# A Sub-Continent of Caries: Prevalence and Severity in Early **Holocene through Recent Africans**

Fawn Carter<sup>1\*</sup> and Joel D. Irish<sup>2</sup> <sup>1</sup>Museum of the North, University of Alaska <sup>2</sup>Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University

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ABSTRACT The most recognizable pathological condition of the human oral cavity is, arguably, dental caries. Beyond a direct impact on oral health, caries presence (or absence) provides important data for bioarchaeologists – to help reconstruct the diet of past populations and individuals. This study explores such data in 44 samples (n=2,119 individuals, 33,444 teeth) dating between 10,000 BP and recent times across the African sub-continent. It is, to date, the most extensive investigation of its kind in this part of the world, entailing descriptions and quantitative comparisons of caries by period, environment, subsistence strategy and sex.

Mann-Whitney U tests and factorial ANOVA results provide expected and some unexpected findings, including: 1) a diachronic increase in caries prevalence across the sub-continent, likely related to diet change from widespread population movement; 2) savanna peoples exhibit more caries than those from other environmental regions; 3) subsistence strategy plays a major role in caries occurrence; and 4) males and females do not evidence significant differences in caries frequencies, but variation does exist in several regional groups. These findings reveal that global trends described by previous researchers often apply, though not always – so it is prudent to consider regions independently.

Here we assess how dental caries frequencies differ by time period, sex, environment, and subsistence strategy among a range of populations across sub-Saharan Africa. Severity is also briefly discussed. Carbohydrate intake, adoption of agriculture, and behavioral and biological differences between the sexes and among populations all influence dental decay, so the latter can be highly informative (Turner, 1979; Newbrun, 1982; Larsen, 1997; Lukacs and Largaespada, 2006; Lukacs and Thompson, 2008). Yet, relatively few dental pathology studies have been conducted within this vast region (Irish, 1993). Those that have, focus largely on qualitative data or are small in spatiotemporal scope (Flower, 1889; Shaw, 1931; Frencken et al., 1986; Morris et al., 1987; Solanki et al., 1991; Sealy et al., 1992; Mackeowen et al., 1995; Steyn et al., 1998; Cleaton-Jones et al., 2000; Ohinata and Steyn, 2001; Pistorius et al., 2002; Steyn, 2003). The present study is much more comprehensive, covering the sub-continent from 10,000 years ago to present. At this large scale, the trends observed can work to support and/or refute those observed elsewhere in the world. The findings are discussed in terms of diet and other biocultural practices known to affect Fairbanks AK dental health.

The present study focuses on four research questions:

1) How did dental caries frequencies change through time? The samples were divided into Late Stone Age, Iron Age, or Recent. Each period was marked by a major shift in diet as new foods were introduced.

2) Is there a significant difference in caries between the sexes? The literature indicates a global trend for higher frequencies in females, particularly with the advent of agriculture (Caselitz, 1998; Lukacs and Largaespada, 2006; Lukacs, 2008; Lukacs and Thompson, 2008; Ferraro and Vieira, 2010). The present results will help test whether the trend holds in sub-Saharan Africa.

3) How do environmental differences affect the dental caries frequencies? Such differences limit what foods are present, so should have an influence. Samples are divided by the ecosystem from

\*Correspondence to: Fawn Carter Museum of the North University of Alaska fmcarter@alaska.edu

which they were derived: coastal, desert, savanna/ grassland, and tropical rainforest.

4) How does subsistence strategy affect the caries rates? Sub-Saharan Africans used a range of strategies to procure food, including hunting and gathering, pastoralism, and agriculture. Because diet is determined by subsistence strategy there should be an impact. To address this likelihood and place sub-Saharan African peoples in broader spatiotemporal context, samples from the current study are compared to Turner's (1979) meta-analysis of populations with different subsistence strategies.

### Materials and Methods

Data on caries prevalence, as well as severity in some instances, were collected from 44 samples (n=2,119 individuals; 33,444 teeth, Table 1) throughout the African sub-continent by Irish during the course of his dental morphological research (1993, 1997). These samples date from ca. 10,000 BP to the 20th century.

The location and severity are recorded for each of the carious lesions present. Caries are ranked on a scale of 1 to 4, with 1 being a small pit that does not penetrate the enamel and 4 being pulp perforation (Buikstra and Ubelaker, 1994). Location is designated as mesial, distal, buccal, occlusal, lingual or a combination in the event of large or multiple lesions. Sex was determined as M, M?, ?, F, F? by the second author using standard methods (e.g., Buikstra and Ubelaker, 1994). Only adults (i.e.,  $\geq$ 18 years of age) were included in the analyses.

Lukacs' (1992, 1996) caries index was calculated to adjust for antemortem tooth loss (AMTL):

### (AMTL) (% teeth with severe caries) + (teeth with caries) (teeth present) + (AMTL)

This method takes into account the number of teeth present with pulp exposure (severity level 4) due to dental caries. The present study compares the percentage of teeth with carious lesions; therefore, results could be skewed if AMTL were not accounted for, since many teeth are removed due to toothache resulting from serious carious lesions or abscesses (Lukacs, 1996).

The caries data were compared using three common statistics. First, Mann-Whitney U tests were used to compare the percent of teeth with carious lesions for the four major categories of independent variables (i.e., period, sex, environment, subsistence). Second, factorial ANOVA accounted for significant differences among subsistence strategy, environment, time period, between- sex, or any combination of these four on the dependent variable (percentage of teeth with caries per individual). The null hypothesis of consistency was tested, followed by a series of post hoc tests (i.e., Tukey) to identify significance between all combinations of the independent variables. Lastly, the Spearman's Rho correlation coefficient was used to simply determine any relationship between attrition and caries. Higher levels of wear should correlate with fewer caries because normal attrition wears away the tooth surface before caries can form (Brothwell, 1963; Scott & Turner, 1988; Hillson, 1996; Caselitz, 1998).

#### Results

The Mann-Whitney U (Table 2) and Tukey (Table 3) test results show a statistically significant difference (p<0.05) for each pair of time periods. The factorial ANOVA found time period to be a significant factor for caries counts with a value of 0.005 (Table 4)

Mann-Whitney U (see Table 2), Tukey (see Table 3) and factorial ANOVA (see Table 4) tests show no statistically significant values for caries frequency differences between the sexes. However, the bar graph (Figure 2) does display a general trend of females with more carious lesions – at least for the Late Stone Age (LSA) and Iron Age samples. In the Recent samples males and females have equal percentages; the only significant difference is among pastoralists (not shown).

ANOVA (see Table 4) results show that environment has a significant impact on caries for the LSA (0.000), Recent (0.009), and Combined groups (0.004). The Mann Whitney U (see Table 2) results reveal no significant difference among environments in terms of caries counts for the Iron Age samples, but some differences do exist for LSA and Recent samples. Tukey (see Table 3) results show significant difference only among the LSA samples. Figure 2 illustrates the different counts of affected individuals for each environment category. Not all environmental categories are represented by time period; as such, some effect on results may occur and these should be interpreted with caution.

Factorial ANOVA (see Table 4) results suggest that subsistence contributes to caries counts for the Recent samples (0.060) and all periods combined (0.000). Outcomes from the Mann-Whitney U (see Table 2) and Tukey (see Table 3) tests show a difference between hunter/gatherers and pastoralists among the LSA samples (0.043) and hunter/ gatherers and agriculturalists when all periods are

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Table 1. Summary of samples including the current country the sample was collected from, the environment, time period, and subsistence strategy category the sample was found to best fit with, and the number of individuals from each sample.

Dental Anthropology

\* information not available

		Significance*			
Variable	Groups	LSA	Iron Age	Recent	Combined
<b>Time Period</b>	LSA & Iron Age	n/a	n/a	n/a	0.003
	LSA & Recent	n/a	n/a	n/a	< 0.001
	Iron Age & Recent	n/a	n/a	n/a	< 0.001
Sex	Male & Female	0.113	0.113	0.564	0.803
Environment	Desert & Savanna	0.942	n/a	0.016	0.625
	Desert & Rainforest	0.127	n/a	0.84	0.771
	Desert & Coastal	0.397	n/a	n/a	0.206
Savanna & Rainforest		< 0.001	0.226	0.007	0.842
	Savanna & Coastal	0.018	n/a	n/a	0.131
	Rainforest & Coastal	0.031	n/a	n/a	0.162
Subsistence	Hunting/Gathering & Pastoralism	0.043	n/a	0.546	< 0.001
	Hunting/Gathering & Agriculture	n/a	n/a	0.975	< 0.001
	Pastoralism & Agriculture	n/a	0.51	0.134	0.654
	*significant at p<0.050				

Table 2. Results of Mann-Whitney U tests

		Significance*			
Variable	Groups	LSA	Iron Age	Recent	Combined
Time Period	LSA & Iron Age	n/a	n/a	n/a	0.057
	LSA & Recent	n/a	n/a	n/a	< 0.001
	Iron Age & Recent	n/a	n/a	n/a	0.041
Sex	Male & Female	0.295	0.415	0.327	0.5
Environment	Desert & Savanna	0.965	n/a	0.156	0.941
	Desert & Rainforest	< 0.001	n/a	0.538	0.583
	Desert & Coastal	0.607	n/a	n/a	0.639
	Savanna & Rainforest	< 0.001	n/a	0.682	0.679
	Savanna & Coastal	0.255	n/a	n/a	0.424
	Rainforest & Coastal	< 0.001	n/a	n/a	0.243
Subsistence	Hunting/Gathering & Pastoralism	n/a	n/a	0.323	0.002
	Hunting/Gathering & Agriculture	n/a	n/a	0.752	< 0.001
	Pastoralism & Agriculture	n/a	n/a	0.236	0.125
	*significant a	at p<0.050			

Table 3. Tukey results

## Table 4. Factorial ANOVA results

Variable	LSA	Iron Age	Re- cent	Combined	
<b>Time Period</b>	n/a	n/a	n/a	0.349	
Sex	0.082	0.675	0.708	0.836	
Environment	< 0.001	0.609	0.009	0.004	
Subsistence	n/a	0.789	0.069	0.037	
*significant at p<0.050					

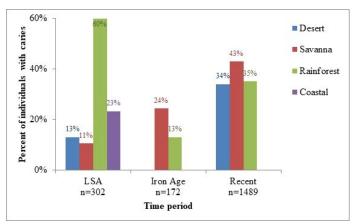


Figure 2. Percent of individuals affected by caries for each environment category in LSA, Iron Age, and Recent sub-Saharan African samples. See text for details. combined (0.000). There is no significant difference in caries number between pastoralists and agriculturalists for any time period. Figure 3 visually represents the differences between subsistence strategies by time period.

Lastly, the correlation between wear and caries prevalence was calculated using Spearman's Correlation Coefficient. The correlation of 0.012 indicates a very weak, yet positive relationship. An insignificant p-value of 0.400 was calculated.

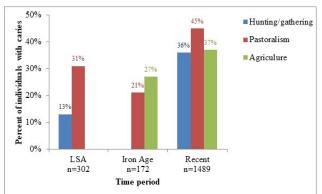


Figure 3. Percent of individuals affected by caries for each subsistence strategy in LSA, Iron Age, and Recent sub-Saharan African samples. See text for details.

### Discussion

1) Did caries frequencies change through time? Results show a definite increase in caries rate through time. Many new crops were introduced through time that may have had an impact. Asian sugarcane and bananas appeared as early as the Iron Age and via the Portuguese in the 17th century (Frencken et al., 1989; Irish and Turner, 1997). Sugarcane has a negative impact on health not only because of high sucrose levels but because of the manner in which it is eaten, which causes severe crown wear (Dreizen & Spies, 1952; Frencken et al., 1989; Irish & Turner, 1997). Bananas and plantains, both a significant crop in central and eastern Africa (Ehret, 2002), are moderately cariogenic due to their sticky and sugary structure (Mundorff-Shrestha et al., 1994; Aurore et al., 2008).

Several cariogenic crops from the Americas were also introduced, including maize and cassava (Larsen et al., 1991; Hillson, 1996; Ehret, 2002); most did not become widespread until the 18th century, which may account for the rise in caries between the Iron Age and Recent samples (Ehret, 2002). Overall, these soft, often sticky high carbohydrate foods are much more cariogenic than the traditional African diet (Hillson, 2008).

2) Is the rate of caries higher among females than males? All tests suggest that an individual's sex did not significantly contribute to the caries frequencies; that said, an examination of the bar chart (Figure 1) reveals a general trend for higher frequencies in females. A common explanation for the disparity is that females collect, prepare and consume more cariogenic foods than do males (Mulder, 1992). Other potential causative factors include genetic and hormone differences; all are said to be accentuated in agriculturalist groups (Lukacs and Largaespada, 2006; Lukacs, 2008), though this is not evident in the present African samples – for reasons we are continuing to investigate.

### *3) Are there environmental differences in the caries frequencies?*

Observing patterns is difficult because not all environmental groups are present by time period. In the Iron Age and Recent periods, caries are more prevalent among those on the savanna. Many of them would have relied on grain foods or pastoralism, i.e., the latter peoples often trade with agriculturalists for grains made into sticky porridge (Forde & Jones, 1950; Skinner, 1973). The naturally high cariogenicity of corn and wheat (Dodds, 1960; Okazaki et al., 2013) combined with the sticky nature of the grain porridge potentially contributes to higher instances of caries in savanna dwellers.

A high caries percentage (23%) occurs in coastal LSA samples. Coastal peoples generally have fewer caries because of grit and fluoride from marine foods (Walker & Erlandson, 1986). Sealy et al. (1992) report similar results with the Oakhurst sample from the Southern Cape. Contradictory to their results with other coast dwellers, where only 2.6% of teeth exhibit caries, 17.7% of teeth from Oakhurst are affected, despite a diet rich in marine resources; the authors state that the explanation for the high rate is the lack of fluoride in local ground water.

4) Does subsistence strategy affect dental health? The results obtained by factorial ANOVA suggests that subsistence strategy is a contributing factor to caries counts when all time periods are combined. No clear pattern is evident in the bar chart (Figure 3), perhaps because not all strategies are present by period. However, the high rate for Recent pastoralists is interesting. As noted, pastoralists eat grains plus milk and other animal byproducts (Forde & Jones, 1950; Skinner, 1973). As well, many Recent pastoralists are actually agro-pastoralists (Krige & Krige, 1954; Skinner, 1973; Zeleza, 1997). Grain porridge combined with maize apparently had a negative impact on dental health (Larsen et al., 1991; Scherer et al., 2007). Cassava would also be a starch source (Ehret, 2002) that prevents carbohydrates being cleaned away to give bacteria more time to feed (Lingstrom et al., 1989, Larsen, 1997; Hillson, 2008).

A comparable caries percentage is evident in the Recent hunter/gatherers and agriculturalists. Perhaps this similarity is related to the fact that modern hunter-gatherers, like the San, are not limited to this lifestyle as they once were. After the arrival of Europeans, many Khoisan worked on farms, where they ate crop- rather than wild foods (Reader, 1997; July, 1998). Modern pygmies also often rely on agriculturalists for trade (Afolayan, 2000). The increase in domesticated foods apparently caused both groups to have caries rates like those of agriculturalists.

Relative to Turner's (1979) analysis of different economies, the sub-Saharan results are complementary. He reports 0.0-5.3% for hunter/gatherers; the sub-Saharan LSA samples fall within this range (2%), but not for recent hunter-gatherers (8%). Most of Turner's samples are from early archaeological sites, so were generally not influenced by an agricultural diet. Recent hunter-gatherers fall within Turner's range for mixed economies (0.4-10.3%), which is likely a more adequate descriptive category. Sub-Saharan pastoralists (5-7%) fall within the mixed economy category, and the agriculturalists (4.0-7%) fit Turner's agriculturalist category (2.3-26.9%).

Finally, caries severity was only recorded in 469 of the total 2119 dentitions; thus, on that basis the Spearman's Rho value of 0.012, though positive, is only very weakly correlated, i.e., essentially random. These results suggest here that while of interest individually, such data may be less useful in a broader study.

### Conclusions

Statistically significant differences in dental caries frequencies have been observed between time periods, environmental groups, and subsistence strategies among 44 sub-Saharan African samples. The introduction of new foods through time, regional specializations, and food collecting strategies have been found to potentially affect dental decay. The results from the current study imply that cultural differences can have major implications for dental health.

### REFERENCES

- Afolayan, F. (2000). Bantu expansion and its consequences. In Falola T, (Ed.), *Africa: volume 1 African history before 1885* (pp. 111-136). Durham, North Carolina: Carolina Academic Press.
- Aurore, G., Pafait, B., & Fahrasmane, L. (2008). Bananas, raw materials for making processed food products. *Trends in Food Science and Technology*, 20(2), 78-91.
- Buikstra, J.E., & Ubelaker, D.H. (1994). Standards for data collection from human skeletal remains: proceedings of a seminar at the Field Museum of Natural History (Arkansas Archaeological Report Research Series). Arkansas: Arkansas Archaeological Survey.
- Caselitz P. (1998). Caries: ancient plague of humankind. In K. Alt, W. Rösing, M. Teschler-Nicola (Eds.), Dental Anthropology: Fundamentals, Limits, and Prospects (pp. 203-225). New York: Springer.
- Cleaton-Jones, P., Williams, S., & Fatti, P. (2000). Surveillance of primary dentition in Germiston, South Africa, 1981-97. *Community of Dentistry and Oral Epidemiology*, 28, 267-274.
- Dodds, M.L. (1960). The cariogenic property of cereal foods. *The Journal of Nutrition*, 71, 317-321.
- Dreizen, S., & Spies ,T.D. (1952). The incidence of dental caries in habitual sugarcane chewers. *Journal of the American Dentistry Association*, 45,193-200.
- Ehret, C. (2002). *The civilizations of Africa: a history to 1800*. Charlottesville: University of Virginia Press.
- Ferraro, M., & Vieira, A.R. (2010). Explaining gender differences in caries: a mulifactorial approach to a multifactorial disease. *International Journal of Dentistry* doi:10.1155/2010/649643.
- Flower, W. (1889). Description of two skeletons of Akkus, a Pygmy race from central Africa. *The Journal of Anthropological Institute of Great Britain and Ireland*, *18*, 3-19.
- Forde, C.D., & Jones, G.I. (1950). Western Africa part III: The Ibo and Ibibio-speaking peoples of southeastern Nigeria. London: International African Institute.
- Frencken, J., Manji, F., & Mosha, H. (1986). Dental caries prevalence amongst 12-year-old urban children in East Africa. *Community Dentistry and Oral Epidemiology*, 14, 94-98.
- Frencken, J., & Rugarabamu, P., Mulder, J. (1989.) The effect of sugar cane chewing on the development of dental caries. *Journal of Dental Research*, 68, 1102-1104.
- Hillson, S. (1989). *Teeth*. Cambridge: Cambridge University Press.

Hillson, S. (2008). Dental pathology. In M.A. Katzenberg & S.R. Saunders (Eds.), Biological Anthropology of the Human Skeleton (pp. 301-340). New Jersey: John Wiley and Sons Inc.

Irish, J.D. (1993). Biological affinities of Late Pleistocene through modern African aboriginal populations: Morris, A.G., Thackeray, A.I., & Thackeray, J.F. the dental evidence. Ph.D. Dissertation, Arizona State University, Tempe.

Irish, J.D. (1997). Characteristic high- and lowfrequency dental traits in sub-Saharan African populations. American Journal of Physical Anthropology, 102, 455-467.

Irish, J.D., & Turner, C.G. (1997). Brief communication: first evidence of LSAMAT in non-native Americans: historic Senegalese from West Africa. American Journal of Physical Anthropology, 102, 141-146.

July, R.W. (1998). A History of the African people. Fifth ed. Long Grove, Illinois: Waveland Press Inc.

Krige, J.D., & Krige, E.J. (1954). The Lovedu of the Transvaal. In C.D. Forde (Ed.), African worlds: studies in the cosmological ideas and social values of African peoples (pp. 5-82). London: Oxford University Press.

Larsen, C.S. (1997). Bioarchaeology: interpreting behavior from the human skeleton. Cambridge: Cambridge University Press.

Larsen, C.S., Shavit, R., & Griffin, M.C. (1991). Dental caries evidence for dietary change: an archaeological context. In M.A. Kelley & C.S. Larsen (Eds.), Advances in Dental Anthropology (pp. 179-202). New York: Wiley-Liss, Inc.

Lingstrom, P., Holm, J., Birkhed, D., & Bjorck, I. (1989). Effects of variously processed starch on pH of human dental plaque. Scandinavian Journal of Dental Research, 97, 92-400.

Lukacs, J.R. (1992). Dental paleopathology and agricultural intensification in South Asia: new evidence from Bronze Age Harappa. American Jour- Scherer, A.K., Wright, L.E., & Yoder, C.J. (2007). nal of Physical Anthropology, 87, 133-150.

Lukacs J.R. (1996). Sex differences in dental caries rates with the origin of agriculture in South Asia. Current Anthropology, 37, 147-153.

Lukacs, J.R. (2008). Fertility and agriculture accentuate sex differences in dental caries rates. Current Anthropology, 46, 901-914.

Lukacs, J.R., & Thompson, L. (2008). Dental caries prevalence by sex in prehistory: magnitude and meaning. In J.D. Irish & G.C. Nelson (Eds.), Technique and Application in Dental Anthropology (pp 136-177). Cambridge: Cambridge University Skinner, E.P. (1973). West African economic sys-Press.

Mackeown, J., Cleaton-Jones, P., & Hargreares, J.

(1995). Energy intake, dental caries and periodontal disease in 11-year-old black children in two regions of southern Africa: KwaZulu and Namibia. Community Dentistry and Oral Epidemiology, 23, 182-186.

(1987). Late Holocene human skeletal remains from Snuifklip, near Vleesbaai, Southern Cape. The South African Archaeological Bulletin, 42, 153-160.

Mulder, M.B. (1992). Demography of pastoralists: preliminary data of the Datoga of Tanzania. Human Ecology, 20, 383-405.

Mundorff-Shrestha, S.A., Featherstone, J.D.B., Eisenberg, A.D., Cowles, E., Curzon, M.E.J., Espeland, M.A., & Shields, C.P. (1994). Cariogenic potential of foods: II relationship of food composition, plaque microbial counts, and salivary parameters to caries in the rat model. Caries Research, 28,106-115.

Newbrun, E. (1982). Sugar and dental caries: A review of human studies. Science, 217, 418-423.

Ohinata, F., & Steyn, M. (2001). Report on human skeletal remains from a Later Iron Age site at Simunye (Swaziland). The South African Archaeological Bulletin, 56, 57-61.

Okazaki, K., Pei-Ying, T., & Kuo-Shyan, L. (2013). Sex difference in oral disease of millet agriculturalists from the Take-vatan lineage of the recent Banun tribe of Taiwan. Anthropological Science, 121, 105-113.

Pistorius, J.C.C., Steyn, M,. & Nienaber, W.C. (2002). Two burials at Malle, a Late Iron Age settlement in the Bankeveld in the North-West Province. The South African Archaeological Bulletin, 57, 55-63.

Reader, J. (1997). Africa: a biography of the continent Africa. New York: Vintage Books a Division of Random House, Inc.

Bioarchaeological evidence for social and temporal differences in diet at Pidras Negras, Guatemala. Latin American Antiquity, 18, 85-104.

Sealy, J.C., Patrick, M.K., Morris, A.G., & Alder, D. (1992). Diet and dental caries among Late Stone Age inhabitants of Cape Province, South Africa. American Journal of Physical Anthropology, 88, 123 -134.

Shaw, J.C.M. (1931). The teeth, the bony palate and the mandible in Bantu races of South Africa. London: John Bale, Sons and Danielsson, Limited.

tems. In E.P. Skinner (Ed.), Peoples and Cultures of Africa: An Anthropological Reader (pp. 205-210). Garden City, New York: Natural History Press.

- Solanki, G., Myburgh, N., & Moola, M.H. (1991). Dental caries in black preschool children in Cape Town. *Community Dentistry and Oral Epidemiology*, 19, 178-179.
- Steyn, M. (2003). A comparison between pre- and post-colonial health in northern parts of South Africa, a preliminary study. *World Archaeology*, *35*, 276-288.
- Steyn, M., Miller, S., Nienaber, W.C., & Loots, M. (1998). Late Iron Age gold burials from Thulamela (Pafuri Region, Kruger National Park). *The South African Archaeological Bulletin*, 53, 73-85.
- Turner, C.G. (1979). Dental anthropological indications of agriculture among the Jomon people of Central Japan. *American Journal of Physical Anthropology*, 51, 619-636.
- Walker, P.L., & Erlandson, J.M. (1986.) Dental evidence for prehistoric dietary change on the Northern Channel Islands, California. *American Antiquity*, *5*, 375-383.
- Zeleza, T. (1997). A modern economic history of Africa: The nineteenth century. V. 1. Nairobi: East African Educational Publishers Ltd.