Contribution of Stable Isotope Analysis to Understanding Dietary Variation among the Maya

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Stable carbon and nitrogen isotope ratios in skeletal tissues are widely used as indicators of prehistoric human diets. This technique distinguishes between the consumption of C3 and C4 plants and assesses the contribution of aquatic resources to otherwise terrestrial diets. Isotopic ratios in bone collagen emphasize dietary protein; those in bone apatite and tooth enamel reflect the whole diet. Bone collagen and apatite represent average diet over the last several years of life, while tooth enamel represents diet during the age of crown formation. The isotopic analysis of all three tissues in individuals at Maya sites in Belize, Guatemala, Honduras and Mexico reveals variation in the importance of maize, a C4 plant, based on age, sex, status, and local ecological factors, as well as dramatic changes in subsistence patterns from the Preclassic to Postclassic periods. These results enable a tentative synthesis of the dynamic relationship between subsistence and sociopolitical developments in ancient Mesoamerica.

Corn (maize) was the single most important New World crop at the time of European contact, and is widely considered to have been fundamentally important
to the rise of indigenous civilizations including the Inca, Aztec, and Maya. Of the triumvirate of maize, beans and squash, there is evidence that at least squash \((Cucurbita \text{ spp.})\) was domesticated by 10,000 years ago \((1-2)\), although domesticated beans \((Phaseolus \text{ spp.})\) appear a few thousand years ago at most \((3)\), and maize was first domesticated somewhere in between. Other plants were also probably cultivated several thousand years prior to the introduction of ceramics and village settlements in several regions of Central and South America \((4-5)\). It is the origins and subsequent importance of maize to these early civilizations that remains the focus of much archaeological and biological research. The focus of this paper will be on the Maya, the cultural group who occupied Belize, Guatemala, and the Yucatan peninsula of Mexico from about 1500 BC to 1500 AD. Using isotopic and other evidence of human diets, Maya subsistence practices will be examined in the context of developments and adaptations in other cultural and environmental areas of Mesoamerica, from its frontier in the highlands of northern Mexico to El Salvador and Honduras in the south.

Maize is widely thought to have been domesticated in the Rio Balsas region of western Mexico \((6)\), although the chronology of its origins and dispersal are less well understood. In the Tehuacán Valley, where maize cobs seemingly were associated with Coxcatlán phase \((7000-5500 \text{ BP})\) levels, direct AMS dating on a dozen cobs produced dates no older than 4700 ± 110 BP \((7-9)\). Two cobs from Guílánt Naquitz have now been dated to 5400 BP and are the oldest maize macrofossils currently known \((10)\), while maize pollen has been found in 6000 BP levels at San Andrés near the Gulf Coast of Tabasco \((11)\), Pope et al. 2001), and maize phytoliths by about 5500 BP at the Aguadulce rockshelter in Panama \((12-13)\).

Even in well documented archaeological excavations, however, the context and dating of archaeobotanical specimens may be problematic \((14)\), and the identification of small numbers and certain forms of maize phytoliths has also been argued by some to be unreliable \((15-16)\). In any event, even after its initial domestication, there was most likely considerable temporal and spatial variability in the incorporation of maize into existing subsistence patterns, and it is extremely difficult to measure its importance relative to other food resources since there is no way to balance the uneven representation and preservation of botanical and faunal remains in the archaeological record. The consumption of maize can, however, be quantified through stable isotope analysis of human skeletal remains \((17-20)\).

**Principles of Stable Isotope Analysis**

Carbon and nitrogen isotope ratios in human bone (and other tissues, when they are preserved) may be used to reconstruct prehistoric diet because of differential fractionation, between certain plant groups, of atmospheric carbon dioxide during
photosynthesis and of nitrogen during fixation or absorption. There are two stable isotopes each of carbon ($^{12}$C, $^{13}$C) and nitrogen ($^{14}$N, $^{15}$N), with $^{12}$C and $^{14}$N by far the most common in nature. Small differences in the ratios of these isotopes ($^{13}$C/$^{12}$C, $^{15}$N/$^{14}$N) can be measured by isotope ratio mass spectrometry using samples smaller than 1 milligram. High precision isotope measurements are reported using the delta notation ($\delta^{13}$C, $\delta^{15}$N) relative to the internationally recognized PDB and AIR standards and are expressed in parts per thousand or per mil ($\%e$).

Empirical and experimental data have indicated that different bone tissues reflect different components of the diet (21-22). In general, bone collagen is produced primarily from the protein portion of the diet, while bone apatite and tooth enamel are produced from a mixture of dietary protein, carbohydrates and fats. Stable isotope analysis of both bone collagen and apatite thus permits quantitative estimates of several dietary components. Both bone collagen and apatite are constantly being resorbed and replenished, so that their isotopic composition reflects dietary averages over at least the last several years of an individual's life. The apatite in tooth enamel, however, is not turned over, and represents diet at the time of tooth formation, often from a pre-weaning age.

Typically, grasses originally native to hot, arid environments follow the C4 (Hatch-Slack) photosynthetic pathway, and will have $\delta^{13}$C values averaging about -12‰; trees, shrubs, and grasses from temperate regions, which follow the C3 (Calvin-Benson) photosynthetic pathway, will have $\delta^{13}$C values averaging about -26‰. Metabolic fractionation in their consumers results in bone collagen $\delta^{13}$C values of about -7‰ and -21‰ and bone apatite $\delta^{13}$C values of about 0‰ and -14‰, respectively, for pure C4 and pure C3 diets.

Stable carbon isotope analysis is particularly useful in New World dietary studies since maize is often the only C4 plant contributing significantly to human diets: its contribution to bone collagen and to bone apatite may be estimated by interpolation. Some caution is warranted, however, if succulent plants were present, since they utilize the alternative CAM (crassulacean acid metabolism) photosynthetic pathway which results in carbon isotope ratios similar to those of C4 plants. Nevertheless, CAM plants are unlikely to have been major sources of dietary protein, whether consumed directly or indirectly through herbivorous faunal intermediaries.

While most plants C3 and C4 plants have similar carbon isotope ratios in most ecological settings, care must be taken in forested or other environments where atmospheric recycling can occur resulting in depleted carbon isotope ratios in plants and their consumers (23). Human diets which include forest animals, therefore, can significantly mask the consumption of maize or other C4 plants with enriched carbon isotope ratios if the values for these food resources have not been established. Carbon isotope ratios in C3 plants also are affected by water stress and
thus correlate to altitude and other factors. This is an important factor to consider in establishing the isotopic baseline for C3 plant foods; C4 plants, with their photosynthetic adaptation to hot and arid environments, do not seem to vary to the same extent, so that a carbon isotope ratio of about -10‰ for maize may be used throughout Mesoamerica unless demonstrated otherwise.

The carbon isotope ratios of marine and freshwater organisms are more variable, depending on local ecological circumstances, and often overlap with those of terrestrial plants and their consumers. These foods typically have much higher nitrogen isotope values, however, and their high protein content will contribute much more carbon to bone collagen than will plants foods which are only 10-20% protein.

For all of these reasons, quantification of the contribution of maize or other plants to human diets is better accomplished through measurement of stable isotope ratios in bone apatite or tooth enamel, rather than bone collagen.

The nitrogen isotope ratios for plants depend primarily on how they obtain their nitrogen - by symbiotic bacterial fixation of atmospheric nitrogen, or from soil nitrates - and these values are similarly passed along through the food chain accompanied by an approximately 2-3‰ positive shift for each trophic level. Human consumers of terrestrial plants and animals typically have δ^{15}N values in bone collagen of about 6-10‰ whereas dedicated consumers of freshwater or marine fish, and sea mammals, may have δ^{15}N values of 15-20‰ (24). Nitrogen isotope ratios also vary according to rainfall and other factors (25), and both carbon and nitrogen isotope ratios vary considerably among marine organisms (26).

It is critical, therefore, to establish a site-relevant isotopic baseline for interpreting human skeletal data. Analyses of faunal remains provide a good estimate both of the animals themselves and the plants they consume. This is particularly important since in many areas while maize may be the only C4 plant cultivated and consumed directly by humans, other C4 grasses may exist and be consumed by grazing herbivores which pass on an enriched isotopic signature to their human consumers. Information from ethnohistoric and other sources, along with isotopic data for relevant food resources, may then be used to propose specific dietary mixing models to account for human bone isotope ratios (27).

**Analytical Procedures**

For bone chemistry studies in Mesoamerica, the extraction of collagen and apatite from bone is often problematic due to rapid degradation in the warm and moist climate. Procedures must be employed which remove carbon and nitrogen from non-biogenic sources, and assess whether the remaining material is sufficiently intact or may have fractionated during decomposition. Bone collagen is usually
obtained by demineralization with HCl or EDTA, followed by treatment with NaOH to remove humic acid contaminants, and with a methanol, chloroform, and water mixture to remove lipids. The use of weak HCl (2%) frequently allows the recovery of collagen from otherwise highly degraded bone, and the visible collagen pseudomorphs produced are a strong indicator of sample reliability. The resulting collagen is often then solubilized, particulate organic contaminants removed by filtration or centrifugation, and recovered as a gelatin powder following evaporation.

CO₂ and N₂ gases are subsequently obtained and introduced to a stable isotope ratio mass spectrometer either (1) by off-line combustion in evacuated quartz tubes, followed by purification and separation by cryogenic distillation, and the use of a manifold ‘cracker’; or (2) by on-line combustion and temporal separation of the gases using a CHN analyzer and chromatographic column directly coupled to the mass spectrometer. The reliability of collagen samples is evaluated by the yield of ‘collagen’ from the bone sample, and the ratio of C:N in the ‘collagen’. Yields under 1% signify very poor preservation and the likelihood that the remaining material may have become fractionated, while ratios outside the range of 2.9-3.7 are not considered typical for intact collagen.

Although normal organic decomposition is the greatest problem affecting bone collagen, contamination and chemical exchange with the burial matrix are the main issues for the reliable isotopic analysis of the carbonate in bone apatite and tooth enamel. The denser, relatively impermeable tooth enamel, however, is easily dealt with even when the tooth is of great antiquity by removal of surface layers followed by an acetic acid wash. Similar procedures have been developed for the more porous bone apatite, with residual organic components dissolved in sodium hypochlorite and non-biogenic carbonates removed with a buffered acetic acid solution. Samples may be further tested for integrity by x-ray diffraction or IR spectroscopy. Purified CO₂ is obtained by reaction with 100% phosphoric acid, either off-line (followed by cryogenic distillation and introduction through a manifold system as described above), or online in automated acid bath systems.

High precision in stable isotope mass spectrometry is achieved through repeated measurements of a reference gas, and inter-laboratory compatibility is maintained through calibration against standard reference materials. Analytical precision for most modern mass spectrometers is about ± 0.1‰ for both δ¹³C and δ¹⁵N.

**Maya Isotope Studies**

One of the first applications of stable isotope analysis in archaeology was the analysis of human remains from the Tehuacan Valley. Unfortunately, of the 12
samples which produced collagen, only two came from contexts earlier than 3000 BP. These limited samples, however, suggest that maize was already a dietary staple several millennia earlier in the El Riego phase ($\delta^{13}C = -13.3\%$), and dominated the diet by the succeeding Coxcatlan phase ($\delta^{13}C = -6.1\%$) (37). The widespread importance of maize by the Formative Period at villages like Monte Alban in the Oaxaca Valley, and along the southeastern coast of Mexico in the Soconusco region, has also been documented by stable isotope studies (38-39). At the southern end of Mesoamerica, maize appears to have been a significant component of Panamanian diets by 4500 BP, at preceramic coastal sites such as Cerro Mangote (40).

A significant amount of research on the diet of the Maya has been done in the last dozen years since the first published study in this central region of Mesoamerica (41). Results are now available for over 600 individuals, representing such diverse areas as the lowlands of Belize and the Petén, the Yucatan peninsula, and the highlands of Guatemala, and spanning more than 2000 years from the Preclassic through Postclassic periods (Figure 1; Table 1). It is now well established that substantial variation in subsistence adaptations existed in this region, and this diversity is mainly attributable to chronology, geographic location, and social factors (42-45). The importance of maize generally increases over time, probably due to intensification and extensification of agricultural production; communities living in diverse ecological zones nevertheless employed different subsistence strategies; and the increasingly hierarchical and complex nature of Maya society allowed for differential patterns of food acquisition, storage, and consumption.

In the Maya region, zooarchaeological and paleobotanical remains as well as ethnohistoric evidence have identified the most important animal and plant foods as including white-tailed and other deer, domestic dog, armadillo, peccary, and freshwater turtle, as well as rabbit, opossum, raccoon, agouti, and tapir; fish and shellfish (in coastal and estuary areas); and maize, beans, squash, root crops, and fruits (46-47). CAM plants such as cactus and pineapple are not thought to have been important to the diet. Trace element analyses strongly argue that most foods were obtained locally, rather than by trade (48), although by the Classic period elites likely would have had preferential access to non-local resources (49).

Most notably, dog was the only domesticated animal available for consumption, and hunting of wild animals remained a significant part of Maya subsistence adaptations long after the establishment of settled villages and urban development. Stable isotope analyses of dog remains from a number of Maya sites generally show similar values to their human masters, but some, especially in later periods, have even higher maize signatures indicating that they were specifically being fed large quantities of maize (42, 45, 50-52). Finds of dog remains in domestic middens, often with cutmarks on the bones, demonstrates that these were indeed comestible canids or corn-dogs (53). Isotopic analyses of deer collagen, however, have
revealed at most a 7-22% level of maize consumption, attributable to occasional browsing in maize fields, and this level of maize consumption does not change over time (42, 45, 52, 54-55).

Figure 1. Map showing Maya archaeological sites for which stable isotope data are available.
For the Maya lowlands in Belize, collagen data are now available for ten sites, including one located on the coast (41-42, 45, 50, 56-62) (Figure 2). These data show that by the Preclassic period, with $\delta^{13}C$ values at non-coastal sites averaging -12.6 ± 1.2‰, C4 sources appear to account for about 50% of the carbon in bone collagen; this is likely the result of consuming significant quantities of maize, as well as C4-enriched animal foods including dog and armadillo. Surprisingly, there is only a modest increase in isotope ratios throughout the Early, Late, and Terminal Classic periods, to -11.3 ± 2.3‰, suggesting that the diversity of foods available in the Maya lowlands had not significantly changed over 2000 years.

It must be noted that the figures presented here are averages of data from multiple sites with different local ecological settings; not all sites individually follow the same trend, for example at Caracol where carbon isotope ratios decrease rather than increase over the course of the Classic period (59-61). The Baking Pot, Barton Ramie and Lamanai sites are located in riverine settings, where consumption of freshwater fish with depleted carbon isotope ratios could offset C4 maize contributions to bone collagen. At Mojo Cay, the enriched carbon isotope ratios are most likely due not to high levels of maize consumption, but rather to the importance of local reef fish and shellfish which do not have enriched nitrogen isotope ratios (42, 45, 56). Intra-site differences based on status are apparent at sites such as La Milpa (unpublished data), Pacbitun (62) and Caracol (59-61), with elites buried in formal tombs near site centers enriched 2-4‰ in collagen carbon compared to non-elites buried away from the site core. At Lamanai, Early Classic elites have the lowest carbon isotope ratios, indicating the least dependence on maize and probably preferential access to reef fish and shellfish (41). Of great significance is the observed shift at Lamanai between the Classic and Postclassic periods, to $\delta^{13}C$ values of -9.3 ± 0.8‰, demonstrating a substantially increased reliance on maize and possibly also a shift from the consumption of freshwater to marine fish as part of coastal trade networks (41).

At Preclassic Maya sites in the Peten region like Altar de Sacrificios and Seibal the average collagen $\delta^{13}C$ values of -10.2 ± 1.2‰ suggest that C4 sources accounted for about 70% of the carbon in bone collagen, a level only reached in Belize during the Postclassic (Figure 3). During the course of the ensuing Classic period, however, we observe the same modest increase of about 1‰ in $\delta^{13}C$ values for Peten sites as we saw for Belize; intensification of maize production was something which was occurring throughout the Maya region. There is no observable difference in carbon isotope ratios between Peten sites located in riverine and inland environments, suggesting that fish were not a significant component of the average Maya diet in this region. At Seibal, there is no change in collagen carbon isotope ratios from the Preclassic to the Terminal classic, although nitrogen isotope ratios decrease nearly 1‰, suggesting stability in maize consumption at this site while terrestrial fauna may have become more important than aquatic fauna over time.
Figure 2. Bone collagen stable isotope data for Maya sites in Belize. 
*Mojo Cay (coastal) not shown.*

Figure 3. Bone collagen stable isotope data for Maya sites in the 
*Peten and Guatemala.*
Individuals from Late Classic Uaxactun notably more closely resemble contemporaries in Belize in their isotope ratios, perhaps because all of the sampled individuals are females from an elite burial context (50). At Copan in Honduras, carbon isotope ratios are similar to contemporary Classic sites in the Peten region; nitrogen isotope ratios, however, are considerably lower, suggesting then greater dependence on beans and/or reduced availability of animal protein (63). Greater variability in isotope ratios is also observed among high-status burial groups, perhaps a result of greater diversity in diets (64). While nitrogen isotope ratios could also be lower at Copan because of its higher altitude (ca. 600 m), there is no systematic difference in the $\delta^{15}$N values for white-tailed deer and other fauna from Copan relative to Peten sites (50). The only Postclassic site for which data are available is Iximche, the Kaqchikel Maya capital in highland Guatemala, with $\delta^{13}$C values reaching -7.8 ± 0.8‰ (65-66), indicating substantially greater maize dependence than at any Classic period site, or contemporary Lamanai in Belize. No faunal samples from this highland area (2200 m asl) have been tested to determine whether the accompanying low nitrogen isotope ratios (7.9 ± 0.4‰) are a result of environmental factors or greater dependence on beans or other plant foods. The collagen data listed in Table 1 for Kaminaljuyu actually come from tooth dentin, with some of the teeth having enriched carbon isotope ratios as a result of the pre-weaning diets that they represent (67-68). This only further emphasizes the differences between Classic and Postclassic diets in the Peten and highland Guatemala.

For omnivorous humans, it is important to remember that isotope data from bone collagen are heavily biased towards consumed protein, making it difficult to compare absolute quantities of maize consumed when the amount of animal (or fish) protein also varied. Bone apatite and tooth enamel, on the other hand, appear to faithfully reflect the whole diet (21), allowing the calculation of the carbon isotope ratios of the average foods consumed. Along with nitrogen isotope ratios from bone collagen, estimated human diets may then be illustrated in the same plot as the foods themselves. Carbon isotope ratios in bone apatite and tooth enamel ratios are offset here by -9.5‰ based on the controlled diet experiments on rats by Ambrose and Norr (21), although an offset of -12‰ has been empirically determined for larger mammals (69); nitrogen isotope ratios are offset by -3.0‰. Values for animal flesh, which contains both protein and fats, were estimated by a -2.0‰ correction relative to the bone collagen results for the faunal specimens tested; when modern samples were used, these were corrected +1.5‰ to account for changes in atmospheric CO$_2$ due to combustion of fossil fuels since the industrial revolution (Figures 4-5).

Bone apatite data are available for a half dozen sites in Belize, and show a similar chronological trend towards increasingly enriched carbon isotope ratios as that observed for bone collagen. A large shift in $\delta^{13}$C from -9.5 ± 1.2‰ to -6.8 ± 1.2‰, however, is observed between the Preclassic and Early Classic at sites
Figure 4. Human diets at Maya sites in Belize based on bone apatite carbon and bone collagen nitrogen isotope ratios. Human bone apatite carbon corrected -9.5, and collagen nitrogen -3.0 to reflect estimated diet. Faunal bone collagen carbon corrected -2.0 to simulate flesh; modern samples corrected +1.5 for industrial effect.

Figure 5. Human diets at Maya sites in the Peten and Guatemala based on bone apatite carbon and bone collagen nitrogen isotope ratios. Corrections as in Figure 4.
including Cuello and Lamanai, while only a statistically insignificant change is then observed through the Late, Terminal, and Postclassic periods. This is in contrast to the timing of changes in carbon isotope ratios in bone collagen, and suggests that the real increase in the importance of maize to the whole diet came during the first millennium BC, and that the collagen shift between the Classic and Postclassic periods may be attributed to changes in the average carbon isotope value for dietary protein. This could be explained by a decrease in the consumption of animal foods, thereby increasing the relative contribution of maize protein; eating animals with more enriched carbon isotope ratios such as dogs, or reef fish if available; or some combination of these.

For the Classic period sites of Holmul, Seibal, and Uaxactun in the Peten region, and Copan in Honduras, there do not appear to be significant differences in the carbon isotope ratios of bone apatite relative to the BelizeClassic period sites, with δ13C values ranging from about -4 to -6‰, suggesting that the overall importance of maize was actually quite similar throughout these regions. Tooth enamel samples from Early Classic Kaminaljuyu average δ13C of -3.0 ± 1.4‰, but the teeth tested include molars and premolars formed at both pre- and post-weaning ages, so that this average value is enriched due to the trophic level effect; the almost-adult diets represented by 3rd molars, with their enamel formed between ages 10 and 12, are therefore similar in isotopic value to those observed for Belize and the Peten. A second and a third molar from Lamanai, which average -2.0‰, are not consistent with bone apatite values from the same individuals and may be the result of small samples representing short-term seasonal diets at the time of tooth formation (70). For Postclassic Iximche, however, only third molars were tested, and the δ13C values of -2.1 ± 1.1‰ obtained are clearly enriched relative to Classic Maya sites in all regions (71). The only contemporary site available for comparison is Lamanai, where bone apatite δ13C averages -6.4±1.7‰, thus strongly supporting the conclusion that dependence on maize was significantly greater in the Mesoamerican highlands than in the lowlands.

Conclusion

Ecological models of the ‘collapse’ of Maya civilization have argued that dietary and health deficiencies mounted throughout the Classic period due to increasing urbanization, deforestation, and climatic instability (72-73), but no pattern of nutritional or health deterioration over time has been documented (43, 74-78). Nevertheless, increasing demands of a political elite certainly encouraged agricultural intensification, monocropping, and unsustainable extensification and use of marginal lands and this is clearly evident in changes in bone isotope ratios. Notable shifts occur in bone apatite values between the Preclassic and Early Classic
periods, and in bone collagen between the Late/Terminal Classic and Postclassic periods, suggesting that overall dependence on maize was largely established and stable by the beginning of the Classic, and that changes in protein sources occurred after the Classic Maya collapse. Decreasing availability of limited wild animal populations may be hypothesized as contributing to increased territorial conflicts among Maya centers. Furthermore, significant variation is apparent on regional levels, with inland and highland populations more dependent on maize in all periods relative to lowland sites with access to aquatic resources or located in more diverse ecological settings. Elite privilege was also important in determining diets during the Classic period, but maize or maize-fed animals were not always the preferred food despite their important role in Maya rituals.

The synthesis presented here is subject to revision as new data become available, both isotopic and from other sources. Results are currently available from only two post-Classical sites, and sites in Honduras, highland Guatemala, and the Yucatan are very sparsely represented. Almost no data are available from the adjacent gulf coast region of Mexico, where the Olmec civilization developed.

Methodologically, bone apatite needs to be analyzed for many more sites to avoid the protein bias of bone collagen, when we know that plant foods formed the bulk of non-coastal Mesoamerican diets. Measurement of isotope ratios in teeth of various formation ages has already been used to reconstruct weaning practices, and in comparison to adult values, changes in diet due to migration or other factors. On a finer scale, microsampling of growth layers in tooth enamel and dentin can also be used to document seasonal variability in diets, which previously was limited to studies in areas where hair samples are preserved. Finally, compound specific isotopic analysis is a new and promising technique which allows comparison of essential vs. non-essential amino acids in collagen, while eliminating the problem of diagenesis in poorly preserved bones.

The continued integration of bioarchaeological data with ethnohistoric, archaeological, faunal, floral, and paleoclimatic evidence ultimately will allow more precise interpretations of the relationships between subsistence and sociopolitical developments in ancient Mesoamerica.

References

### Table I. Stable Isotope Data for the Maya

<table>
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<tr>
<th>Site</th>
<th>n</th>
<th>δ(^{15})N</th>
<th>δ(^{13})C(_{\text{collagen}})</th>
<th>δ(^{13})C(_{\text{apatite}})</th>
<th>δ(^{13})C(_{\text{enamel}})</th>
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<td></td>
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<td>Baking Pot: LC</td>
<td>9,9,4</td>
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### Table I (continued)

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Abbreviations: Preclassic (PreC); Early Classic (EC); Middle Classic (MC); Late Classic (LC); Terminal Classic (TC); Postclassic (PC); Historic (H)