: 1854) and 1.ANT3 (between 1801 and 1924; median date: 1875). The estimates of chronological brackets derive from probability calculations conducted using BEAST (Bayesian Evolutionary Analysis Sampling Trees) – a cross-platform program used to perform molecular dating (Figure 1) – and should be taken only as a very rough guide.

Sub-branch 1.ANT3 is associated with genomes from Kenya and the DRC; 1.ANT2 is related to genomes from Tanzania, Kenya and Yemen, while 1.ANT1 genomes come from Uganda and the DRC. Importantly, as Mas Fiol et al. demonstrated, other African regions – in both North Africa (Algeria and Morocco) and Sub-Saharan Africa (Senegal, Namibia, Zimbabwe and South Africa) – are represented by a different lineage: 1.ORI with its sub-branches and strains (and, indeed, the study found no evidence of the 0.PE3 branch, supposedly associated with Angola, anywhere in Africa). As several other studies have established, 1.ORI sub-branches are associated with the so-called 'Third Plague Pandemic', which although already ravaging the Yunnan

[14] G. Chouin, 'Reflections on plague in African history (14th–19th c.)', *Afriques*, 9 (2018), https://journals.openedition.org/afriques/2228; D. Gallagher and S. Dueppen, 'Recognizing plague epidemics in the archaeological record of West Africa', *Afriques*, 9 (2018), https://journals.openedition.org/afriques/2198; M.-L. Derat, 'Du Lexique aux talismans: occurrences de la peste dans la corne de l'Afrique du XIIIe au XVe siècle', *Afriques*, 9 (2018), https://journals.openedition.org/afriques/2090.

[15] D. Seidensticker et al., 'Population collapse in Congo Rainforest from 400 CE urges reassessment of the Bantu expansion', *Science Advances*, 7 (2021), 8352–56. Seidensticker et al.'s paper attracted criticism in the respective replies of Giresse et al., and of Clist et al., as well as Seidensticker et al.'s rejoinders, in the same volume of *Science Advances*.

[16] G.D. Sussman, 'Scientists doing history: Central Africa and the origins of the First Plague Pandemic', *Journal of World History*, 26, 2 (2015), 325–54.

[17] G. Mas Fiol et al., 'Global evolutionary patterns of *Yersinia pestis* and its spread into Africa', *BioRxiv [Preprint]* (2024), doi: 10.1101/2024.11.26.625443.

[18] *ibid.*; P. Slavin, 'Out of the west: formation of a permanent plague reservoir in South-Central Germany (1349–1356) and its implications', *Past & Present*, 252, 1 (2021), 24–28.

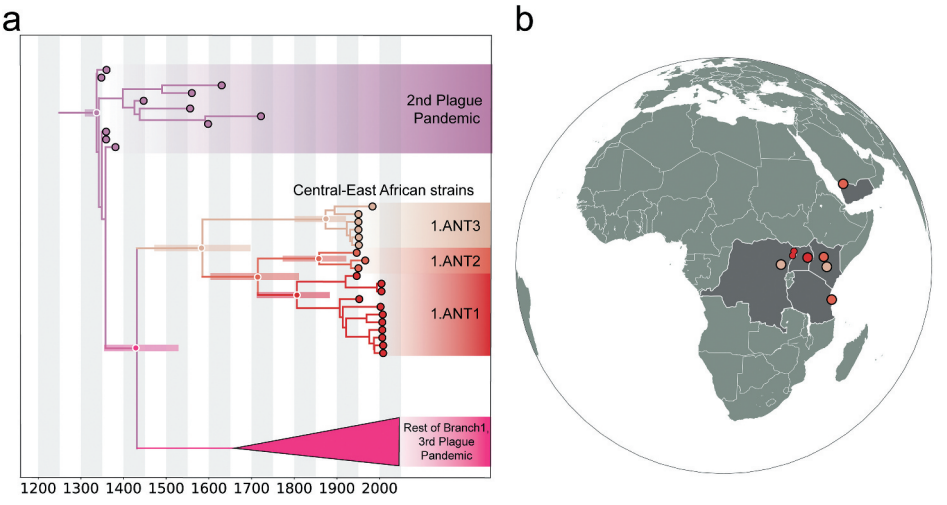

Figure 1. Phylogenetic positioning of African *Yersinia pestis* strains from the 1.ANT lineage and genomes associated with the Second and Third Plague Pandemics. (a) Phylogenetic tree summarising the molecular dating analyses by Mas Fiol et al., 'Global evolutionary patterns', describing the emergence and evolution of 1.ANT lineage, and Spyrou et al., 'Source of the Black Death', SI, focusing on the origin of the Second Plague Pandemic; (b) Geographic distribution of 1.ANT strains in Central-Eastern Africa and Yemen. Nodes and branches in the tree are coloured according to their associated lineages. Horizontal bars indicate the highest posterior density (HPD) interval for the divergence year of the node. The HPD represents the range of dates that are most consistent with the data and Bayesian phylogenetic inference analysis used in Mas Fiol, 'Global evolutionary patterns' and Spyrou et al., 'Source of the Black Death', SI, and thus contains the divergence dates with the highest inferred probabilities. Circles with white contour over the selected nodes represent the median inferred value for their divergence date. The tree and map plots were generated using the Baltic library (https://github.com/evogytis/baltic).

province of China in 1772, became global with the 1894 outbreak in Hong Kong and spread into Asian, African, European, American and Australian ports in the course of the next 25 or so years.[19] By contrast, 1.ANT had emerged long before the Third Plague Pandemic, with its sub-branches and their strains being confined, seemingly, only to East Africa and South Arabia.

The phylogenetic positioning of sequenced 1.ANT genomes may hint at an earlier phylogeographic history of their branches. As noted above, 1.ANT3 was the first one to branch off. Since this branch occurs in eastern DRC and Kenya, while 1.ANT1 and 1.ANT2 are spread across DRC, Tanzania, Kenya and Uganda, the 1.ANT3 lineage likely emerged between eastern DRC and Kenya, with later 1.ANT1 and 1.ANT2 diversification occurring elsewhere in the Great Lakes region. Historical sources support this, pointing to Buganda Kingdom in Uganda – midway between eastern DRC and Kenya – as the probable origin of the common ancestor of the three 1.ANT sub-branches.

To test these assertions, we must situate these evolutionary developments and their chronology within the broader historical context, considering biological, environmental, socio-

[19]C. Benedict, *Bubonic Plague in Nineteenth-Century China* (Stanford, 1996); M. Echenberg, *Plague Ports: The global urban impact of bubonic plague, 1894–1901* (New York, 2007); B. Bramanti et al., 'The Third Plague Pandemic in Europe', *Proceedings of the Royal Society B: Biological Sciences* 286, 1901 (2019): article 20182429; P.N. Barr, *Uncertainty and Emotion in the 1900 Sydney Plague* (Cambridge, 2024).

economic and political changes in the Great Lakes and specifically the Kingdom of Buganda, where plague was present from around 1700. This article synthesises historical evidence from pre-colonial and early colonial periods, combining it with DNA data, to shed light on the emergence, early spread, and external introduction of plague in East Africa.

Early spread of plague in East Africa

The first phase: early plague spread in Buganda, c.1700–1840

Local polities around the Great Lakes did not have a written culture; their historical traditions were passed down orally until the early twentieth century, when European missionaries and local intellectuals began collecting and codifying them. As the earliest history of plague in the region is related to the Kingdom of Buganda (situated on the north-western shore of the Lake Victoria), it is appropriate to begin our discussion with this polity.[20]

Arguably, the single most prominent Baganda historian was Sir Apollo Kagwa (1864–1927), a political and intellectual leader of British Uganda and the author of several books, including *Bassekabaka ba Buganda* (*The Kings of Buganda*; 1901) and *Empisa z'Abaganda* (*The Customs of Baganda*; 1907), both based on local oral tradition of pre-colonial Uganda.[21] The *Kings of Buganda* traces the history of Buganda's *kabakas* (kings) back to the fourteenth century, covering 30 kings up to the reign of Mutesa I (1854–1885). Although a highly valuable work, it has to be approached with caution. Firstly, its chronology is vague; instead of precise or approximate years, each *kabaka* (in some instances there were two or three co-rulers) represents one 'generation', interpreted as '30 years'. This has meant that historians of Buganda disagree on historical chronology.[22] Secondly, owing to the nature of human memory and oral tradition, some aspects of chronologically remote periods are prone to have been transmitted inaccurately or incorrectly down through many generations before Kagwa composed his text.[23] Nevertheless, *The Kings of Buganda* clearly placed plague in Buganda long before the arrival of European missionaries, doctors and colonialists. In the Luganda language, spoken by the natives of Buganda, the word for 'plague' is *kawumpuli*. According to the *Kings of Buganda*, Kawumpuli was an historical figure, the son of *kabaka* Kayemba (c.1670–1700), born limbless and expelled, together with his mother, by his father, out of fear. According to the Baganda tradition, during the latter's reign, there was a harsh plague outbreak in Buganda, with many peasants fleeing their homes, and it was Kawumpuli who stopped the epidemic.[24] After his death, Kawumpuli was declared the *lubaale* (a prominent historical figure becoming a godlike spirit upon death) of plague, and locals made offerings to him, to avert plague in the future. Kayemba built Kawumpuli a temple in Buyego (a 'no man's land' between the kingdoms of Buganda and Bunyoro in the Luweero District of Central Uganda, near today's Bombo), where his remains were kept in a deep hole covered by wild cat skins, to prevent him from leaving the temple and

[20]'Buganda' is the name of the polity; 'Baganda' is the name of the people living in Buganda; 'Luganda' is the name of the language spoken by Baganda.
[21]A. Kagwa, *The Kings of Buganda*, M.S.M. Kiwanuka (trans.) (Nairobi, 1971); A. Kagwa, *The Customs of the Baganda*., E.B. Kalibala (trans.) (New York, 1934).
[22]Kagwa, *Kings of Buganda*, *op. cit*., 195–96; H. Médard, 'Croissance et crises de la royauté du Buganda au XIXe siècle' (Ph.D., Université Paris, 2001), vol. 1, 29.
[23]J. Vansina, *Oral Tradition as History* (Madison, 1985); A. Portelli, *The Death of Luigi Trastulli and Other Stories: Form and meaning in oral history* (New York, 1991).
[24]J. Roscoe, *The Baganda: An account of their native customs and beliefs* (London, 1911), 309–11; Kagwa, *Customs of the Baganda, op. cit*., 121–22.

causing a plague outbreak. The Kawumpuli Temple priest protected locals during plague outbreaks by distributing metal amulets, cleansing plague-affected homes and gardens, and sheltering victims' families and cattle at the temple until the outbreak ended, after which the families returned home to mourn and later offered Kawumpuli beer and barkcloths in gratitude.[25]

Thus, it appears that plague arrived and was focalised somewhere in Buganda at some point in the late seventeenth or early eighteenth century. The precise location of its reservoir is unknown, but it may be tentatively inferred from references to plague outbreaks in Kagwa's *Kings of Buganda*. The fact that the cult of Kawumpuli appears to have originated around his temple in Buyego may hint that the reservoir associated with earliest outbreaks was confined to this region. Importantly, the dating of the earliest plague outbreaks in Buganda and the emergence of the cult of Kawumpuli fall into the upper chronological bracket estimated for the branching-off of 1.ANT branch. If the earliest outbreaks in Buganda and the emergence of 1.ANT are indeed related, then the branch in question may have indeed risen in Buganda (possibly in the Buyego region).

Since the beginning of the cult of Kawumpuli c.1700, the Kingdom of Buganda experienced a series of outbreaks of plague (invariably referred to in Luganda language as *kawumpuli*), as reported by Kagwa. Thus, a local tradition holds that King Juuko, Kayemba's brother (and Kawumpuli's uncle), died of plague around 1700.[26] During Kayabaggu's reign (c.1760–1790), there were plagues of rats attacking the capital. The king understood the connection between rat over-abundance and human plague and ordered his subjects to hunt and kill the vermin with sticks.[27] The capital in question was situated on the Masajja Hill (between Kampala and Kaazi), indicating that the geographic range of plague expanded southwards to the northern shore of Lake Victoria at that point.[28] Possibly, the 'rats' in question were either (or both) Natal multi-mammate mice (*Mastomys natalensis*) or African grass rats (*Arvicanthis niloticus*), both reported to have been the main vector in the late pre-colonial era, as shown below.

Under Kayabaggu's successor, Jungu (c.1790–1800), there were harsh plague outbreaks, with many settlements abandoned because of it, with the *kabaka* moving his court on no less than five occasions.[29] Having moved initially from Lubya (in Kyadondo, north of Kampala) to Mugongo (in Busiro, south of Kampala), Jungu then moved westwards – to Migo (Singo, near Mubende; roughly, some 100 km west of Lake Wamala), then eastwards to Kasalaga (Busujju, on the eastern shore of the Lake Wamala), then Kiwawu (in the same county) and finally to Nsozibbirye (in Butambala, halfway between Wamala and Victoria lakes). This may hint that by c.1800, the plague range had expanded farther west of Wamala.[30] During Semakokiro's reign (c.1800–1812), there was an outbreak which killed, among others, Kaduwamala, a deposed prime minister.[31] Around the same time, the king had Prince Kamaanya arrested and confined to houses of people who had recently died of plague, hoping he would die of the disease too.[32]

[25]Roscoe, *Baganda, op. cit.*, 309–11; Kagwa, *Customs of the Baganda, op. cit.*, 121–22; Médard, 'Croissance et crises', *op. cit.*, vol. 1, 48–49; Green, 'Putting Africa on the Black Death map', *op. cit.*, 21.
[26]M.S.M. Kiwanuka, *A History of Buganda from the Foundation of the Kingdom to 1900* (New York, 1972), 71.
[27]Kagwa, *Kings of Buganda, op. cit.*, 83–84; Kiwanuka, *History of Buganda, op. cit.*, 81, 150.
[28]Kagwa, *Kings of Buganda, op. cit.*, 83.
[29]*ibid.*, 93.
[30]*ibid.*, 223.
[31]*ibid.*, 83.
[32]*ibid.*, 98.

Unfortunately, Kagwa's works do not describe the symptoms of *kawumpuli*, but it is clear that in these early contexts, this name was associated with plague. This can be inferred from the reports of both early missionaries and colonial medical practitioners (discussed below), who, in describing plague in Buganda and its 'classical' symptoms (buboes, first and foremost), invariably noted that the same disease was referred to by locals as *kawumpuli*.[33] Obviously, retrospective diagnoses are often problematic because disease categories, conceptualisations and pathogens change over time. However, in this instance, these references support the retrospective diagnosis of *kawumpuli* and its association with plague. The Luganda word for smallpox, *ndawula*, is named after a Buganda *kabaka* (c.1700–1730) who, allegedly the first Baganda to die of the disease, became its *lubaale* with a dedicated temple on Mubende Hill; following his death, smallpox outbreaks recurred several times in Buganda.[34] In other words, the commencement of the cults of Kawumpuli and Ndawula appears to have been clearly associated with the earliest instances of outbreaks of their associated diseases.

The second phase: plague spread around the Great Lakes, c.1840s/1850s–1898

While plague was confined primarily to Buganda territories during the first phase (c.1700–-1840), the second phase (c.1840/1850–1898) was characterised by its gradual expansion into other Great Lake regions (see Figure 2).[35] During his 1858–1859 travels, Richard Francis Burton, one of the first European explorers in the Great Lakes region, met Arab merchants in Unyanyembe (northern Tanzania) who told him they had witnessed plague devastation there on their earlier visits. Burton, fluent in Arabic, noted that the merchants used the term *ṭāʿūn* usually meaning 'plague', and described buboes as well as the fast progression of the disease.[36] It is unfortunate that Burton's interlocutors did not indicate when exactly they had first arrived in Unyanyembe, so we can only surmise that the plague outbreak in question had occurred at some point in the 1840s or 1850s.[37] Towards the end of Ssuuna II Kalema's reign (c.1830–1857), the warlord Kayira invaded Busoga kingdom, but many of his soldiers died from plague on their return.[38] The plague was still ravaging upon the ascension of his successor Mutesa I in 1856 or 1857.[39] The fact that the disease was found in Karagwe and Busoga around roughly the same time indicates that by the 1850s, the pathogen had left Buganda territories and migrated farther south and east, around the hinterland of Lake Victoria. To reach and become established in the kingdom of Karagwe in north-western Tanzania before or by the 1840s–1850s, the pathogen would have had to travel via Buganda's south-western neighbour – the kingdom of Ankole.

[33]H. Médard, 'La Peste et les missionnaires: santé et syncrétisme médical au royaume du Buganda à la fin du XIXe siècle', *Outre-Mers: Revue d'histoire*, 346–47, (2005), 79–101, here 84, 89, 96; C. Christy, 'Bubonic plague ("Kaumpuli") in Central East Africa', *British Medical Journal*, 14, 2 (1903), 1265–67.
[34]Médard, 'Croissance et crises', *op. cit.*, 647–49.
[35]See also SI Table 1.
[36]R.F. Burton, 'The Lake regions of Central Equatorial Africa, with notices of the lunar mountains and the sources of the White Nile', *The Journal of the Royal Geographical Society of London*, 29 (1859), 1–454, here 387. For the use of *ṭāʿūn* in Arabic sources, see L.I. Conrad, 'Tāʿūn and Wabāʾ: Conceptions of plague and pestilence in early Islam', *Journal of the Economic and Social History of the Orient*, 25 (1982), 268–307. However, there were some instances when the same word appears to have signified, more vaguely, 'epidemic': J. Brack, M. Biran and R. Amitai, 'Plague and the Mongol conquest of Baghdad (1258)? A reevaluation of the sources', *Medical History*, 68, 4 (2024), 392–410, here 394.
[37]J. Koponen, 'War, famine, and pestilence in late precolonial Tanzania: a case for a heightened mortality', *International Journal of African Historical Studies*, 21, 4 (1988), 637–76, here 657–59, even suggested, without foundation, that it may have happened as early as the late 1830s or early 1840s.
[38]Kagwa, *Kings of Buganda, op. cit.*, 123.
[39]Médard, 'La Peste et les missionnaires', *op. cit.*, 90.

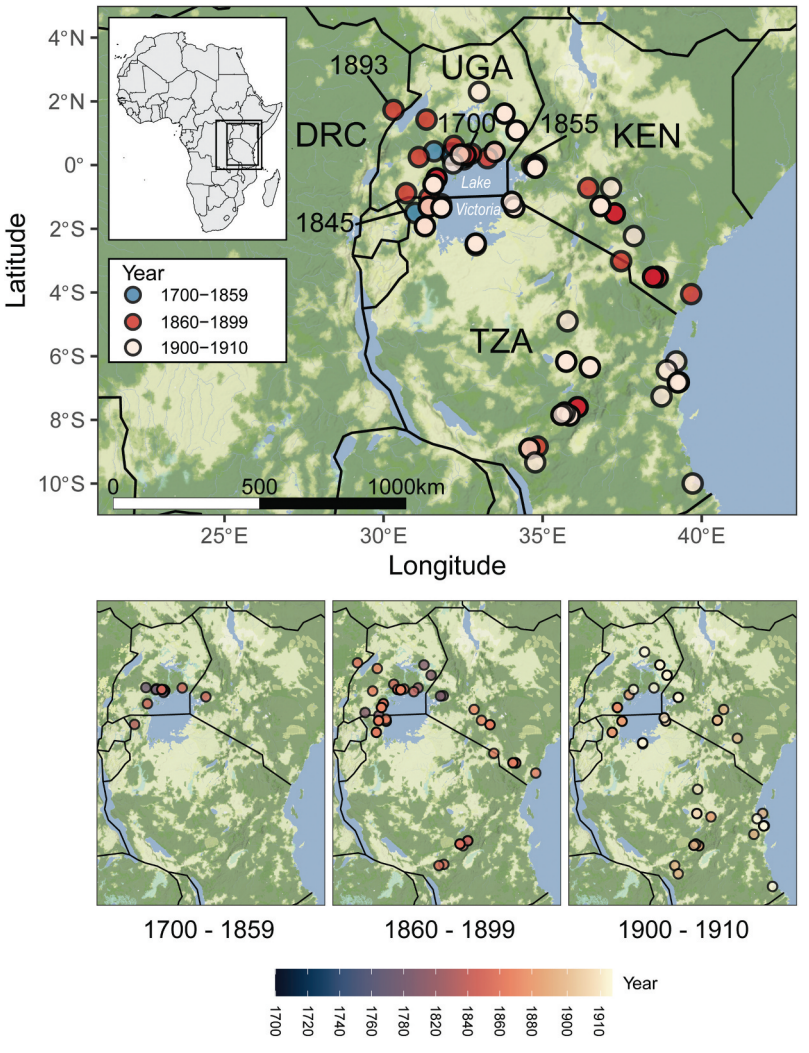

Figure 2. Locations of putative plague outbreaks in East Africa, c.1700–1910. Source: See SI, Table 1. The main map represents the temporal and geographic distribution of outbreaks described in the historical records consulted. Labelled years indicate the earliest recorded outbreak described in present-day Democratic Republic of the Congo (DRC), Kenya (KEN), Tanzania (TZA) and Uganda (UGA). The three lower maps represent snapshots summarising the recorded outbreaks across three different periods in the Great Lakes region. Maps were generated in R 4.4.0 using the ggmaps package (https://www.R-project.org/).

Indeed, the spread into Ankole and neighbouring territories in the later 1850s can be inferred from the following. During his plague research in Dar es Salaam in 1897–1898, Robert Koch studied not only samples but also the history of plague spread in German Tanzania. He asked his assistant, colonial doctor Maximilian Zupitza, stationed in Bukoba since 1896, to interview locals and missionaries about plague history; their 1897–1898 interviews showed that plague repeatedly entered Kiziba from Buddu over the past eight years, with Buddu having had the disease

for 30–40 years, originating from northern Uganda where it was known 'since time immemorial'.[40]

In the 1850s, the plague wave may have spread farther east still. In 1905, D. Milne, a colonial doctor stationed in Kenya, noted local informants' testimonies about a bubonic plague outbreak in the Kibuye Hills (in the Kisumu region) which had occurred about 50 years earlier (c.1855). The same outbreak prompted local upland villagers to migrate some 10 miles into a lowland region.[41]

When plague was ravaging the Busoga, Ankole, Buddu, Karagwe and Kisumu regions in the 1850s, the disease was a novel phenomenon there. It appears that plague was confined to and radiating out of its reservoir/s in Buganda until the 1840s–1850s, and it was not until then or later that it started spreading into other regions of the Great Lakes (Figure 2). This is confirmed by the fact that plague is not mentioned in any non-Baganda dynastic histories.[42] Plague's absence from Tito Winyi's '*Abakama ba Bunyoro Kitara*' ('*The Kings of Bunyoro-Kitara*'; 1935–1937) is somewhat surprising, given the geographic proximity of Kawumpuli's Temple in Buyego to Bunyoro.[43] However, Winyi is corroborated by the assertion of French missionaries in 1890 that the plague was either rare or non-existent in Bunyoro.[44] Similarly, references to plague or plague-like diseases do not appear in either of the dynastic histories of neighbouring Rwanda or of Kiziba (north-western Tanzania).[45] By contrast, some of the same sources mention smallpox and cattle pestilence, as well as some 'epidemics', whose nature cannot be identified.[46]

Thus, on the basis of present evidence, it was not until the 1840s and 1850s that plague left its endemic region in Buganda and started spreading into its neighbouring territories around the Great Lakes – Busoga, Ankole, Buddu, Karagwe and Kisumu regions (Figure 2). Though uncertain, the disease may have established local reservoirs in these regions, which means that the mid-1870s trans-regional wave originated not from Buganda but from a newly formed reservoir elsewhere in the Great Lakes. Secondary sources infer that one of these local reservoirs may have been situated somewhere in a north-eastern region of Lake Victoria. According to F.X. Lwamgira's *Amakuru Ga Kiziba Na Abakama Bamu* (*The History of Kiziba and Its Kings*), it was around 1875 that plague was exported from Ishanzhe (Nkore/Ankole) into Kanyigo (northern Kiziba in northern Tanzania) by a traveller, who ignored several forewarnings about the epidemic ravaging in Ankole territories; thus it is suggested that the disease had been previously unknown in Kiziba.[47] According to oral history collected c.1914 by William John Simpson, the colonial health

[40]R. Koch, *Gessamelte Werke*, Vol. 2.2 (Leipzig, 1912), 742; M. Zupitza, 'Die Ergebnisse der Pestexpedition nach Kisiba am Westufer des Victoria-Sees 1897/98', *Zeitschrift für Hygiene und Infectionskrankheiten*, 32 (1899), 268–94, here 291.
[41]A.D. Milne, 'Plague in the East Africa Protectorate', *Journal of Tropical Medicine and Hygiene*, 8 (1905), 178–79.
[42]Most obviously, T. Winyi, 'Abakama Ba Bunyoro Kitara' ('The Kings of Bunyoro-Kitara'), *Uganda Journal*, 3, 2 (1935), 155–60; *Uganda Journal*, 4, 1 (1936), 75–83; *Uganda Journal*, 5, 2 (1937), 53–68; A.G. Katete and L. Kamugungunu, *Abagabe B'ankole* (*The History of the Kings of Ankole*) (Dar-es-Salaam, 1955).
[43]Winyi, *op. cit*.
[44]Médard, 'La Peste et les missionnaires', *op. cit*., 89.
[45]P. Schumacher, 'Lebensgeschichte des Grossfürsten Kayijuka und seiner Ahnen deit Sultan Yuhi Mazimpaka, König von Ruanda: Von ihm selbst Erzählt', *Mitteilungen der Ausland-Hochschule an der Universität Berlin*, 41 (1938), 103–61; L. Dalmas, *Généalogies de la noblesse (les Batutsi) du Ruanda* (Kabgayi, 1950); A. Kagame, *Un Abrégé de l'ethno-histoire du Rwanda*, vol. 1 (Butare, 1972); Edmond Césard, 'Le Muhaya (l'afrique Orientale)', *Anthropos*, 30, 1–2 (1935), 75–106; *Anthropos*, 30, 3–4 (1935), 451–62; *Anthropos*, 31, 1–2 (1936), 97–114; *Anthropos*, 31, 3–4 (1936), 489–508; *Anthropos*, 31, 5–6 (1936), 821–49; *Anthropos*, 32, 1–2 (1937), 15–60; F.X. Lwamgira, *The History of Kiziba and Its Kings: A translation of Amakuru Ga Kiziba Na Abakama Bamu*, G.B. Kamanzi (trans.) (Dar es Salaam, 2020).
[46]For instance, Winyi, 'Abakama Ba Bunyoro Kitara', *op. cit., Uganda Journal*, 3, 2 (1935), 159; *Uganda Journal*, 5, 2 (1937), 64.
[47]Lwamgira, *op. cit*., 324–25.

officer stationed in Uganda, plague had occurred on the Usemi hills (Kisumu region in North-East Kenya) 30–50 years earlier (that is, around the time of the c.1875 outbreak in Ishanzhe and Kiziba). The outbreak prompted local inhabitants of the Jaluo tribe to abandon the hills and migrate to the plains, only to import the disease there.[48] According to British doctor Clement John Baker, who worked in Uganda from 1903 and gathered local testimonies, a severe plague outbreak struck Bukedi on Lake Victoria's north-eastern shore around 1876 during the Baganda invasion. The Baganda retreated at once, bringing the plague back to their homeland, causing a major outbreak there.[49]

When the first British missionaries arrived in Buganda in 1877 they encountered an ongoing plague outbreak.[50] After another outbreak in 1881, Buganda experienced annual outbreaks annually through the period 1883–1889. After a respite, interrupted by sporadic cases in Kampala in 1897–1899, plague was constantly present for some 37 years (1910–1947) in Buganda. Concurrently, plague was becoming more and more commonplace in other regions of Uganda, largely mimicking the situation in Buganda.

From the later 1880s onwards, the plague expanded its range considerably (Figure 2). In or around 1888, plague was introduced from Buddu into Kiziba, where its outbreaks occurred virtually without pause until 1900.[51] Two years earlier, in 1886, the epidemic was reported in Imagi and Uhehe (Tanzania), having been introduced from the north during Wahehe chief Mkwawa's campaigns.[52] Thereafter, the plague reappeared in that region on a regular basis every few years, as it did in 1889 and 1893–1894, 1903, 1905 and beyond.[53] From Uhehe, the disease spread southwards – all the way to Ubena and Ilembula (South-West Tanzania, close to the Malawi border, some 150 km north-east of Lake Malawi), where it broke out in, respectively, 1891 and 1893.[54] In 1900, the plague spread into the Mpwapwa and Dodoma regions in Central Tanzania.[55]

Concurrently, the plague was spreading in the north, throughout Kenyan territories. In 1892, the disease was reported at the foot of Ndara Hill (introduced from the south according to local inhabitants) – some 140 km from Mombasa and the Swahili Coast.[56] In the following year, it spread around Ndara Hill and Sagalla.[57] The disease made itself known in Machakos (some 60 km south-east of Nairobi) in either 1895 or 1897, spreading farther east to the Taita-Taveta region in 1897–1898 (some 190 km north-west of Mombasa).[58] In 1898, plague appeared for the first time on the Swahili Coast when an infected passenger arrived in Mombasa on a ship to Zanzibar, but no outbreak occurred and local authorities did not investigate it further.[59] In December 1898, the SS *Bhundara* from Karachi, carrying 1000 Indian labourers, of whom six

[48]The National Archives (UK), CO 879/115/10, W.J. Simpson, *Report on Sanitary Matters in the East Africa Protectorate* (1915), 24.
[49]C.J. Baker, 'Rats in Uganda and their relation to plague', *Reports of the Medical Department of Uganda for 1921* (1922), 38–41.
[50]G.H.E. Hopkins, *Report on Rats, Fleas and Plague in Uganda* (Entebbe, 1949), 32–33.
[51]Kolonial-Abteilung des Auswärtigen Amts, 'Deutsch -Ostafrika', *Medizinal-Berichte über die deutschen Schutzgebiete* (1903–1904), 59.
[52]Kolonial-Abteilung des Auswärtigen Amts, *op. cit.*, 59; E.N. Thornton, *A Report on an Investigation into Plague in the Protectorate of Uganda* (Entebbe, 1930), 212–13.
[53]Kolonial-Abteilung des Auswärtigen Amts, *op. cit.*, 62; *Reports of the Medical Officer of the Privy Council and Local Government Board for 1904–5* (London, 1906), 275–76.
[54]Kolonial-Abteilung des Auswärtigen Amts, *op. cit.*, 62; S. Neerinckx, E. Bertherat and H. Leirs, 'Human plague occurrences in Africa: an overview from 1877 to 2008', *Transactions of the Royal Society of Tropical Medicine and Hygiene*, 104 (2009), 97–103, SI, 112.
[55]Neerinckx, Bertherat and Leirs, *op. cit.*, SI, p. 112.
[56]C.W. Hobley, *Kenya from Chartered Company to Crown Colony* (London, 1970), 63.
[57]Thornton, *op. cit.*, 5.
[58]Simpson, *op. cit.*, 16; Thornton, *op. cit.*, 6; J.I. Roberts, 'The endemicity of plague in East Africa', *The East African Medical Journal*, 12 (1935), 200–19, here 214.
[59]Simpson, *op. cit.*, 19.

were dead and an unknown number infected with plague, entered Mombasa harbour. The ship's crew and passengers were taken to Manda Island, where they were isolated, and thus, the plague did not spread into Mombasa on that occasion.[60]

Importantly, the geographic spread of plague was not only eastbound. At some point between 1888 and 1898, the pathogen crossed Lake Albert into the Nizi region of eastern Congo (the Ituri province), leading to the first documented outbreak there. Local testimonies collected by Belgian doctor Jacques Schwetz during the 1928 Nizi outbreak indicate plague was first imported 30–40 years earlier from Uganda via Lake Albert's northern or southern shore, possibly through Mfulayembe migration.[61]

The third phase: plague spreads to the Swahili Coast and beyond, c.1898–1917

The appearance of plague in Mombasa in 1898, albeit not causing an epidemic there, marks a new era in the global history of the disease. With the exception of 1433–1435, when a plague wave, which may have commenced in Ethiopia around 1431–1432, crossed into Berbera (on the Somaliland coast) and other coastal regions and then Yemen, there is no evidence that the disease was ever found in the Swahili Coast and other coastal regions.[62] After the Mombasa outbreak, plague appeared in Zanzibar (1905) and Dar es Salaam (1908), despite various preventive and surveillance measures implemented by local authorities.[63] Yet before it reached Zanzibar and Dar es Salaam, it crossed the sea into Oman, ravaging Muscat and its hinterland in 1899, and spreading farther into Yemen in the following year.[64] The plague started moving southwards later, in a piecemeal fashion, reaching Malawi in late 1916 and the Eastern Province of Zambia in early 1917.[65] As noted, one 2018 study established the presence of 1.ANT in the East Province of Zambia, possibly hinting that that region constituted the southernmost frontiers of 1.ANT.[66] No plague isolates from Malawi have been sequenced or genotyped to date. When plague reached southern Mozambique and Transvaal in 1899, it carried 1.ORI strains originating from China and imported via Hong Kong, India, Mauritius and Madagascar during the Third Pandemic's global phase. Mas Fiol et al.'s study confirms that all sequenced genomes from South Africa, Namibia and Zimbabwe belong to the 1.ORI branch. There is no evidence of 1.ANT and 1.ORI strains coexisting in the same reservoir or region in southern Africa – in marked contrast with some regions in Central Asia, where several strains co-exist in the same reservoir.[67]

[60] A.A. Issa, 'Bubonic Plague and state control in Zanzibar (ca. 1897–1905)' in P. Bala and R. Viljoen (eds), *Epidemic Encounters, Communities, and Practices in the Colonial World* (Lanham, 2023), 67; A.H. Hardinge, *A Diplomatist in the East* (London, 1928), 237–39.

[61] J. Schwetz, L. Fornara and A. Collart, 'La Peste dans la région du Lac Albert (Congo Belge)', *Annales de la Société belge de médecine tropicale*, 9, 3 (1929), 219–63, here 228.

[62] For these outbreaks, see C. Conti Rossini, 'Il Gadla Filpos E Il Gadla Yohannes Di Dabra Bizan', *Memorie della Reale Accademia dei Lincei*, 8 (1900), 62–170, here 157; Derat, *op. cit.*, 8–10; É. Vallet, *L'Arabie marchande: État et commerce sous les sultans Rasūlides du Yémen (626–858/1229–1454)* (Paris, 2010), 670–71; P. Slavin, 'Jinn in the Mountains: Ecology, climate and plague reservoir in the Yemeni highlands, c.839/1436–965/1558', *Nouvelles Chroniques du manuscrit au Yémen*, NS 21, 40, (2025), 67–104 (esp. 71–73).

[63] Issa, *op. cit.*, 72–78; Neerinckx, Bertherat and Leirs, *op. cit.*, SI, 112.

[64] J.E. Peterson, *Historical Muscat: An illustrated guide and gazetteer* (Leiden, 2006), 35; S.C. Zavitziano, 'Turkey: Report from Constantinople', *Public Health Reports*, 15, 20 (1900), 1226.

[65] M. Hokkanen, 'The Government medical service and British missions in colonial Malawi, c.1891–1940' in A. Greenwood (ed.), *Beyond the State: The Colonial Medical Service in British Africa* (Manchester, 2015), 49–50.

[66] S.S. Nyirenda, B.M. Hang'ombe, and B.S. Kilonzo, 'Factors that precipitated human plague in Zambia from 1914 to 2014 – an overview for a century (100 Years)', *Journal of Zoonotic Diseases* 1, 1 (2016), 1–14, here 9.

[67] V. Kutyrev et al., 'Phylogeny and classification of *Yersinia pestis* through the lens of strains from the plague foci of Commonwealth of Independent States', *Frontiers in Microbiology*, 9 (2018), doi:10.3389/fmicb.2018.01106; Y. Li et al., 'Different region analysis for genotyping *Yersinia pestis* isolates from China', *PLoS One*, 3 (2008), e2166; G. Eroshenko et al., '*Yersinia pestis* strains of ancient phylogenetic Branch 0.ANT are widely spread in the high-mountain plague foci of Kyrgyzstan', *PLoS One*, 12 (2017), e0187230.

Although there is no evidence that plague ever reached Muscat or other regions in Oman prior to 1899, there had been a long series of plague waves in Yemen from the disease's introduction there in 1433/1434 until at least 1558, and then again from 1815 until the 1969 outbreak in the Khawlan region (the north-western highlands) – the same outbreak that one of the genomes sequenced by Mas Fiol and colleagues is associated with.[68] It has been argued that plague outbreaks in Yemen – including the 1969 one – radiated out of a putative reservoir in the Asir mountains region (in south-western Saudia).[69] Most likely, the Asir reservoir was seeded late (perhaps in the early nineteenth century), and the fifteenth- and sixteenth-century outbreaks were associated with a different reservoir, situated somewhere in the Yemeni highlands, possibly in the Ibb region.[70] In any event, it is likely that up until the initial importation of 1.ANT strains into Yemen – presumably in 1900, via Muscat – those earlier outbreaks were caused by different strains.

In 1899, plague spread across southern Mozambique and Transvaal, reaching Cape Town by 1900; unlike the Swahili Coast and South Arabia with 1.ANT strains, the South African coast was dominated by 1.ORI strains.[71] As several DNA studies have established, 1.ORI strains were associated with the Third Plague Pandemic, which, although already ravaging the Yunnan province of China in 1772, became global after the 1894 Hong Kong outbreak, and reached the South African coast in 1899 via Mauritius and Madagascar, arriving there from India in 1898.[72] Thus, by 1900, there were two epicentres of plague circulation in the western Indian Ocean: the Swahili Coast, associated with 1.ANT strains, and the South African coast, associated with 1.ORI strains.

When and where did plague focalise around the Great Lakes?

The same historical sources reveal not only the spatio-temporal trends of plague spread around the Great Lakes, but also its focalisation in that region. Today, East Africa boasts some two dozen limited-range reservoirs or 'meso-foci', some apparently existing since pre-colonial times (including the Buganda one), others emerging during the twentieth century; some reservoirs became 'dormant' and others died out.[73] The geography of these 'modern' foci derives from plague field studies and surveillance by modern scientists. Establishing likely historical reservoirs on the basis of textual evidence is a much trickier task. At the most basic level, this requires identifying regions in which recurrent plague outbreaks occurred independently of other

[68]On the absence of plague from Oman before the close of the nineteenth century, see W. Floor, *Muscat: City, society and trade* (Washington, DC, 2015), 134. The years of documented outbreaks in inland Yemen are 1433/1434–1437/1438, 1445, 1523, 1526/1527–1528, 1532–1533, 1545–1546, 1557–1558, 1815–1816, 1826, 1830–1832, 1836–1837, 1844, 1853–1854, 1858–1859, 1868, 1874, 1879–1880, 1887, 1889, 1891, 1893–1900, 1906, 1951 and 1969; see P. Slavin, 'Jinn in the Mountains', *op. cit.* The 1969 isolate in question is IP1865H, associated with one of the two samples (previously labelled as PYH-1 and PYH-2) taken from the village of Al-Maddah during the outbreak in June 1969 and sent to the Pasteur Institute in Tehran (before transferral to the Pasteur Institute in Paris in the early 1970s). See M. Bahmanyar, 'Human plague episode in the district of Khawlan, Yemen', *American Journal of Tropical Medicine and Hygiene*, 20, 5 (1972), 123–28, here 126–27; B.W Hudson et al., 'An electrophoretic and bacteriologic study of *Yersinia pestis* isolates from Central Java, Asia, and the Western Hemisphere', *American Journal of Tropical Medicine and Hygiene*, 22, 5 (1973), 642–53, here 642–43 (Hudson et al. misdated the samples to 1968).

[69]Bahmanyar, *op. cit*.

[70]Slavin, 'Jinn in the Mountains', *op. cit*.

[71]Mas Fiol et al., *op. cit*.

[72]Benedict, *op. cit.*; Sussman, *op. cit*., 332; G. Campbell, *Africa and the Indian Ocean World from Early Times to Circa 1900* (Cambridge, 2019), 253.

[73]On plague reservoirs in Uganda, see Hopkins, *op. cit*., 34–37 and Maps I–II; for Tanzania, see A.S. Msangi, 'Observations on the Endemicity of Plague in Tanzania' (Ph.D., University of London, 1968), 20–62 and 166, and M. Ziwa et al., 'Plague in Tanzania: an overview', *Tanzania Journal of Health Research*, 15 (2014), 252–58.

affected areas – that is, regions with putative reservoirs rather than outbreaks imported from elsewhere.[74]

Figure 3 shows the approximate geography of such regions with putative plague reservoirs, emerging over time.[75] As argued above, plague may have initially focalised somewhere in Buganda, most likely not far from Kawumpuli's temple in Buyego in the late seventeenth or early eighteenth century, sporadically breaking out of its reservoir/s. From the mid-nineteenth century on, or possibly slightly earlier, plague seeded additional reservoirs around Lake Victoria. From the mid-nineteenth century, plague established new reservoirs around Lake Victoria – arriving in Karagwe (north-western Tanzania) by the 1840s or 1850s via Buganda trade, spreading by the 1850s to Busoga, Buddu (possibly in/around the Masaka region, which acted as a plague epicentre in 1921–1930) and Kisumu, and by the 1870s to Ankole, Bukedi and northern Kiziba.[76] From 1883 onwards, plague broke out endemically in and around Kampala, with Lubaga/Rubaga Hill possibly serving as a local reservoir.[77]

In the last two decades of the nineteenth century, plague reservoirs expanded their range considerably, with the disease focalising in south-western and south-central Tanzania (Iringa, Ilembula and Mpwapwa), Sagalla and Kilimanjaro highlands on today's Tanzania–Kenya border, as well as in the Nizi region of Congo (the Ituri province), just west of Lake Albert. During the first decade of the twentieth century, new reservoirs emerged around Kondoa (eastern Tanzania), Ukamba (south-eastern Kenya), as well as North Mara and Mwanza, both in north-western Tanzania. In 1916, the plague moved to Nyasa/Lake Malawi and seemingly seeded a local reservoir there, while a year later it focalised in the Tembwe/Nyimba region of Zambia.

The reconstructed geography of putative plague reservoirs, based on the available textual evidence, is by no means accurate or complete, and there is some room for uncertainty. Thus, it is possible that there were some additional meso-foci, whose activity cannot be inferred from written sources. In addition, it is unclear whether some of these meso-foci were indeed separate reservoirs or merely parts of larger foci. As of today, no attempt has been made to systematise and name different plague reservoirs in Sub-Saharan Africa as has been done for the former Soviet Union, Mongolia, China and Brazil since the 1960s.[78] Hence, reservoir nomenclature used here is tentative.

Two characteristics are common to all these meso-foci. Firstly, they are all upland/highland reservoirs, situated at different altitudes, varying from about 1050 m (Luweero) to 2700 m (Kilimanjaro). Secondly, as can be inferred from twentieth-century evidence, these reservoirs were maintained in the pre-colonial era by Natal multimammate mice (*Mastomys natalensis*, also known as *Rattus mastomys coucha Ugandae*) and, from the late nineteenth century, also by black rats (*Rattus rattus*), with the latter becoming the most prolific plague carrier in East Africa,

[74]Slavin, 'Out of the west', *op. cit.*, 7–12 and M. Keller et al., 'A refined phylochronology of the Second Plague Pandemic in Western Eurasia', *BioRxiv* [Preprint] (2023), doi:10.1101/2023.07.18.549544.
[75]See SI Table 1.
[76]For plague outbreaks around the Masaka region in 1921–1930, see Neerinckx, Bertherat and Leirs, *op. cit.*, SI, 105.
[77]Neerinckx, Bertherat and Leirs, *op. cit.*, SI, 102.
[78]V.M. Dubyanskiy and A.B. Yeszhanov, 'Ecology of *Yersinia pestis* and the epidemiology of plague' in R. Yang and A. Anisimov (eds), *Yersinia pestis: Retrospective and perspective* (Dordrecht, 2016), 147–63; Kutyrev et al., *op. cit.*; Li et al., *op. cit.*; D.B. Verzhutskii and Z. Ad'yasuren, 'Prirodnye Ochagi Chumy v Mongolii: Annotirovannyi Spisok', *Baikal'skii Zoologicheskii Zhurnal*, 2, 25 (2019), 92–103; A.M. Paiva de Almeida et al., 'Isolamento da *Yersinia pestis* nos focos pestosos do Nordeste do Brasil no período de 1966 a 1982', *Revista do Instituto de Medicina Tropical de São Paulo*, 27, 4 (1985), 207–18.

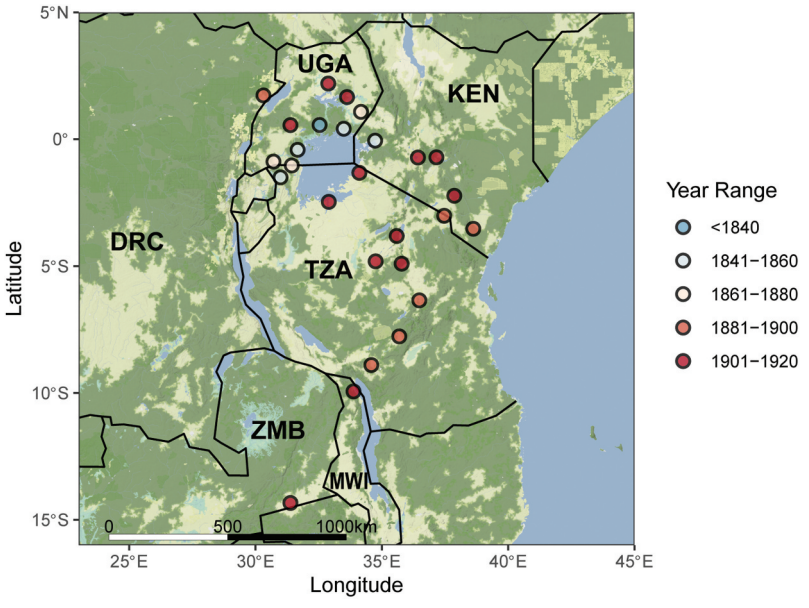

Figure 3. Approximate locations of plague focalisation in East Africa, c.1700–1920. Source: See SI, Tables 1–2.

because of their invasive nature.[79] The role of different rodents and their fleas in plague spread in East Africa will be discussed in the following section.

Exogenous plague spread enablers: vectors and hosts

As we have seen, it was not until 1898 that the plague reached the Swahili Coast. This may be linked to the trajectory of the movement of cotton, the single most important commercial import to the region and an attractor of both fleas and rodents. Raw (unginned) cotton, imported primarily from Gujarat, travelled inland westwards from one of the Swahili Coast ports towards the Great Lakes. The impact of cotton imports and, from 1902, its cultivation, on plague outbreaks in Kenya and Uganda has been stressed in several publications based on first-hand accounts.[80] It is, therefore, possible that cotton movement and cultivation facilitated plague circulation within the inland regions of the Great Lakes – but not its spread towards the Swahili Coast, precisely because of the opposite trajectory.

What about other crops? As far as consumable crops are concerned, millet, known since pre-colonial times, continued to be cultivated in small proportions. Wheat cultivation was introduced by early missionaries and colonial authorities but it did not gain ground until the late 1920s.[81] By contrast, maize, a novel crop introduced in the later nineteenth century and initially cultivated on a limited scale, became increasingly widespread by 1900, before becoming a

[79] R. Enscore et al., 'The changing triad of plague in Uganda: invasive black rats (*Rattus rattus*), indigenous small mammals, and their fleas', *Journal of Vector Ecology*, 45 (2020), 333–55.
[80] Simpson, *op. cit.*, 27–35; J.I. Roberts, 'The relationship of the cotton crop to plague, and its role as a vehicle for rats and fleas in East Africa', *Journal of Hygiene*, 35, 3 (1935), 388–403; Sussman, *op. cit.*, 348–49.
[81] F.F. Pinto and E.A. Kurd, 'Seventy years with wheat in Kenya', *East African Agricultural and Forestry Journal*, 36, Issue Sup. 1 (1970), 1–24.

paramount crop in the 1930s.[82] Cotton and maize cobs attracted rodents as well as their fleas. In the context of plague history, it is important to distinguish between wild (or sylvatic) and domestic (or commensal) rodents. In the case of the Great Lakes region, however, this distinction is problematic because the same association of 'wild' rodents with 'wild' space and 'commensal' rodents with 'domestic' space, as it is largely known in West Eurasia, does not hold. Thus, during the 1905–1906 expedition to the Rwenzori Mountains region (between Lake Albert and Lake Edward, on the Uganda–Congo border), Oldfield Thomas and Robert Wroughton caught several *Rattus rattus* species from local plains and woodland.[83] Conversely, early European explorers described local landscapes teeming with local 'wild' rats, both within and outside villages in savanna and shrubland. In his July 1887 diary, reflecting on his sojourn around Lake Albert, Emin Pasha stated that he had never seen such a multitude of rats 'jumping cheerfully around me and climbing onto my writing desk during the day, as I write, and performing grand dances jumping at night'.[84] Elsewhere, he complained of rats disturbing his sleep at night.[85] Arthur Jermy Mounteney Jephson, while staying at newly built Fort Bodo (near Lake Albert) in February 1888, noted the multitude of hungry rats, whose presence prompted members of the Pasha Relief Expedition to hang corn sacks nine feet above the ground.[86] The multitude of local rats, always attracted to maize, was also described by William Stairs, another member of the expedition, in his autumn 1887–winter 1888 diary. Stairs also noted that rats and fleas were in tandem disturbing his party's rest.[87] Clement John Baker, working on plague in Uganda since 1903, noted that natives' granaries, made of wicker works supported on rocks and standing only a foot or two above the ground, consistently attracted rats that not only spread the disease but also inflicted colossal losses to stored crops.[88]

Importantly, the rats described by Emin Pasha and other European explorers were undoubtedly native rodents – most likely, Natal multimammate mice and African grass rats (*Arvicanthis niloticus*), both notorious destroyers of cultivated and stored crops (initially millet, and later maize and cotton) and plague carriers in the region – rather than black rats (*Rattus rattus*).[89] Although *Rattus rattus* has been documented archaeologically in the coastal area of Kenya since the eighth to tenth century CE (as well as in South Africa since the eighth century), there is no evidence, textual, archaeological or palaeogenetic, of their presence in the Great Lakes region before the end of the nineteenth century.[90] It is assumed that the black rats invaded the Great Lakes landscapes either from India or the Swahili Coast (facilitated by the Uganda Railway), or

[82] C.C. Wrigley, *Crops and Wealth in Uganda: A short agrarian history* (Nairobi, 1970), 13–43, 75; M.P. Miracle, 'The introduction and spread of maize in Africa', *Journal of African History*, 6, 1 (1965), 49–50.

[83] O. Thomas and R.C. Wroughton, 'Zoological results of the Ruwenzori Expedition, 1905–1906: 17. Mammalia', *Transactions of the Zoological Society of London*, 19 (1909–10), 503.

[84] *Die Tagebücher von Dr. Emin Pascha: Band III*, F. Stuhlmann (ed.) (Hamburg, 1922), 370. On local rats, see 288.

[85] A.J. Mounteney-Jephson, *Emin Pasha and the Rebellion at the Equator* (London, 1890), 428.

[86] *The Diary of A.J. Mounteney Jephson: Emin Pasha Relief Expedition 1887–1889*, D. Middleton (ed.) (Cambridge, 1969), 222–23.

[87] *African Exploits: The diaries of William Stairs, 1887–1892*, R. Maclaren (ed.) (Montreal, 1998), 133–34, 159.

[88] Baker, *op. cit.*, 41.

[89] Hopkins, *op. cit.*, 41–43; J. Borchert et al., 'Invasive rats and bubonic plague in Northwest Uganda' in G.W. Witmer, W.C. Pitt and K. A. Fagerstone (eds), *Managing Vertebrate Invasive Species: Proceedings of an international symposium* (Fort Collins, 2007), 283–93; L.A. Fiedler, 'Rodent problems in Africa' in I. Prakash (ed.), *Rodent Pest Management* (Boca Raton, 1988), 42–45.

[90] H. Yu et al., 'Palaeogenomic analysis of black rat (*Rattus rattus*) reveals multiple European introductions associated with human economic history', *Nature Communications*, 13, 1 (2022), 2399, Data S2.1; D.M. Avery, 'Hitching a ride: the early history of black rat immigration into Southern Africa', *Biological Invasions*, 25 (2023), article 1061. The earliest evidence of *Rattus rattus* around the Great Lakes comes from Stuhlmann's expedition to Bukoba in 1892, in the course of which he caught some rats and brought their skulls to the Berlin Museum; see F. Dieterlen, 'Zur Ausbreitungsgeschichte der Hausratte (*Rattus rattus*) in Ostafrika', *Zeitschrift für angewandte Zoologie*, 66 (1978), 173–84, here 178. Stuhlmann's Bukoba expedition was followed by that of Thomas and Wroughton's 1905 to the Rwenzori Mountains region, in the course of which they caught several *Rattus rattus* species: Thomas and Wroughton, *op. cit.*, 503.

from Egypt and Sudan via the Nile.[91] Following the introduction of *Rattus rattus*, native inhabitants living in everyday proximity to various types of rat learned quickly to distinguish between plague outbreaks caused by *Rattus rattus* (referred to in Luganda dialects as *nsolima*), those triggered by *Mastomys natalensis* (previously classified as *Rattus coucha* and called *mvugu* in Luganda) and those caused by *Arvicanthis niloticus* (known as *messe* in Luganda).[92] In theory, there might have been another potential mechanism of plague spread – rat hunting and consumption. The Baganda prized giant rats (*Cricetomys gambianus*) as a delicacy, grilling them whole without removing the entrails, but, unlike for native *Mastomys coucha* or invasive *Rattus rattus*, there is no evidence that they were primary plague hosts.[93] The connection between rats, their mass die-outs, and plague outbreaks in humans has been understood by native communities since at least *kabaka* Kayabaggu's reign (c.1760–1790) when the latter ordered the destruction of rats attacking the capital.[94] The plague in the Imagi and Uhehe regions in 1886 was preceded by rat mortality.[95] Likewise, the 1902 plague in Nairobi, commencing in early March, was preceded by mass rat die-outs in late February.[96]

We have also to account for ectoparasites transmitting plague from rodents to humans (fleas) and/or directly between humans (fleas and lice). Investigations in Kenya and Uganda in 1926–1927 and 1930–1932 established that various types of flea, including *Xenopsylla brasiliensis* and *Xenopsylla cheopis*, had been thriving in cotton bales and on rats.[97] That fleas were abundant in East Africa was noted by early European explorers of the region. Mounteney Jephson complained about the multitude of fleas in the Lake Albert region of Uganda during the Emin Pasha Relief Expedition (1887–1889).[98] While studying local flora and fauna in 1877, Emin Pasha himself noticed the prevalence of fleas all over Uganda.[99] In late 1891 Franz Stuhlmann described the legs of local Baganda porters as literally covered with fleas, causing them to aggressively scratch themselves.[100] The multitude of lice, along with fleas and bugs, in human huts was noted by Johann Ludwig Krapf during his September 1844 travels east of Mombasa into the mainland.[101] In a similar vein, the ubiquitous presence of lice was discussed by Emin Pasha in his exploration diaries.[102] John Roscoe, an Anglican missionary living in East Africa from 1884 until 1909, mentioned that the bark clothes of the Banyoro people attracted a great multitude of body-lice, to the point that the barkcloth had to be destroyed.[103] Despite cotton's introduction under Kabaka Semakookiro (1800–1812) and industry growth from 1902, most Ugandan and Kenyan commoners continued wearing barkcloth, which might attract lice and fleas.[104] Lice were confirmed as plague vectors during the 2004–2009 outbreak in north-

[91]Dieterlen, *op. cit.*, 174–80; E. Schwarz, 'The origin of African house-rats', *Proceedings of the Zoological Society of London*, 104, 4 (1934), 723–26.
[92]Bodleian Library, Oxford, Mss. Afr. s. 1091, Papers of Dr Clement John Baker and Lt George Baker, Box 3/7 (Appendix); Hopkins, *op. cit.*, 41.
[93]Roscoe, *Baganda, op. cit.*, 449–50; Hopkins, *op. cit.*, 44; Enscore et al., *op. cit.*
[94]Kagwa, *Kings of Buganda, op. cit.*, 83–84; Kiwanuka, *op. cit.*, 81, 150.
[95]Kolonial-Abteilung des Auswärtigen Amts, *op. cit.*, 62.
[96]M.F. Hill, *Permanent Way: The story of the Kenya and Uganda Railway* (Nairobi, 1949), 240.
[97]Thornton, *op. cit.*; Roberts, 'The relationship of the cotton crop', *op. cit.*
[98]*Diary of A.J. Mounteney Jephson, op. cit.*, 311; Mounteney-Jephson, *Emin Pasha, op. cit.*, 339.
[99]*Emin-Pascha: Eine Sammlung von Reisebriefen und Berichten* (Leipzig, 1888), 52, 171; *Emin Pasha in Central Africa: Being a Collection of His Letters and Journals* (London, 1888), 23, 55, 173.
[100]F. Stuhlmann, *Mit Emin Pascha ins Herz von Afrika* (Berlin, 1894), vol. 2, 150.
[101]J.L. Krapf, *Reisen in Ost-Afrika, Ausgeführt in dem Jahren 1837–55* (Stuttgart, 1858), 221.
[102]For instance, *Die Tagebücher von Dr. Emin Pascha. Band II*, F. Stuhlmann (ed.) (Hamburg, 1919), 3, 69.
[103]J. Roscoe, *The Bakitara or Banyoro* (Cambridge), 238.
[104]Roscoe, *Baganda, op. cit.*

eastern Congo near Uganda.[105] Importantly, Mas Fiol et al.'s study analysed 15 genomes from the same outbreak, all of which were caused by strains of 1.ANT1.[106]

Endogenous plague spread enablers: anthropogenic factors

Human movement: the slow phase (before c.1840)

No study of plague spread can ignore the fact that transported goods themselves – especially grains and textiles – acted as 'moveable reservoirs' in which fleas and bacteria could thrive for weeks without hosts and their bloodmeals.[107] Hence, both the pace and geographic range of plague spread mirrored those of the transported goods and people who were involved in local and trans-regional trade. Indeed, the movement of humans and goods – most commonly through trade, migration and warfare (with these categories often overlapping) – is the single most important trigger of trans-regional plague spread. Plague spread depends on regional interconnectedness, with more commercialised, urbanised, densely populated and developed areas experiencing faster and more pervasive spread of plague – and the other way around.

At first, the initial confinement of plague to Buganda, its limited spatio-temporal spread within local territories and its absence from other regions around the Great Lakes during the first phase of spread (c.1700–1840) appears surprising – especially when compared to the fast spread and wide coverage of plague waves in Eurasia and North Africa during the Second Pandemic. To appreciate this phenomenon, it is necessary to consider factors that may have accounted for its slow and limited circulation within the kingdom and hindered its spread outside of it. Although plague bacteria are capable of spreading without human mediation in rodent colonies (and the Great Lakes were rife with rodents), human institutions and agency facilitate their circulation and transmission in space and time.

Before c.1830, the Great Lakes area was one of the most isolated regions of the globe, largely unknown to the outside world. Even within the Interlacustrine region itself, however, it was not until the late eighteenth century that we witness the first traits of inter-regional trade between neighbouring kingdoms – and Buganda was no exception. Thus, there are occasional findings of Entebbe-type pottery (c.1000–1500) on coastal sites of western Kenya, on the Uganda border, but no farther than that.[108] There is no evidence – archaeological or textual – of any change in the subsequent centuries. Some change came under *kabaka* Junju (1790–1800), who was the first ruler to procure copper and metalware from the kingdom of Karagwe.[109] Under his son Semakookiro (1800–1812), the Baganda cemented their commercial ties with Karagwe, which became famous for its wealth towards the end of the eighteenth century and maintained trade relations with its neighbours since the reign of King Ruhinda VI Orushongo (c.1794–1819).[110] The trade was based on the acquisition of cotton and cowrie shells (harvested off the Swahili Coast) in exchange for ivory. Allegedly, Semakookiro sought to promote ivory harvesting and

[105]R. Piarroux et al., 'Plague epidemics and lice, Democratic Republic of the Congo', *Emerging Infectious Diseases*, 19 (2013), 505–06.
[106]Mas Fiol et al., *op. cit*.
[107]O.J. Benedictow, *The Complete History of the Black Death* (Woodbridge, 2021), 53–56.
[108]S. Amin, 'The Archaeology of the Sesse Islands and their Contribution to the Understanding of Great Lakes Ceramics' (Ph.D., University College London, 2015), 84; C.Z. Ashley, 'Ceramic Variability and Change: A Perspective from Great Lakes Africa' (Ph.D., University College London, 2005), vol. I, 243, 422.
[109]Kagwa, *Customs of the Baganda, op. cit.* 161; M.S. Kiwanuka, 'The Traditional History of the Buganda Kingdom; with Special Reference to the Historical Writings of Sir Apolo Kaggwa' (Ph.D., University of London, School of Oriental and African Studies, 1965), 441; Kagwa, *Kings of Buganda, op. cit*., 99.
[110]Kagwa, *Kings of Buganda, op. cit*., 99; I.K. Katoke, *The Making of the Karagwe Kingdom* (Dar es Salaam, 1970), 22.

trade as a response to overgrazing of elephants in his kingdom.[111] In addition, Semakookiro expanded the barkcloth industry, whose goods were imported to Busoga, Bunyoro, and farther to Karagwe and Rwanda.[112] Around the same time or slightly later, Baganda traders began acquiring salt from Tooro and Bunyoro kingdoms.[113] In addition, beads were procured from the kingdom of Kiziba (on the Central-Western shore of Lake Victoria).[114]

No large-scale migrations occurred around the Great Lakes after the late seventeenth-/early eighteenth-century movements of the Luo/Lwoo from southern Sudan into Nyanza (Kenya), the Iteso from the Usuku district (north-eastern Uganda) southwards into Bukedi, and the Alur around Lake Albert.[115] Ironically, the Luo/Lwoo and Iteso migration, as will be suggested below, may have been the actual source of the initial introduction and spread of *Yersinia pestis* in the Great Lakes region around the same time. There were some instances of small-scale regional migration, with local chiefs and their subjects moving from one part of Buganda to another, or to other neighbouring kingdoms, seeking refuge. For instance, during Kikulwe's and Mawanda's reigns (c.1730–1760), some families of the Elephant clan fled the country because of their conflict with the rulers.[116] Similarly, Semakookiro's reign (c.1800–1812) saw the exile of the so-called Bakunta – political opponents, associated primarily with the Lungfish clan – to Bunyoro, Tooro, Ankola and Nyanza province in Kenya (on today's border with Uganda).[117] Political persecution resulting in exile was likewise occurring under Ssuuna II (1830–1856/1857).[118] However, these migrations involved parts of clans, rather than ethnic groups, and as such appear to be small in scale (as well as in geographic range).

As far as armed conflicts are concerned, these were small-scale regional raids either confined within Buganda or limited to neighbouring territories, often for the purpose of slave and cattle plunder. In the course of the seventeenth and eighteenth centuries, there were frequent mutual raids between Bunyoro and Buganda.[119] Thus, *kabaka* Junju (c.1790–1800) invaded Buddu, upon the rumours that it became abundant in cattle, and once victorious, took much livestock.[120] Junju also invaded Kiziba (on the Central-Western shore of Lake Victoria) at some point.[121] During Ssuuna II's invasion of Busoga, towards the end of his reign (1856/1857), Abasigulu people raided women and cattle on Wamakofu island.[122] During his 1865 expedition to Busoga, the army of *kabaka* Mutesa I captured many cattle and slaves.[123] Although some of these campaigns may have facilitated the spread of plague, their limited scale and range also imply their limited ability to do so.

Whatever form human movement took – trade, migration or warfare – it was being conducted on a small scale with limited range. Moreover, human movement facilitates long-distance spread of plague efficiently only as long as fleas and bacteria can be transported in

[111]Kagwa, *Kings of Buganda, op. cit.*, 99.
[112]J. Tosh, 'The Northern Interlacustine region' in R. Gray and D. Birmingham (eds), *Pre-Colonial African Trade: Essays on trade in Central and Eastern Africa before 1900* (Oxford, 1970), 106.
[113]Roscoe, *Baganda, op. cit.*, 438–39.
[114]Kiwanuka, 'The traditional history', *op. cit.*, 451.
[115]J.C.D. Lawrance, *The Iteso: Fifty years of change in a Nilo-Hamitic tribe of Uganda* (Oxford, 1957), 9–10; A. Southall, 'Alur tradition and its historical significance', *Uganda Journal*, 18, 2 (1954), 148–51.
[116]Kiwanuka, 'The traditional history', *op. cit.*, 438.
[117]*ibid.*, 432–36; R. Oliver, 'The Baganda and the Bakonjo', *Uganda Journal*, 18 (1954), 31–33.
[118]Kiwanuka, 'The traditional history', *op. cit.*, 438.
[119]*ibid.*, 448.
[120]Kagwa, *Kings of Buganda, op. cit.*, 90.
[121]*ibid.*, 91.
[122]*ibid.*, 128.
[123]*ibid.*, 156.

temporary storage (grain sacks or textiles).[124] In contrast with much of Eurasia and North Africa, Baganda communities hardly relied on either. The only grain grown and consumed in Buganda was, as noted, millet, but it was grown in small quantities in local gardens rather than fields, and was used for brewing, rather than baking.[125] The majority of calories were derived from meat (beef, mutton, chevon and poultry), yams and fish, supplemented with plantation fruit and legumes (peas and beans).[126] As far as clothing goes, barkcloth, attracting human lice, remained virtually the only type of material until the colonial era. It was not until the reign of Semakookiro (c.1800–1812) that cotton was introduced to Buganda from Karagwe – but its use remained limited to the elites until Mutesa I's reign (1856/1857–1884).[127] While there was potential for plague to spread from human to human, mediated by ectoparasites, its speed and trajectory were likely to have been inefficient.[128] In other words, there was a series of barriers to a trans-regional spread of plague in the pre-1840 era.

Commercialisation of the Great Lakes region (from c.1840)

The real change came with the arrival of Muslim traders from Khartoum and Oman and their settlement in the region from the 1830s onwards. This meant a significant expansion of the commercial range and scale of the Baganda. There is evidence of Arab commercial activity around Lake Tanganyika as early as 1831, and by 1839 they were actively present in Unyanyembe (northern Tanzania).[129] In Buganda proper, Arab merchants are attested since 1844.[130] The commercial networks of the Arabs were facilitated by the Omani capture of Mombasa in 1837 and the subsequent shift of the sultan's court from Muscat to Zanzibar three years later.[131] During the following two decades, the Muslims founded a series of trade hubs between the Swahili Coast and the Great Lakes – including Puge, Tabora (both south of Lake Victoria), Kafuro (on the east bank of the Kagera river) and Ujiji (on the eastern shore of Lake Tanganyika).[132] In the 1850s, three main trade routes linked the Great Lakes to the outside world: north via the White Nile to Sudan, north-east to Mombasa, and south-east via Tabora to the port of Bagamoyo.[133] Both Mombasa and Bagamoyo housed large Indian communities, primarily from Gujarat – Hindis, Parsis and Ismaili Muslims.[134] Those routes and settlements were sketched, albeit in a highly imprecise manner, on the maps of the earliest European explorers, including Johann Ludwig Krapf, Jakob Erhardt and Richard Burton.[135]

When explorers reached the Great Lakes in the 1850s, they found it thriving in regional and long-distance trade, with Arabs linking it to the Swahili Coast and Sudan, and Gujaratis connecting the coast to Oman and India. Regionally, trade goods included wild coffee from

[124]Roscoe, *Baganda, op. cit.*, 108, 432.
[125]*ibid.*, 432, 434.
[126]*ibid.*, 161, 432–42.
[127]*ibid.*, 225, 227–28.
[128]Piarroux et al., 'Plague epidemics', *op. cit.*, 505–06.
[129]A. Oded, *Islam in Uganda: Islamisation through a centralised state in pre-colonial Africa* (Jerusalem, 1974), 25.
[130]J.M. Gray, 'Ahmed bin Ibrahim – the first Arab to reach Buganda', *Uganda Journal*, 11, 2 (1947), 82.
[131]Oded, *op. cit.*, 26.
[132]Sussman, *op. cit.*, 350; Tosh, *op. cit.*, 111.
[133]Oded, *op. cit.*, 24.
[134]On Gujarati merchants in East Africa, see E.A. Alpers, 'Gujarat and the trade of East Africa, c. 1500–1800', *The International Journal of African Historical Studies*, 9, 1 (1976), 22–44; E.A. Alpers, *East Africa and the Indian Ocean* (Princeton, 2009).
[135]J. Erhardt, 'Mémoire zur Erläuterung der von ihm und Johannes Rebmann Zusammengestellten Karte von Ost- und Central-Afrika', *Petermanns Geographische Mitteilungen*, 2 (1856), Tafel 1; Krapf, *Reisen in Ost-Afrika*, vol. 2, 523; https://library.princeton.edu/visual_materials/maps/websites/africa/burton/burton-map.html (accessed 1 January 2026).

Bunyoro and Buganda to Karagwe, tobacco from Ankole to Karagwe and Bunyoro, and salt from Kibero and Busongora to Buganda.[136] To these, we should add the exchange of ivory for brass between Acholiland and Buganda, and of ivory for ironware between Lango and Iteso. Likewise, Bunyoro was producing and exporting good-quality iron, prized as a durable material for spears all over the Great Lakes.[137]

As far as long-distance trade is concerned, the two main articles of export from the Great Lakes region, including Buganda, were ivory and slaves.[138] Ivory was exported from both Khartoum and Zanzibar from the 1850s, primarily into Europe and North America, where it was used as a material for piano and organ keys, billiard balls, cutlery, toiletries, figurines, chess and many other articles.[139] The total volume of East African ivory imported to the United Kingdom annually rose from about four tonnes in 1855 to 140 tonnes in 1875.[140] Accordingly, the prices rose from 47 to 90 'Maria Teresa Dollars' per *frasela* (35 lbs), in Zanzibar markets.[141] The expansion of ivory trade led to the emergence of professional elephant hunters in Bunyoro – an area abundant in elephants, especially after their forced driving from Buganda during Semakookiro's reign (c.1800–1812).[142]

Slaves were brought from the interior to markets in both Zanzibar and Khartoum, where the slave trade appears to have reached its peak from the 1840s until the 1870s. Around that time, about 15,000 slaves were exported annually from the area overlapping with today's Tanzania, with an average price per slave in Zanzibar markets rising from about eight 'Maria Teresa Dollars' in 1849 to 25–30 in 1871.[143] From Zanzibar, most slaves were sent to Muscat, then to Arabia for work in pearling, date plantations, or (in the case of women) domestic service. Triggered by a rising international demand and thus price for dates and pearls, both sectors saw considerable expansion from the 1870s.[144] From Khartoum slaves were taken to Egyptian cities to be employed in domestic sectors, and to eastern Arabia to be used in agriculture.[145]

The penetration of European powers into East Africa led to the abolition of the slave trade in the region. Under British pressure, both Zanzibar and Khartoum shut their slave markets in, respectively, 1873 and 1880.[146] In the following two decades, the slave trade similarly declined and disappeared from the coast of Banaadir and Bajun in southern Somalia, territories gradually placed under Italian rule.[147] Likewise, the slave trade was gradually suppressed in Egypt, under indirect British rule, from 1877.[148] In the interior, however, slavery and the slave trade persevered somewhat longer – until the British, German and Belgian takeover in the late 1880s–1890s.[149]

[136]Tosh, *op. cit.*, 104–07.
[137]*ibid.*, 115–16.
[138]*ibid.*, 115–16.
[139]R.W. Beachey, 'The East African ivory trade in the nineteenth century', *Journal of African History*, 8, 2 (1967), 269–90, here 287–88.
[140]A. Sheriff, *Slaves, Spices and Ivory in Zanzibar: Integration of an East African commercial empire into the world economy, 1770–1873* (Woodbridge, 1987), 258.
[141]Sheriff, *op. cit.*, xix and 255–56.
[142]Tosh, *op. cit.*, 116; Kagwa, *Kings of Buganda, op. cit.*, 99.
[143]P. Manning, *Slavery and African Life: Occidental, Oriental and African slave trades* (Cambridge, 1990), 81; Sheriff, *op. cit.*, 68–69.
[144]R.C. Allen, 'Slavery in Arabia and East Africa, 1800–1913' (Working Paper #0066 New York University, Abu Dhabi, 2021).
[145]G. Baer, 'Slavery in nineteenth century Egypt', *Journal of African History*, 8, 3 (1967), 417–41; B. Reilly, *Slavery, Agriculture, and Malaria in the Arabian Peninsula* (Athens, OH, 2015).
[146]A. Moore-Harell, 'Slave trade in the Sudan in the nineteenth century and its suppression in the years 1877–80', *Middle Eastern Studies*, 34, 2 (1998), 113–28; A. Sheriff, *op. cit.*, 223–44.
[147]E.B. Martin and T.C.I. Ryan, 'The slave trade of the Bajun and Benadir Coasts', *Transafrican Journal of History*, 9, 1 (1980), 103–32.
[148]Baer, *op. cit.*
[149]See various studies in H. Médard and S. Doyle (eds), *Slavery in the Great Lakes Region of East Africa* (Woodbridge, 2007).

The main exchange article for ivory and slaves was Gujarati cotton and cotton textiles. It has been estimated that between 1850 and 1890, the annual volume of cotton cloth imports into East Africa rose from less than 0.1 to about 1.6 yards *per capita per annum*. Within colonial Uganda, equivalent figures rose from about 0.95 to 6.6 yards between 1903 and 1913.[150] At the turn of the twentieth century, cotton cultivation was introduced into the Great Lakes by colonial authorities: first into German Tanganyika (1900) and two years later into Kenya and Uganda.[151] In Uganda annual output rose exponentially from fewer than 1,000 bales of lint in 1907 to nearly 200,000 in 1925.[152] The impact of cotton trade and production on plague in Uganda has already been noted. In addition to cotton, there were more minor products, including firearms, opera glasses, parasols, scissors, cooking pots, rings, daggers, picture books and dolls.[153]

The colonial economy and labour migration

From the 1850s the integration of East African Interior into Indian Ocean trade expanded the inter-regional movement of people and goods, inadvertently spreading pathogens via infected rodents and ectoparasites; the influx of Arab, Gujarati and European traders also created new jobs for native communities that further increased mobility. The proliferation of migratory workers was partly associated with mass slave ransoming and manumission, encouraged by colonial authorities in the 1880s and 1900s.[154]

Remarkably, all transportation was done by caravans of human porters, also acting as security providers.[155] Although inter-regional porterage involved different ethnic groups, the Wanyamwezi (Nyamwezi) people of western Tanzania played a particularly important role. Arab merchants relied upon the services and local knowledge of Wanyamwezi porters from their initial arrival around Lake Tanganyika in 1831.[156] The fact that East African trade was reliant on human porterage rather than animal traction, wheel-carts and paved roads, was due to both cultural and environmental factors. The dense tropical rainforest covering much of Congo to the west and western Kenya to the east made the development of inter-regional infrastructure challenging. The situation was exacerbated further by the endemic presence of the tsetse fly (widespread all over rainforest and savannah regions of Sub-Saharan Africa), causing the infamous 'sleeping sickness' in both humans and animals and limiting livestock use to meat and dairy. Missionary and colonial efforts to improve transport by paving roads and using donkeys, oxen, carts and Indian elephants failed due to environmental conditions, tsetse infestation and local resistance, especially from caravan porters and traders.[157] The adoption of donkey packing by the Wanyamwezi around Tabora was an exception rather than the rule.[158]

[150]K. Frederick, 'Global and local forces in deindustrialization: the case of cotton cloth in East Africa's Lower Shire Valley', *Journal of Eastern African Studies*, 11, 2 (2017), 266–89, here 269.
[151]T. Sunseri, 'The Baumwollfrage: cotton colonialism in German East Africa', *Central European History*, 34, 1 (2001), 31–51; Roberts, 'The relationship of the cotton crop', *op. cit*.
[152]Roberts, 'The relationship of the cotton crop', *op. cit*. One bale = 400 lbs.
[153]Beachey, *op. cit*., 274.
[154]T. Sunseri, *Vilimani: Labour migration and rural change in early colonial Tanzania* (Portsmouth, 2002), 32–40.
[155]A. Greiner, *Human Porterage and Colonial State Formation in German East Africa, 1880s–1914* (Cham, 2022).
[156]A. Roberts, 'Nyamwezi Trade' in R. Gray and D. Birmingham (eds), *Pre-Colonial African Trade: Essays on trade in Central and Eastern Africa before 1900* (Oxford, 1970), 39–74; Oded, *op. cit*., 25–26.
[157]K. Pallaver, 'Donkeys, oxen and elephants: in search for an alternative to human porters in nineteenth century Tanzania', *Africa: Rivista Trimestrale di Studi e Documentazione*, 65 (2010), 289–309.
[158]Pallaver, *op. cit*., 296.

The failure to introduce animal traction in the Great Lakes region may have slowed the speed of plague spread, but it certainly did not hinder it. From the 1850s, and especially the 1870s, commercialisation spurred long-distance human traffic within the Great Lakes and between the lakes and the Swahili Coast. Professional porters, such as the Wanyamwezi, were hardy individuals, capable of covering 13 miles a day with 70 lbs of goods on their head and shoulders.[159] Lighter loads could be carried faster (17–22 miles a day), with some light messengers allegedly covering 40–50 miles a day.[160] In German Tanganyika, local authorities saw porters as un-sanitary workers and super-spreaders of infectious diseases, including plague, with caravan routes acting as highways of plague. From 1902 they founded special military posts to monitor and quarantine infected or suspected porters. However, this strategy failed and many porters moved undetected, potentially spreading pathogens.[161]

Agricultural plantations growing primarily cotton, tobacco and coffee also attracted migratory labour. The earliest colonial plantations in the region appeared in German Tanganyika in the 1880s, although it was not until the early 1900s that they gained ground.[162] Likewise, the first cash crop plantations in British Uganda appeared in 1902 with the introduction of cotton cultivation; this subsequently expanded, together with tobacco and coffee.[163] These new opportunities resulted in an influx of migratory workers belonging to different ethnic groups: for instance, the Wanyamwezi into Tanganyika, and the Soga, Nyoro, Toro and Ziba into Buganda.[164]

Many native labourers worked on the German Usambara Railway (350 km from Tanga to Moshi) and the British Uganda Railway (1060 km from Mombasa to Kisumu) during the 1890s.[165] This implied not only laying the tracks but also cutting and carrying forest trees – causing massive deforestation along the rail lines and potentially facilitating the mass migration of sylvatic rodents.[166] German colonial authorities encouraged the Wanyamwezi to settle in the Tanga region with preferential tax and landholding terms, leading thousands to work on the Usambara Railway in the 1890s.[167] Likewise, large numbers of Wanyamwezi and individuals from other ethnic groups worked on the Uganda Railway (1896–1902). By 1898, 5,096 of the 13,738 workers were local, the rest migrants from British India.[168] The number of Indian workers rose to nearly 17,000 of a total of around 19,500 by 1902, when construction ended and most returned home.[169] The construction of railways, requiring people to work close together in gangs and be housed in crowded temporary lodgings, was another potential mode of plague transmission. For example, the plague outbreak in Nairobi in spring–summer 1899 coincided with the completion of the Mombasa–Nairobi section of the Uganda Railway, opened in

[159]Greiner, *op. cit.*
[160]S.J. Rockel, *Carriers of Culture: Labour on the road in nineteenth century East Africa* (Portsmouth, 2006), 81–82.
[161]Greiner, *op. cit.*, 169–70.
[162]Sunseri, 'Baumwollfrage', *op. cit.*
[163]Wrigley, *op. cit.*, 13–43.
[164]Sunseri, *Vilimani, op. cit.*; P.G. Powesland, 'History of the migration in Uganda' in A. I. Richards (ed.), *Economic Development and Tribal Change: A study of immigrant labour in Buganda* (Cambridge, 1954), 20.
[165]Sunseri, *Vilimani, op. cit.*
[166]N. Aselmeyer, 'The Shadow Line: railway and society in colonial East Africa, c. 1890–1914' (Ph.D., Florence, European University Institute, 2022), 231–71.
[167]Sunseri, *Vilimani, op. cit.*, 60, 138 and 168.
[168]Aselmeyer, *op. cit.*, 52–53.
[169]*ibid.*, 53; Hill, *op. cit.*, 240.

August that year.[170] The completion and opening of the Uganda Railway in 1902 and the Usambara Railway in 1911 facilitated increased volume, speed and frequency of long-distance movement of people, goods and pathogens. From 1904 human plague broke out annually in Uganda until 1947 (and again from 1986 until the present) and in Kenya until 1964, while in Tanzania, annual outbreaks with occasional short breaks continued until 2011.[171]

Plague, conflict and refugees

Local plague outbreaks themselves sometimes led to human migration, which contributed to the regional or trans-regional spread of the disease. During the c.1874 outbreak in the Usemi hills (Kisumu, North-East Kenya), Jaluo communities left their upland villages for the plains, inadvertently spreading plague, which then ravaged the region for two years.[172] When plague reached the Nizi territories of East Congo (c.1888–1898), locals blamed migrating Mfulayembe people for bringing it from Uganda.[173] Moreover, plague outbreaks often coincided with military conflicts, local expansionism, or civil strife. In Buganda, expansionism reached its peak under Mutesa I (1854–1884). In or around 1876, Mutesa's soldiers invaded Bukedi territories on the north-eastern shore of Lake Victoria, only to contract plague and spread the disease into Buganda while retreating.[174] In 1880, there was a plague outbreak in Busoga, during a Baganda campaign there.[175] The same expansionist policies were promoted by other rulers of the Great Lakes. Thus, when the plague spread, apparently for the first time, to the Uhehe region of Central Tanzania in 1886, it was said to have been introduced from the north during Chief (Sultan) Mkwawa's expansionist campaigns.[176] The 1860s–1880s saw the climax of regional and trans-regional conflicts in the Great Lakes area.[177] In other instances, plague spread was a result of more local conflicts. Thus, the 1899–1900 plague outbreak in Kiziba Kingdom was partly facilitated by the emigration of King Rwehabula's opponents from his domains.[178]

How did plague spread into the Great Lakes around the end of the seventeenth century?

The remainder of this article returns to the question, long tackled by both historians and plague scientists, of how plague spread into the Great Lakes around the end of the seventeenth century. Arguably, the most common theory is that the bacteria were introduced from the East (Oman or India) via the Swahili Coast. Several researchers, including Simpson (1915),

[170]J.H. Patterson, *The Man-Eaters of Tsavo and other East African Adventures* (London, 1912), 296; Hill, *op. cit.*, 172.
[171]Neerinckx, Bertherat and Leirs, *op. cit.*, SI, 39–46, 101–23; L. Haikukutu et al., 'Plague in Tanzania: first report of sylvatic plague in Morogoro region, persistence in Mbulu focus, and ongoing quiescence in Lushoto and Iringa foci', *International Journal of Infectious Diseases*, 4 (2022), 105–10.
[172]Milne, *op. cit.*, 178–79; Simpson, *op. cit.*, 24.
[173]Schwetz et al., *op. cit.*, 228.
[174]Baker, *op. cit.*, 38–41.
[175]Kiwanuka, 'The traditional history', *op. cit.*, 559.
[176]Kolonial-Abteilung des Auswärtigen Amts, *op. cit.*, 62; Thornton, *op. cit.*, 5; Roberts, 'The endemicity of plague', *op. cit.*, 212–13.
[177]Koponen, *op. cit.*, 648–55.
[178]M.K. Webel, *The Politics of Disease Control: Sleeping sickness in Eastern Africa, 1890–1920* (Athens, OH, 2019), 136–37.

Thornton (1930), Roberts (1935), Twigg (1984), Ziwa and colleagues (2013) and Green (2018), linked the initial introduction to the 1696–1697 Omani siege of Portuguese Mombasa, during which 'swelling sickness' (*inchaçaes*) struck.[179] They interpret the term as a possible plague outbreak, with some suggesting it was likely introduced by either the Portuguese fleet from Goa or the Omanis.[180] Several issues make this scenario impossible. Firstly, a close analysis of the *História de Mombaça* – the only source about the siege episode, written shortly after the event itself – reveals that the mysterious *inchaçaes* was not plague, but another disease. According to the same source, some corpses of the Mombasa epidemic were subjugated to dissection by Portuguese garrison members, who discovered enlarged liver and lungs 'swollen as barrels', and nobody knew what the disease was.[181] It is likely that the Portuguese garrison (which would have included at least one medic) knew what plague was, given the harsh outbreak in Portugal in 1680–1681 and the availability of countless plague treatises for consultation.[182] Significantly, one 1522 Portuguese document mentions a ship arriving in India (most likely, Goa), whose passengers arrived 'swollen' (*inchados*), because of their appallingly bad working and diet conditions, and filled local hospitals.[183] Hence, the *inchaçaes* appear to have been associated with some tropical disease, possibly related to navigation conditions in the Indian Ocean. Secondly, there is no evidence of any plague outbreak in Mombasa, Oman and Goa around 1700 – or, in fact, until a much later date. Again, the earliest reference to plague in Mombasa comes from 1898, apparently brought from the Great Lakes region.[184] Likewise, it appears that both Oman and Goa were plague free until, respectively, 1899 and 1901.[185] Both Mombasa (until the Omani conquest of 1698) and Goa are well endowed with Portuguese administrative records, while Muscat boasts abundant Portuguese and Dutch records – all mentioning different epidemic outbreaks, including smallpox, cholera and fevers, but not plague.[186] Likewise, no plague outbreak is mentioned in the so-called *Pate Chronicle* – a native North Swahili Coast history, completed in the late nineteenth century (with some early twentieth-century additions), but going back to the early thirteenth century.[187] Finally, if plague were imported from Mombasa, Oman or Goa, then it would have had to travel westwards to reach the Great Lakes from the Swahili Coast. As noted, plague moved in the opposite direction, from the Great Lakes to the Swahili Coast and then across the Indian Ocean to South Arabia in the closing years of the nineteenth

[179]Simpson, *op. cit.*, 17; Thornton, *op. cit.*, 5–6; Roberts, 'The endemicity of plague', *op. cit.*, 206; G. Twigg, *The Black Death: A biological reappraisal* (London, 1984), 27–28; Ziwa et al., *op. cit.*, 2; Green, 'Putting Africa on the Black Death map', *op. cit.*, 23. Médard, too, suggested that the early outbreaks in Buganda might be associated with plague activity in the Indian Ocean or, Egypt: Médard, 'Croissance et crises', *op. cit.*, vol. 1, 74. Kilonso anachronistically suggested that plague 'is thought to have been introduced to East Africa from Egypt, Arabia and India by various medieval traders including slave and caravan traders': B.S. Kilonso, 'A survey of rodents and their flea ectoparasites in North-Eastern Tanzania', *East African Journal of Medical Research*, 3, 3 (1976), 117–26, here 117.

[180]H. Sassoon, 'The sinking of the Santo António de Tanná in Mombasa harbour', *Paideuma: Mitteilungen zur Kulturkunde*, 28 (1982), 101–08, here 103–04; Green, 'Putting Africa on the Black Death map', *op. cit.*, 23–24.

[181]Lisbon, Biblioteca Nacional de Portugal, Fundo Geral, Códice 584, fols. 81–82; J. Strandes, *Die Portugiesenzeit von Deutsch und Englisch-Ostafrika* (Berlin, 1899), 259.

[182]M.H.V. Barbosa and A. de Deus Godinho, *Crises de mortalidade em Portugal desde meados do século XVI até ao início do século XX* (Guimarães, 2001), 13.

[183]*Documentos sobre os Portugueses em Moçambique e na África Central, 1497–1840, Vol. VI (1519–1537)* (Lisbon, 1969), 77.

[184]Simpson, *op. cit.*, 19.

[185]Floor, *op. cit.*, 134; F. da Silva Gracias, *Health and Hygiene and Colonial Goa, 1510–1961* (New Delhi, 1994), 266–67.

[186]Floor, *op. cit.*, 133–37; da Silva Gracias, *op. cit.*, 266–68. In her handlist of historical outbreaks of epidemic diseases in Goa, da Silva Gracias lists 'Plague (bubonic)' in 1570, without reference or substantiation (*op. cit.*, 266). Elsewhere in the book, she identifies the 1570 outbreak as '[c]holera of virulent nature' (88), and with 'fevers' (90). Hence, the association of the 1570 outbreak with plague cannot be accepted.

[187]*The Pate Chronicle*, M. Tolmacheva (ed. and trans.) (East Lansing, 1993).

century. In light of all this, the Swahili Coast can be excluded as a point of plague entry into the Great Lakes region.

In her 2018 article, Monica Green suggested, in addition to the Swahili Coast, three other potential routes: (1) from North Africa, across the Sahara, into the Chad basin; (2) from Ethiopia; and (3) from Egypt and Sudan, via the White Nile.[188] However, the first two of these theories are problematic. As far as the trans-Saharan route is concerned, there is no evidence that plague had ever crossed into central or eastern Sahel via the Chad basin. No native chronicle mentions plague outbreaks at any point.[189] The earliest references to plague outbreak in Nigeria and Cameroon come from, respectively, 1923 and 1961, while in Niger, Chad and Central African Republic there appears to be no history of plague at all in the twentieth century.[190] In Ethiopia there were recurrent waves of epidemics, of which at least some appear to have been caused by plague, between the early fifteenth century and 1635 (c.1403, at some point between c.1414 and 1430, c.1431–1435, at some point between c.1454 and 1468, in 1490, 1497, 1508, c.1520, 1535–1537, 1563–1564, 1567–1568, possibly 1579, 1603, possibly 1611, 1618–1619, 1626–1627, and 1634–1635), but none reported ever since – in contrast with other epidemic diseases.[191] Likewise, no plague epidemics are reported in Ethiopia in the twentieth century.[192] Hence, we may discard the Ethiopian theory as well.

This leaves us with only one remaining possibility: Egypt via the White Nile. On the most basic level, this scenario is more plausible than all the others because of the geographic proximity of the earliest recorded outbreaks of *kawumpuli* – confined to the Kawumpuli Temple built by *kabaka* Kayemba (c.1670–1700) in Buyego – to the Nile.[193] Buyego is situated about 75 km to the west of the Nile's origin, implying that the disease may have initially been introduced from the north, by the way of the Nile, rather than from elsewhere.

In Egypt, plague had established itself since the Black Death, seemingly local reservoirs in Upper Egypt and around Cairo. To reach the Great Lakes, the pathogen would need to travel some 4500 km along the Nile from its Mediterranean delta to Lake Victoria, or some 3700 km from a middle point of Upper Egypt. The travel would involve crossing all six cataracts, before merging into the White Nile near today's Khartoum. At first glance, transferring plague in these circumstances appears anything but possible, for two reasons. Firstly, such a journey, without long stops or delays, would have taken four or five months, assuming a camelback travel speed of 30 km a day from Egypt to Sennar (the capital of the Funj Sultanate) and then

[188]Green, 'Putting Africa on the Black Death map', *op. cit*., 22–25.
[189]For example, H.R. Palmer, 'The Kano Chronicle', *Journal of the Royal Anthropological Institute of Great Britain and Ireland*, 38 (1908), 58–98, covering North Nigeria c.1000–1892; *A Sudanic Chronicle: The Borno expeditions of Idrīs Alauma (1564–1576) according to the account of Aḥmad b. Furṭū*, D. Lange (ed. and trans.) (Wiesbaden, 1987); *Chronologie et histoire d'un royaume Africain (de la fin du 10e siècle jusqu'à 1808): le diwan des sultans du (Kanem-) Bornu*. D. Lange (ed. and trans.) (Wiesbaden, 1977); *Un manuscrit arabe sur l'histoire du Royaume Peul de Kontcha dans le Nord-Cameroun (XIXe–XXe siècle)*, H. Adama and T.M. Bah (eds) (Rabat, 2001).
[190]Neerinckx, Bertherat and Leirs, *op. cit*., SI, pp. 10, 89.
[191]Derat, *op. cit*., 5–9; R. Pankhurst, 'The history of famine and pestilence in Ethiopia prior to the founding of Gondär', *Journal of Ethiopian Studies*, 10, 2 (1972), 37–64; Slavin, 'Jinn in the Mountains', *op. cit*.
[192]S. Neerinckx et al., 'Geographic distribution and ecological niche of plague in Sub-Saharan Africa', *International Journal of Health Geographics*, 7, 54 (2008), https://doi.org/10.1186/1476-072X-7-54, 2.
[193]Médard, 'Croissance et crises', *op. cit*., vol. 1, 48–49.

either the faster speed of 40–50 km a day by canoe boats or a much slower speed if travelling by foot.[194] Secondly, according to both historians and travellers, plague was very rare in northern Sudan and seemingly absent altogether from southern Sudan. Thus, Leo Africanus noted in 1526, in perhaps an arbitrary manner, that plague in 'Nubia' (roughly, the area between the First Cataract of the Nile and the confluence of the Blue and White Niles in Central Sudan) would happen only once every hundred or so years, while in the 'Land of Blacks', it did not exist at all.[195] Evliya Çelebi, travelling in 1672–1673, claimed plague was rare in Qasr Ibrim (the Christian site on today's Egyptian–Nubian border) and unknown in Sennar, attributing this to locals oiling themselves with ghee, which he believed repelled fleas, lice and bedbugs – although, as noted later, he was wrong about ectoparasites.[196] In 1813, Johann Ludwig Burckhardt was told that while smallpox often devastated Sudanese communities, plague never spread beyond Aswan and the First Cataract, let alone to the Second.[197]

So how did the disease reach the Great Lakes via the Nile? Obviously, no precise spatio-temporal reconstruction of plague introduction into that region is possible at this stage, but a plausible hypothesis may be suggested. The only recorded plague south of the Second Cataract comes from the 1698–1699 travelogues of French physician Charles-Jacques Poncet and Jesuit Father de Brevedent, en route from Cairo to treat Emperor Iyasu I and his son.[198] Poncet and de Brevedent were among the first Europeans to have crossed into Sudan. Prior to his Sudanese–Ethiopian voyage, Poncet had been living in Cairo since 1687, making his living as a physician and pharmacist. While in the city, he witnessed the 1695–1696 plague outbreak of which he left a detailed description.[199] Crossing the Third Cataract between Moshu (north of Argo Island) and Dongola (the capital of the Northern provinces of the Funj Sultanate), Poncet and de Brevedent observed deserted villages, abandoned churches, and uncultivated fields, resulting from a plague that had struck in 1696. According to Poncet, it was the same plague that he had witnessed in Cairo in 1695–1696, which also occurred in Upper Egypt and the 'Land of the Barbarins' (largely overlapping with the Funj Sultanate).[200]

The 1695–1696 outbreak in Egypt and Sudan is of importance here not only because of its high mortality rates (as mentioned by both Poncet and a number of Egyptian chroniclers) but also because of its wider eco-climatic context.[201] The outbreak was preceded by a disastrous famine, triggered by two back-to-back harvest failures of 1694 and 1695, caused by the very low levels and fast recession of the Nile.[202] According to Egyptian chroniclers, the famine resulted in starvation-related mortality of exceptional

[194]The rough equivalent of 30 km a day derives from the itineraries of Charles-Jacques Poncet (1698–1699), Theodor Krump (1701–1702), Lenoir de Roule (1704) and James Bruce (1772). W. Foster (ed.), *The Red Sea and Adjacent Countries at the Close of the Seventeenth Century* (London, 1949), 93–105; O.G.S. Crawford, *The Fung Kingdom of Sennar: With a geographical account of the Middle Nile region* (Gloucester, 1951), 318–19. It took 34 days for John Speke and James Grant to paddle from Gondokoro (southern Sudan) to Khartoum in February/March 1863 (about 1600 km).

[195]*Johannes Leo der Afrikaner: Seine Beschreibung des Raumes zwischen Nil und Niger nach dem Urtext*, D. Rauchenberger (ed.) (Wiesbaden, 1999), 368–69.

[196]R. Dankoff, N. Tezcan and M.D. Sheridan (eds), *Ottoman Explorations of the Nile* (London, 2018), 243, 288.

[197]*Travels in Nubia by the Late John Lewis Burckhardt* (London, 1819), 144 and 229–30.

[198]J.O. Udal, *The Nile in Darkness: Conquest and exploration, 1504–1862* (Norwich, 1998), 36–53.

[199]Foster, *op. cit*., 99.

[200]*ibid*., 99; Crawford, *op. cit*., 294.

[201]Poncet, grossly exaggerating, claimed that during its peak, up to 10,000 individuals had died in Cairo: see Foster, *op. cit*., 99.

[202]*'Abd al-Raḥmān al-Jabartī's History of Egypt: 'Ajā'ib al-āthār fī 'l-tarājim wa'l-akhbār, Volumes I & II*., T. Philipp and M. Perlmann (trans.) (Stuttgart, 1994), vol. 1, 41.

proportions and people resorted to cannibalism.[203] With the many gaps in annual Nilometre readings between 1523 and 1698, we are lucky to have one for 1693 (preceding the 1694–1695 famine): according to one Coptic chronicle, the flood levels stood at only 16 cubits – one of the lowest levels for the period 1573–1921, with 21.9 cubits (on the 26 cubit crest employed by the Ottomans) being the average figure for that period (see Figure 4).[204]

Like the ensuing plague, the subsistence crisis of 1694–1696 appears to have been a pan-Nilean rather than Egyptian phenomenon. The 1694–1695 drought is mentioned in a biographic work of the Funji scholar Muḥammad al-Nūr b. Ḍayf Allāh (d. 1809), based on earlier non-surviving sources.[205] Both Poncet and de Brevedent, travelling in October 1698, mentioned the multitude of camel and donkey carcases and bones covering the desert, possibly reflecting the drought crisis.[206] Intriguingly, the 1694–1696 crisis was part of a wider wave of environmental disasters in the Nile region in the late seventeenth century. A late nineteenth-century Funj Chronicle, drawing on lost sources, records that in 1095 AH/1684 CE a famine – euphemised as *ʾUmm Laḥm* ('Mother of Meat') and coupled with smallpox – devastated communities,

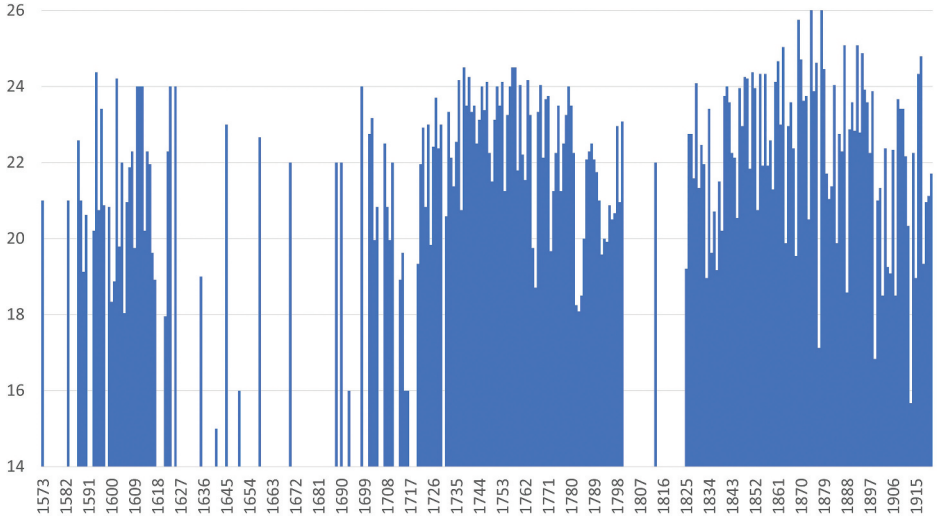

Figure 4. Annual Nile flooding levels, 1573–1921 (in Ottoman-style cubits; max = 26). Source: Omar Toussoun, *Mémoire sur l'histoire du Nil, Tome 2*. Cairo: Imprimerie de l'Institut français d'archéologie orientale, 1925), pp. 394–404. We are indebted to Prof. Stuart Borsch for supplying us with a tabulated version of this data (which included all the years, except 1693, not included in Toussoun's list and added by us from the *History of the Patriarchs of the Egyptian Church* chronicle).

[203] A. Raymond, 'Les grandes épidémies de peste au Caire aux XVII et XVIII siècles', *Bulletin d'études orientales*, 25 (1972), 205; *'Abd al-Raḥmān al-Jabartī's History of Egypt, op. cit., vol. 1*, 43.

[204] *History of the Patriarchs of the Egyptian Church, Known as the History of the Holy Church*, A. Khater and O.H.E. Khs-Burmester (eds), (Cairo, 1970), vol. 3.3, 279. The average figure of 21.9 cubits derives from O. Toussoun, *Mémoire sur l'histoire du Nil* (Cairo, 1925), vol. 2, 366–404. For the annual levels in the pre-Ottoman periods, utilising a 24- rather than a 26-cubit crest, see W. Popper, *The Cairo Nilometer: Studies in Ibn Taghrî Birdî's Chronicles of Egypt* (Berkeley, 1951), 219–23.

[205] *Muḥammad al-Nūr b. Ḍayf Allāh: Kitāb al-ṭabaqāt fi khuṣūṣ al–awliyā' wa 'l-sāliḥīn wa 'l–'ulamā' wa 'l–shu'arā' fi 'l–Sūdān*, Yūsuf Faḍl Ḥasan (ed.) (Khartoum, 1974), 357.

[206] Foster, *Red Sea and Adjacent Countries, op. cit.*, 96; Crawford, *op. cit.*, 292.

driving them to eat dogs.[207] The same famine appears to have ravaged all over the sultanate, with some individuals coming to purchase grain from southern parts.[208] Ḍayf Allāh also mentions a drought in 1099 AH/1686–1687 CE.[209] Unfortunately, both sources – the only surviving Funji compositions describing that period – skipped the plague years 1107 and 1108 AH/1695–1696 and 1696–1697 CE altogether in their respective narratives.

The late seventeenth-century crisis undoubtedly created much stress for human communities around the Nile. One inevitable consequence of subsistence crises is human migration, and the 1694–1696 crisis was no exception. In August 1695, at the height of the famine and in the course of the plague outbreak, a crowd of hungry Egyptian countrymen flocked to Cairo, causing food riots.[210] According to a Coptic chronicle, all of Upper Egypt became devoid of hungry and poor people during the crisis.[211] Amid intense human movement, the pathogen likely spread along the Nile through Egypt into Sudan and possibly farther south towards the Great Lakes, aided by regional migrations. The late seventeenth-century crisis may have coincided with the migration of several Nilotic groups between southern Sudan and Lake Victoria's northern shore. Most notably, there was a migration of the Luo/Lwoo people from southern Sudan into what is now Nyanza Province of Kenya (on the north-eastern shore of Victoria). According to J.C.D. Lawrance (not stating his source of this information), this migration was caused by drought, famine and invasions.[212] The route of the migration went along the Nile, via the Shilluk, Dinka, Nuer and Anuak polities.[213] The drought may have facilitated the crossing of the often impenetrable Sudd swamp. Approaching their new homes on Lake Victoria, the Luo/Lwoo were bound to come into contact, or conflict (or both) with the Iteso, Baganda and Basoga natives and it could be in these circumstances that the plague was introduced into the Great Lakes region. It is possible that it was the Luo/Lwoo invasion that pushed the Iteso people from their original land in the Usuku district (north-eastern Uganda) southwards into their new home in Bukedi – the Iteso migration is dated to the late seventeenth/early eighteenth century.[214] The westernmost frontiers of Bukedi were situated some 200 km east of the site of Kawumpuli's temple in Buyego (in proximity to the putative plague reservoir) and 125 km east of the Nile's origin. The Luo/Lwoo migrants may have split into several groups, one of which, the Jaluo, continued farther south-east, establishing themselves in what is today the Nyanza province of north-western Kenya (on the north-eastern shores of Lake Victoria).[215] The late seventeenth-century Nilean crisis, the arrival of the Luo/Lwoo and the migration of the Iteso all seem to overlap with the chronology of the earliest plague outbreaks in Buganda.

Could the Luo/Lwoo and Iteso migrations have brought plague to the Great Lakes in the late seventeenth century, perhaps in the context of the 1695–1696 outbreak around the Nile? Our sole knowledge based on twentieth-century oral traditions is very patchy, so the connection remains hypothetical – although, if indeed driven by the same crisis, the Luo/Lwoo could plausibly have introduced the disease and the Iteso facilitated its spread. Given the severity of the

[207] Aḥmad b. al-Ḥājj Abū 'Ali Kātib al-Shūna, *Makhṭūṭat Kātib al-Shūna: Taḥqīq al-Shāṭir Buṣaylī 'Abd al-Jalīl* (Cairo, 1961), 17; H.A. Macmichael, *A History of the Arabs in the Sudan* (Cambridge, 1922), vol. 2, 263; P.M. Holt, *The Sudan of the Three Niles: The Funj Chronicle 910–1288/1504–1871* (Leiden, 1999), 11–12.
[208] Holt, *Sudan of the Three Niles, op. cit.*, 11–12.
[209] *Muḥammad al-Nūr b. Ḍayf Allāh: Kitāb al-ṭabaqāt, op. cit.*, 210.
[210] *'Abd al-Raḥmān al-Jabartī's History of Egypt, op. cit., vol. 1*, 42–43.
[211] *History of the Patriarchs of the Egyptian Church, op. cit.*, vol. 3.3, 279–80.
[212] Lawrance, *op. cit.*, 9.
[213] J. P. Crazzolara, *The Lwoo: Part I. Lwoo Migrations* (Verona, 1950).
[214] Lawrance, *op. cit.*, 9–10; J. H. Driberg, *The Lango: A Nilotic Tribe of Uganda* (London, 1923), 23–26.
[215] Lawrance, *op. cit.*, 9–10; Driberg, *op. cit.*, 23–26.

late seventeenth-century Nilean crisis, we may speculate that both the Luo/Lwoo and Iteso migrated fast. Fast migration would be facilitated by their mobile lifestyles and socio-economic regimes, with the Luo/Lwoo practising agro-pastoralism, while the Iteso were primarily nomadic pastoralists. The omnipresent drought, depressing both food resources for humans and grassland for livestock, would most certainly have encouraged Luo/Lwoo communities to flee south from their home in southern Sudan. As they relied heavily on cattle, it is likely that they would have driven their bovids along while migrating. As such, cattle would act as mobile wealth and food resources, though not as beasts of burden since Nilotic farmers of Sudan were reluctant to use them in this capacity as late as 1960.[216] This, however, would not have precluded a long-distance importation of plague: as we have seen, human porters, especially if carrying flea- and rodent-attracting items, such as barkcloths and grain seeds, could act as successful plague spreaders.

The long-distance spread of plague would have been further facilitated by the multitude of potential vectors and hosts. As noted, Evliya Çelebi claimed in 1672–1673 that plague was unknown in Sennar,[217] although obviously wrong about the absence of ectoparasites in Sudan. Burckhard's lexicon of Kenzi and Nuba languages, compiled during his 1813 voyage in Sudan, has both 'lice' and 'fleas' (in addition to 'plague').[218] Wilhelm (Vasilii) Junker, a German–Russian explorer sojourning in Sudan in 1876–1878 and 1884–1885, noted that while fleas were not plentiful in Egyptian Sudan, they were abundant in Equatoria (southern Sudan).[219] *Xenopsylla cheopis*, the main vector of human plague, was first described scientifically by Rothschild and Jordan in 1901 in Shendi and it remains the chief parasite of African grass rats (*Arvicanthis niloticus*) in Sudan.[220] As for rodents, these feature prominently in explorers' travelogues and diaries. Thus, Çelebi, while travelling in the southern limits of Funj in early 1673, noted local 'earth rats' and stated that locals, albeit Muslims, consumed them.[221] Ignaz Pallme, while in Sudan (1837–1839), observed abundant 'tame' mice and rats living under humans' feet, fed rather than killed.[222] Likewise, Junker's travelogue is full of encounters with rats in different parts of Sudan.[223] Staying in villages of Otuho/Lotuxo people in Equatoria in April 1881, Emin Pasha mentioned the abundance of rats in and outside local huts.[224]

Finally, it is important to reflect further here on the nature of the 1694–1696 crisis, encompassing drought, famine and plague. Researchers have long pointed out the impact of climate on plague activity. In particular, it has been shown that a prolonged wet spell (producing much grass and encouraging the growth of both vector- (fleas) and host- (rodents) populations), followed by a drought (which decimates these), can have far-reaching repercussions for plague activity.[225] In this context a zoonotic spillover tends to occur, whereby hungry fleas jump onto humans as a result of either mass rodent die-outs or migration, or rodent migration closer to

[216] I.M. Khalil, 'Developing the animal wealth of the Sudan', *Sudan Notes and Records*, 41 (1960), 12.
[217] Dankoff, Tezcan and Sheridan, *op. cit.*, 288.
[218] *Travels in Nubia, op. cit.*, 154–55.
[219] *Dr. Wilhelm Junkers Reisen in Afrika, 1875–1886: Erster Band (1875–1878)*, R. Buchta (ed.) (Vienna, 1889), 445.
[220] Natural History Museum (An open source project by the Natural History Museum's Biodiversity Informatics Group), Data Portal: https://data.nhm.ac.uk/dataset/collection-specimens/resource/05ff2255-c38a-40c9-b657-4ccb55ab2feb/record/7936169 (accessed January 2026); D. Fagir, and E.A. El-Rayah, 'Parasites of the Nile rat in rural and urban regions of Sudan', *Integrative Zoology*, 4 (2009), 179–87.
[221] Dankoff, Tezcan and Sheridan, *op. cit.*, 293.
[222] I. Pallme, *Beschreibung von Kordofan und Einigen angrenzenden Ländern* (Stuttgart, 1843), 140, 146.
[223] *Dr. Wilhelm Junkers Reisen in Afrika, op. cit., Erster Band*, 238, 380, 403, 464, *Zweitter Band (1879–1882)*, 53, 65–66, 83, 110.
[224] *Die Tagebücher von Dr. Emin Pascha: Band II, op. cit.*, 179–80.
[225] Slavin, 'The birth of the Black Death', *op. cit.*, 314–20.

human habitats in hope of securing food. Could plague, transmitted among rodents and to humans, and possibly accelerated by human migration, have spread from Egypt down the Nile to the Great Lakes in this context? Obviously, this is a hypothetical scenario, based on all the available textual data, and without additional evidence – textual, archaeological and aDNA – it may be, for now, the best educated guess.

Conjoining historical reconstruction and DNA evidence

Now that the introduction and early spread of plague in the Great Lakes region has been reconstructed using historical sources, we may conjoin it with DNA evidence deriving from Mas Fiol et al.'s 2024 publication to achieve a more integrative picture. As noted, 1.ANT branch diverged from 1B lineage (responsible for the *pestis secunda* of 1356–1366) at some point between 1344 and 1537 (median date: 1431), followed by its first diversification at some point between 1471 and 1712 (median date: 1591). The emergence of 1.ANT3, whose genomes are attested in the twentieth and twenty-first centuries in East DRC and Kenya, was followed by a parallel rise of two additional sub-branches – 1.ANT1 and 1.ANT2, at some point between 1616 and 1823 (median date: 1728). All three sub-branches underwent a process of diversification, whereby new sub-lineages diverged from each main sub-branch, during the nineteenth century. Sub-branch 1.ANT1 was the first to undergo the diversification event between 1736 and 1897 (median date: 1826), followed by 1.ANT2 (between 1771 and 1918; median date: 1854) and 1.ANT3 (between 1801 and 1924; median date: 1875). 1.ANT1 strains are present in East DRC and Uganda; those of 1.ANT2 are found in Tanzania, Kenya and Yemen, while the 1.ANT3 strains are associated with East DRC and Kenya.

If the pathogen reached the Great Lakes via the Nile in the late seventeenth century, perhaps during the 1695–1696 outbreak in Egypt and Sudan, we may hypothesise the following. During the *pestis secunda* wave (1356–1366), Branch 1B strains would have reached several geographic 'dead ends' – regions representing eco-climatic barriers to their further spread and, hence, further survival and evolution. Of 100+ sequenced genomes from post-Black Death Europe (c.1357–1771), only nine – all from *pestis secunda* contexts – belong to branch 1B, implying the latter had left its South-Central German reservoir, and Europe, for good.[226] To evolve further, 1B strains had to seed a new reservoir/s in wild rodents and/or soil, either during or at the end of its spread, having reached a 'dead end' region. One of these regions was Egypt, where the *pestis secunda* is attested between February and July 1363.[227] A close analysis of the subsequent plague outbreaks in Egypt reveals that although some of these were introduced from elsewhere (the Maghreb, Syria or elsewhere in the Mediterranean via sea), some appear to have started in Egypt, before spreading to the north. There are two indications of the latter trend: (1) that there were no plague outbreaks in adjacent regions in the same or previous year; and (2) that a plague wave is said to have commenced in Upper Egypt or around Cairo, before reaching Alexandria and farther north. Such

[226]Slavin, 'Out of the west', 7–15, 44–48; C. Parker et al., '14th-century *Yersinia pestis* genomes support emergence of *pestis secunda* within Europe', *PLoS Pathogens*, 19, (2023), e1011404.

[227]For a referenced (but not exhaustive) catalogue of plague outbreaks in Egypt between 1347 and 1514, see B. Shoshan, 'Notes sur les épidémies de peste an Égypte', *Annales de Démographie Historique* (1981), 395–400.

outbreaks were reported in Egypt in 1358, (possibly 1363), 1367–1368, 1377, 1388–1389, 1395–1396, 1406–1407, 1413, 1415–1416, 1418–1420, 1428, 1436, 1438, 1444, 1449, 1454–1455, 1477, 1505, 1507, and 1513–1514.[228] Although much more research is needed to confirm this hypothesis, it is possible that any of these outbreaks may have originated in a putative Egyptian plague reservoir, potentially situated around Cairo and/or Upper Egypt. Moreover, any of these waves may have been associated with the divergence of 1.ANT branch from 1B lineage.

Importantly, there are 10 single nucleotide polymorphisms (SNPs) defining Branch 1B between the node leading to the youngest sequenced 1B genome – that of Bolghar (Tatarstan), which has been externally dated to 1364 – and the divergence of 1.ANT from 1B.[229] Despite variation in SNP acquisition rates across and within the same branches, we can use a median of one SNP per five years – based on three branch-defining SNPs between the Black Death genomes (1348–1350) and the Bolghar genome (c.1364) – as a rough guideline. If the speed of SNP substitution did not change drastically between the Bolghar node and the branching-off of 1.ANT, we may place the latter event in the early fifteenth century. However, this approximation could well be a red herring – especially if 1B strains indeed seeded a reservoir in Egypt during their migration there in 1363. As has recently been hypothesised, focalisation in a new environment may lead to some drastic molecular changes, including large deletion on the chromosome and elevation in substitution rates.[230]

If 1.ANT3 (the common ancestor of the three 1.ANT sub-branches) arose in the Great Lakes, and plague only arrived there in the late seventeenth century, its emergence must also date to then – at the upper end of its computational bracketing (1471–1712; median date: 1591). This is by no means impossible: before Spyrou et al.'s 2022 study determined that the Big Bang (or the 'Great Polytomy') occurred in the late 1330s or early 1340s (on the basis of precisely dated genomes from Kara-Djigach, northern Kyrgyzstan), the same event had been dated, on the basis of probability computations, to a period between 1142 and 1339 (with the median date of 1268, which was later recalibrated to 1170 or 1196 ± ~200 years).[231]

The period between the emergence of 1.ANT3 (possibly in the late seventeenth century and most likely in Buganda), whose strains have been documented only in eastern DRC and Kenya, and the diversification of 1.ANT sub-branches (between 1736 and 1897; median date: 1826) may

[228]The 1358–1359 outbreak: 'Abd al-Bāsiṭ Ibn Khalil, *Nayl al-Amal fi Dhayl al-Duwal*. (Sidon: Al-maktabah al-'aṣrīyah, 1992), vol. 1: 312; the 1367–1368 outbreak: *al-Maqrīzī, Kitāb al-Sulūk li-Ma'rifat Duwal al-Mulūk, vol. 3.1*, M.M. Ziyāda (ed.) (Cairo, 1956), 162; the 1388–1389 outbreak: Ibn al-Ṣayrafī, *Nuzhat al-Nufūs wa-l-Abdān fī Tawārīkh al-Zamān*, Ḥ. Ḥabashī (ed.) (Cairo, 1970–1994), vol. 1, 168, 170, 172; the 1395–1396 outbreak: Shoshan, *op. cit*., 396; the 1406–1407 and 1413 outbreaks: *al-Maqrīzī, Kitāb al-Sulūk li-Ma'rifat Duwal al-Mulūk, vol. 4.1*. S.ʿA.F. ʿĀshūr (ed.) (Cairo, 1970), 19–20, 43, 257–58; the 1415–1416 outbreak: *al-Maqrīzī, Kitāb al-Sulūk, op. cit*., vol. 4.1, 301, 310, 312; the 1418–1420 outbreak: *al-Maqrīzī, Kitāb al-Sulūk li-Ma'rifat Duwal al-Mulūk*, vol. 4.2, S.ʿA.F. ʿĀshūr (ed.) (Cairo, 1972), 481–83, 486–87, 492; *History of Egypt, 1382–1469 AD, Translated from the Arabic Annals of Abu l-Maḥâsin Ibn Taghrî Birdî*, W. Popper (trans.) (Berkeley, 1954–1963), vol. 3, 30, 39–40; the 1428 outbreak: *al-Maqrīzī, Kitāb al-Sulūk li-Ma'rifat Duwal al-Mulūk*, vol. 4.3, S.ʿA.F. ʿĀshūr (ed.) (Cairo, 1973), 772; the 1436 and 1438 outbreaks: *Ibn Iyās al-Ḥanafī, Badā'i' al-Zuhūr fī Waqā'i' al-Duhūr*, vol. 2, M. Muṣṭafā (ed.) (Wiesbaden, 1975), 169; *al-Maqrīzī, Kitāb al-Sulūk, op. cit*., vol. 4.3, 1109, 1126–27; *History of Egypt, 1382–1469 A.D, op. cit*., vol. 4, 144–53; the 1444 outbreak: *History of Egypt, 1382–1469 A.D, op. cit*., vol. 5, 92–93; the 1454–1455 outbreak: *Kitāb Ḥawādith al-Duhūr fī Madā al-Ayyām wa-al-Shuhūr*, W. Popper (ed.) (Berkeley, 1930), 206, 224, 228, 230; the 1507 outbreak: *Ibn Iyās al-Ḥanafī, Badā'i' Al-Zuhūr Fī Waqā'i' Al-Duhūr*, vol. 4., M. Muṣṭafā (ed.) (Wiesbaden, 1984), 109; the 1513–1514 outbreak: *Journal D'un Bourgeois Du Caire: Ibn Iyâs, Histoire Des Mamlouks, vol. 1*., G. Wiet (trans.) (Paris, 1955), 277–78, 280.

[229]SNP is a variation (or mutation) in a single nucleobase (A for adenine, C for cytosine, G for guanine, or T for thymine) at a certain genomic position.

[230]Keller et al., *op. cit*., Sl, 125, 141–42.

[231]Cui et al., *op. cit*., 580, table 1; M.A. Spyrou et al., 'Analysis of 3800-year-old *Yersinia pestis* genomes suggests Bronze Age origin for bubonic plague', *Nature Communications*, 9 (2018), supplementary table 9.

have corresponded to what has been referred to in this article as 'the first phase: early plague spread in Buganda, c.1700–1840'. During this phase, plague was confined entirely to Baganda territories, radiating out of one or several nearby reservoirs (one of which was possibly situated in the Buyego region, in the vicinity of Kawumpuli's temple) and accumulating 24 SNPs. The diversification of 1.ANT1 into new sub-lineages may have occurred during the 'the second phase: plague spread around the Great Lakes, c.1840s/1850s–1898', whereby plague started spreading outside Buganda into adjacent territories along the northern and western shores of Lake Victoria in the 1840s–1870s. It was during the subsequent spread of plague to the east in the 1880s and 1890s that 1.ANT2 and 1.ANT3 underwent a similar process of genetic diversification and geographic expansion, seeding reservoirs in Kenya, Tanzania, and (in the case of 1.ANT2) crossing into South Arabia in the closing years of the nineteenth century.

Conclusions

Taken together, historical texts and new DNA evidence reveal how plague – previously unknown in East Africa – entered the Great Lakes, became established, and spread east to the Swahili Coast and across the Indian Ocean to southern Arabia. While studied before, a full reconstruction of its early East African spread has only become possible with recent DNA data from Mas Fiol et al.[232]

On the basis of current evidence, the plague was initially imported into Buganda – most likely from the north by the Nile – in the late seventeenth or early eighteenth century. After its introduction, plague remained in Baganda territories (c.1700–1840s) before spreading across the Great Lakes and reaching the Swahili Coast by the late nineteenth century, aided by the new commercial, technological and political reality of the early colonial era. The most likely route of introduction is via the Nile, from Egypt and Sudan, in the context of the late seventeenth-century climatic, bio-ecological and socio-economic crises that befell different parts of the Nile region. Although it cannot, at this stage, be proven, the same crisis may have driven the Luo/Lwoo migration from southern Sudan into present-day Nyanza Province (Kenya), displacing the Iteso from Usuku (north-eastern Uganda) south into Bukedi, near the putative plague reservoir at Buyego.

If this hypothetical reconstruction is not too far removed from reality, then we have a perfect example of a biological crisis initiated by exogenous forces and exacerbated by endogenous (anthropogenic) and demographic factors. The plague outbreak commenced, naturally, in its wildlife reservoir, possibly situated somewhere in Egypt. Likewise, its spillover to humans in spring 1695 was triggered by environmental factors – most likely, the drought. Yet its subsequent spread was caused by purely anthropogenic and demographic factors: famine (which is, mostly, a man-made phenomenon) and human migration. Hence, the connection between these variables must be regarded as potentially key factors triggering some plague outbreaks. This, in turn, strengthens the idea that environmental crises – famines, epidemics and epizootics – are triggered by a complex interaction of exogenous, endogenous and demographic factors.[233]

[232]Mas Fiol et al., *op. cit.*

[233]P. Slavin, *Experiencing Famine in Fourteenth-Century Britain* (Turnhout, 2019); P. Slavin, 'Mites and merchants: the crisis of English wool and textile trade revisited, c.1275–1330', *Economic History Review*, 73 (2020), 885–913; Slavin, 'From the Tian Shan to Crimea', *op. cit.*, 573.

A key finding here is plague's ability to travel long distances into impenetrable and isolated regions despite difficult terrain and climate, and the lack of transport, infrastructure and, by extension, migration and trans-regional trade. Before Arab merchants arrived in the 1830s, the Great Lakes were among the world's most cut-off regions, yet plague still entered Buganda (likely via the Nile) around 1700, where it seeded reservoirs – an anomalous scenario for plague spread given the usual trade- and/or migration-driven transmission.[234] It is an important reminder that although trans-regional plague spread was often associated with the interconnected world, this connection should not be taken for granted.

Lastly, this article underscores the importance of adhering to an inherently transdisciplinary perspective when studying the history of infectious diseases – and particularly for those regions where there were no native written sources until the colonial era. Plague is a highly complex phenomenon and, as such, it can only be studied efficiently if we bring together textual and non-textual sources: DNA evidence, in this instance. By doing so, this article has provided a reconstruction of how plague entered and became established in the Great Lakes long before intensive outside contacts or early written records of the region. This would not have been possible without the new DNA evidence and without marrying the same evidence with historical sources. Thus, it proves once more that only an interdisciplinary vision and approach can improve our ability to study and understand infectious disease, past, present – and, potentially, future.

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[234]See (in relation to the Black Death), Benedictow, *Complete History, op. cit.*; Barker, *op. cit.*; Slavin, 'From the Tian Shan to Crimea', *op. cit.*