Early Ceremonial Constructions at Ceibal, Guatemala, and the Origins of Lowland Maya Civilization

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The spread of plaza-pyramid complexes across southern Mesoamerica during the early Middle Preclassic period (1000 to 700 BCE) provides critical information regarding the origins of lowland Maya civilization and the role of the Gulf Coast Olmec. Recent excavations at the Maya site of Ceibal, Guatemala, documented the growth of a formal ceremonial space into a plaza-pyramid complex that predated comparable buildings at other lowland Maya sites and major occupations at the Olmec center of La Venta. The development of lowland Maya civilization did not result from one-directional influence from La Venta, but from interregional interactions, involving groups in the southwestern Maya lowlands, Chiapas, the Pacific Coast, and the southern Gulf Coast.

During the early Middle Preclassic period (1000 to 700 BCE), sedentary communities using ceramics began to appear in the Maya lowlands (Figs. 1 and 2). Many of their neighbors were already leading sedentary ways of life and were using ceramics during the Early Preclassic period (before 1000 BCE) (*1*). In particular, the inhabitants of southern Veracruz and western Tabasco, generally called the Gulf Coast Olmec, were building a large center at San Lorenzo and were producing elaborate stone sculptures (*2*, *3*). Scholars have long debated the influence that the Gulf Coast Olmec had on the development of lowland Maya society. Some view the Gulf Coast Olmec as the mother culture: the source of cultural innovations from which characteristic art styles and centralized political organization spread to the Maya and other Mesoamerican groups (*4*–*6*). Others contend that the lowland Maya received only limited Olmec influence or interacted with them as competing peers (*7*–*9*). A critical issue is the development of formal architectural complexes consisting of plazas and pyramids, which eventually became the hallmarks of Mesoamerican civilizations. San Lorenzo did not have substantial mounds or pyramids (*2*, *10*). The subsequent Gulf Coast center of La Venta, in contrast, exhibited a highly formalized arrangement of a pyramid, platforms, and plazas, and it has been suggested that this architectural template developed there spread to the Maya lowlands and other parts of southern Mesoamerica (*5*, *11*). Here we describe excavations at the Maya center of Ceibal that provide evidence of earlier architecture and thus imply a more complex process.

Ceibal (also spelled Seibal) is located in the southwestern part of the Maya lowlands and was explored extensively in the 1960s by a team from Harvard University (*12*). These studies showed that its occupation began during the early Middle Preclassic period characterized by Real ceramics (*13*). We targeted group A, where the Harvard team found concentrations of Real ceramics (Fig. 3). Our excavations revealed early Middle Preclassic buildings in four areas: the core of structure A-20 and the plaza in front of structure A-20, as well as in the lower levels of the A-24 platform and the East Court. Structure A-20 appears to have at least 11 construction stages, of which 5 or more date to the Real phase (Fig. 4). The excavation results and radiocarbon dates indicate that around 1000 BCE, the early residents of Ceibal made the first version of structure A-20 (Ajaw) by carving a high point of the limestone bedrock and placing black soil with high clay content on top (fig. S1). This building measured 2.0 m in height and 4.0 m in the east-west dimension of its summit. Thus, the first version of A-20 was a low flat platform rather than a pyramid. On the eastern side of the building, a ramp carved out of natural marl (decaying limestone bedrock) provided access to the summit. A major renovation took place during the Real 2 phase (850 to 800 BCE), and the expanded building (B'ehom) appears to have reached a height of 3 to 5 m and had a pyramidal shape. We estimate that the building measured roughly 6 to 8 m in height by the end of the Real phase around 700 BCE. Fifty meters to the east of structure Ajaw, we uncovered a long platform (Xa'an) buried under later plaza fills. Structure Xa'an was also carved out of natural marl around 1000 BCE, and it measured 1.0 m in height and probably 42 to 55 m in length. Structures Ajaw and Xa'an represent the earliest known example of the so-called "E-Group assemblage," a ceremonial compound consisting of a western square structure and an eastern long platform that became ritual foci of many lowland

Fig. 1. Map of southern Mesoamerica with the locations of Ceibal and the sites discussed in the text.

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Maya centers during later periods. At the same time, the residents scraped off the surface soil in the area between structures Ajaw and Xa'an to create a leveled plaza and used the exposed whitish marl as the first plaza floor. Numerous offerings, including greenstone axes, were deposited in this plaza, indicating that this space served as the primary stage of communal ritual throughout the Middle Preclassic period. During the Real 3 phase (800 to 700 BCE), the Ceibal residents expanded this plaza by burying structure Xa'an in a plaza fill and constructing a new version of the eastern long platform (Saqpusin) farther to the east.

The earliest version of the A-24 platform (Sulul), revealed in operation (Op.) 200B, was also built around 1000 BCE (Fig. 5 and fig. S2). It consisted of sticky dark clay that appears to have been taken from the wetlands and was placed directly over the irregular natural ground surface. This fill measured 1.3 m in thickness, but the platform's horizontal dimensions are unknown. Platform Sulul was soon expanded horizontally to reach an east-west dimension of more than 34 m, as indicated by the find of the same wetland-soil fill in Op. 200A. The total thickness of platform Sulul's fill in Op. 200A measured more than 2.5 m because of the sloping natural terrain, suggesting that the construction of this platform involved a substantial investment of labor. During the latter part of the Real 1 phase, the Ceibal residents expanded this platform vertically using clay mixed with silt and sand. Through at least 17 episodes of construction by the end of the Real 2 phase, the renovated version of the platform (Ch'och') reached total fill thicknesses of 3.5 m in Op. 200B and roughly 6 m in Op. 200A. During the Real 3 phase, the A-24 platform received little renovation, and the focus of construction activity shifted to the northeastern platform, the East Court. This platform started with one or two episodes of substantial construction with earthen fills (K'at), possibly during the Real 2 phase, which measured 1.4 to 1.7 m in total thickness. By the end of the Real phase, platform K'at had received at least 15 episodes of reflooring and rebuilding, reaching a fill thickness of 2.0 to 2.3 m. In contrast to structures Ajaw, Xa'an, and Saqpusin of a public and ceremonial nature, platforms Sulul/Ch'och' and K'at appear to have supported multiple residential structures, which consisted of low clay or clay-and-stone foundations and perishable walls and roofs. Excavations of the East Court revealed parts of three structures dating to the late Middle Preclassic Escoba phase, which appear to have surrounded a square patio. We suspect that a residential complex in a similar configuration existed during the Real phase.

We obtained 54 radiocarbon dates, to which we applied Bayesian modeling to develop a site chronology (figs. S3 and S4 and table S1). Multiple dates associated with the earliest versions of structures Ajaw and Xa'an and platform Sulul concentrate around 1000 BCE, marking the beginning of the Real 1 phase. The following Real 2 phase is dated to 850 to 800 BCE with 13 overlapping radiocarbon dates. This facet is more precisely dated because the radiocarbon calibration curve of this span is steep, and the radiocarbon dates obtained from a sequence of numerous floors in platform Ch'och' made Bayesian modeling effective. The date of the Real 3 phase is less precise because of the flattening of the calibration curve, but we estimate that it spanned from 800 to 700 BCE.

The beginning date of 1000 BCE for Ceibal corresponds roughly with the onset of sedentary settlements with ceramics in other parts of the Maya lowlands, including Cuello, Cahal Pech, Blackman Eddy, and Tikal (*14*–*17*). Although some of these sites have yielded earlier calibrated dates, acceptable dates from secure contexts tend to fall around 1000 BCE or later (*18*). Furthermore, these sites share ceramics with postslip incisions characteristic of the early Middle Preclassic period. However, formal ceremonial complexes dating to 1000 to 800 BCE have not been found at these other sites; excavations have revealed only humble residences, consisting of postholes dug in the natural ground or small platforms less than half a meter in height. The Ceibal E-Group assemblage consisting of structures Ajaw and Xa'an thus predates other known examples from the Maya lowlands by two centuries or more. Komchen may have substantial platforms dating to the early Middle Preclassic period, but their initial configuration is not clear, and their dates remain imprecise. During the Real 2 phase, the Ceibal E-Group assemblage grew to be the earliest known plaza-pyramid complex in the Maya lowlands, and structure

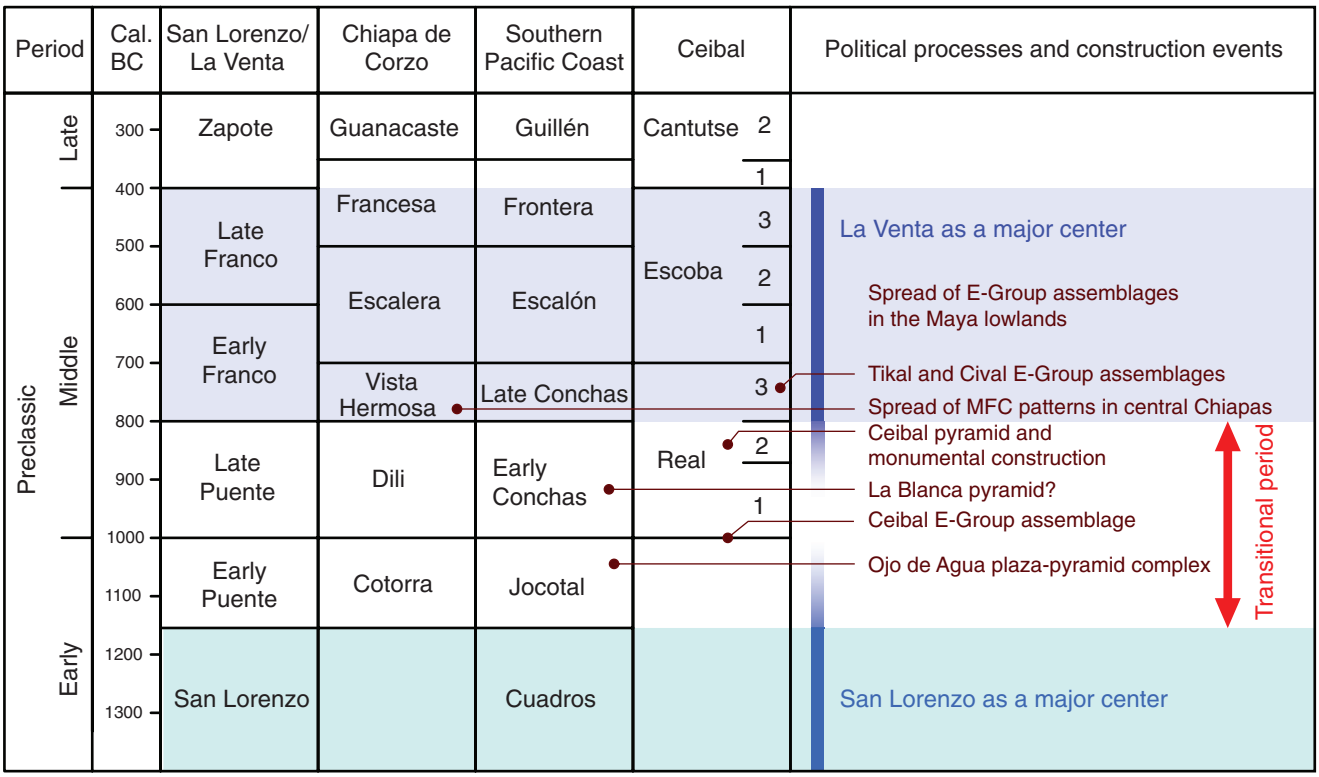

Fig. 2. Chronology of southern Mesoamerica.

B'ehom and platform Ch'och' represented the earliest monumental constructions. The next oldest E-Group assemblages in the Maya lowlands have been found at Tikal and Cival (*7*, *17*). They are associated with ceramics contemporaneous with the Real 3 and Escoba 1 phases (800 to 600 BCE). During the late Middle Preclassic period (700 to 400 BCE), E-Group assemblages with pyramids spread to numerous lowland Maya centers, including Nakbe.

Outside the Maya lowlands, interpretations hinge on a comparison with La Venta. Much of our knowledge of this Olmec center comes from excavations in the 1940s and 1950s, and a large part of the site is unexplored. Its chronology has been a vexing problem. New radiocarbon dates and the cross-dating of ceramics and figurines, however, suggest to some that the rise of La Venta as a major center occurred after 800 BCE (*19*–*21*). We applied Bayesian statistics to these radiocarbon dates, using the improved regional ceramic sequence (*22*, *23*). Out of 10 significant cultural features excavated in complexes E and G near the La Venta ceremonial core, 9 belong to the Franco ceramic phase (800 to 400 BCE), characterized by composite-silhouette bowls and plates (round bases and walls that are straight or curve out), black serving vessels, and hatched triangles and other incised or grooved motifs (figs. S5 and S6 and table S2). These results support the interpretation that the population of La Venta grew rapidly after 800 BCE. The construction of La Venta's ceremonial core may have started earlier (fig. S7 and table S3), but before 800 BCE La Venta was probably a smaller, less influential center and may have had mutually stimulating interactions with Ceibal and other contemporaneous communities. These dates also indicate that there was a substantial gap between the decline of San Lorenzo and the growth of its successor. The interpretation of San Lorenzo's fall has been equally uncertain, although the date of 1000 BCE has traditionally been used (*2*). However, a Bayesian model of available dates suggests that San Lorenzo's heyday more likely ended around 1150 BCE (figs. S8 and S9 and table S4). Moreover, archaeological data from central Chiapas and the Chiapas Pacific Coast, as well as the Bayesian statistics of radiocarbon dates from there (figs. S10 and S11 and table S5), indicate that the influence of San Lorenzo diminished around this date (the end of the Cuadros phase on the Pacific

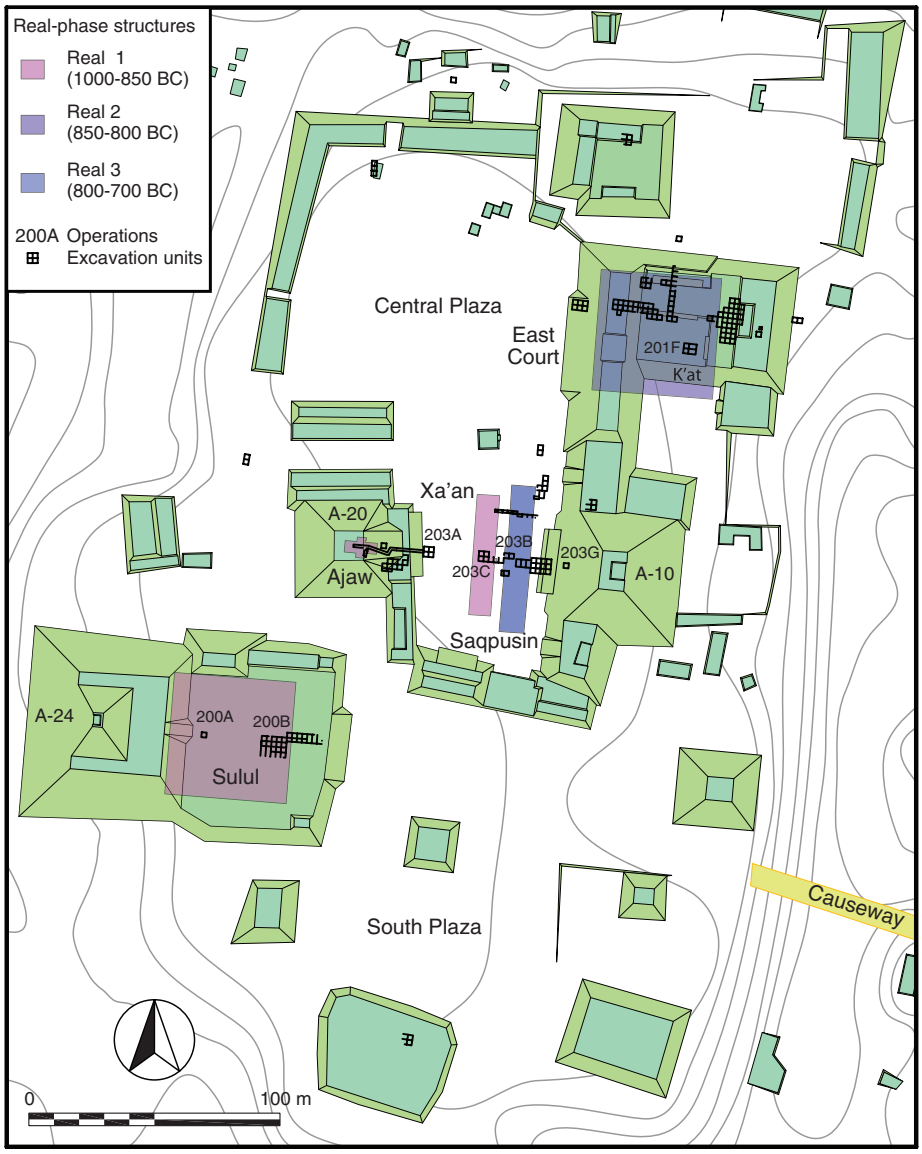

Fig. 3. Map of Ceibal group A with the locations of excavation units and Real-phase structures.

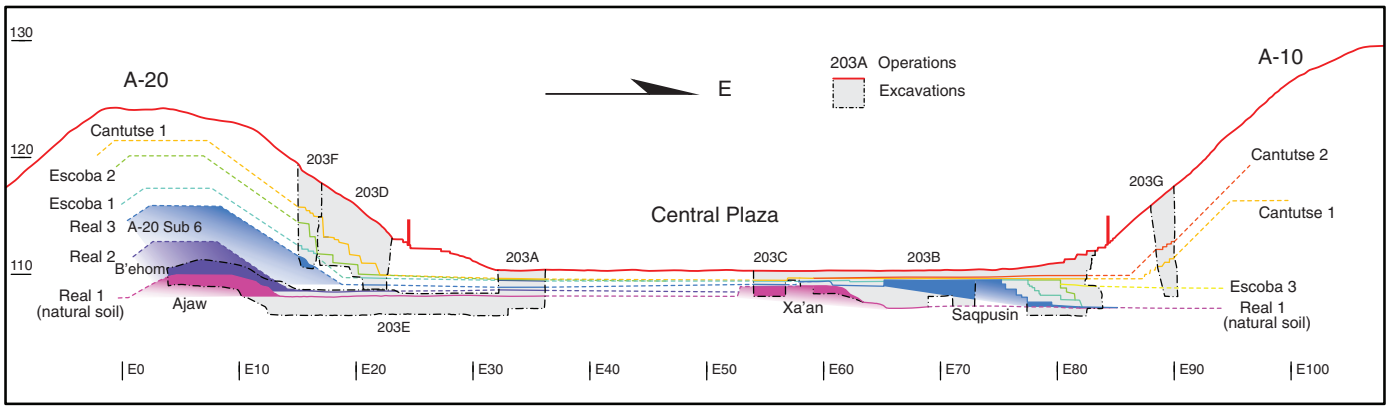

Fig. 4. East-west section of the central plaza and structures A-10 and A-20.

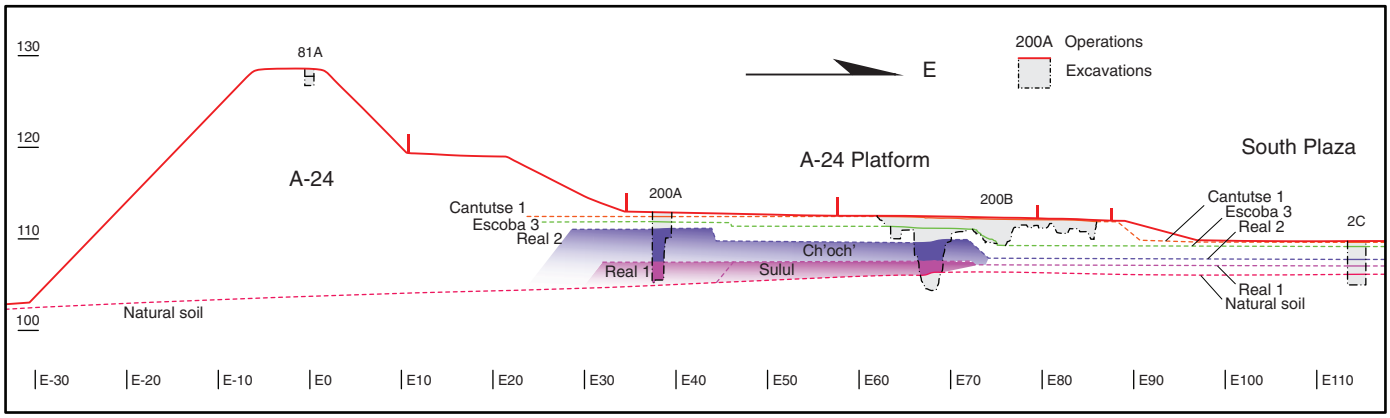

Fig. 5. East-west section of the A-24 platform.

Coast and that of the Cacahuanó phase in the western Grijalva River basin) (*19*, *24*, *25*). The establishment of formal ceremonial spaces and their growth into plaza-pyramid complexes probably occurred during this transitional period between the two Gulf Coast powers.

An important area for the development of ceremonial complexes was probably central Chiapas along the Grijalva River. Clark, following McDonald and Lowe (*5*, *11*, *26*), noted that Middle Preclassic centers in this region, including Mirador, San Isidro, Ocozocoautla, Chiapa de Corzo, Finca Acapulco, and La Libertad, as well as Tzutzuculi on the Pacific Coast, shared highly standardized spatial plans, each consisting of an E-Group assemblage and large platforms placed along the north-south axis of the settlements. This configuration, which Clark called the Middle Formative Chiapas (MFC) pattern, closely resembles that of Ceibal. Many of the MFC-pattern complexes, including those at Tzutzuculi, Mirador, San Isidro, and La Libertad, were not constructed until 800 or 700 BCE (*26*–*29*). The E-Group assemblage at Chiapa de Corzo may be slightly earlier (*30*). Excavations also suggest that, at the beginning of the Middle Preclassic, the central part of Chiapa de Corzo was leveled off, and scraped surface soils along with remains of the Early Preclassic period were dumped to the slope near the ceremonial core (*31*). This means that the early residents of Chiapa de Corzo and Ceibal shared similar manners of preparing the areas at the onset of ceremonial constructions, apparently emphasizing a break from the previous era. The excavation results of Finca Acapulco have not been fully described, but it is possible that this site with significant Early Preclassic occupations had ceremonial constructions contemporaneous with those of Ceibal (*25*). An even earlier plaza-pyramid complex may have existed on the Chiapas Pacific Coast. During the Jocotal phase (1200 to 1000 BCE), when the influence of San Lorenzo weakened, a series of extensive mounds were constructed near estuaries, but the most impressive was Ojo de Agua in an inland area (*32*). Its pyramids, substantial platforms, and plazas exhibit a vague resemblance to the MFC pattern. The southern Pacific Coast had a tradition of building residences on raised platforms associated with plazas dating back at least to the Locona phase (1600 to 1500 BCE) (*33*). However, during the Cuadros phase (1350 to 1200 BCE), when influence from San Lorenzo was notable, the largest community of the area, Cantón Corralito, adopted San Lorenzo–like constructions lacking tall mounds but consisting of an extensive low terrace that supported residential buildings with low foundations (*24*). This sequence suggests that the plaza-pyramid complex of Ojo de Agua did not derive from the Gulf Coast. During the following Conchas phase (1000 to 600 BCE), the center of La Blanca across the Guatemalan border grew, with a large pyramid, mound 1, eventually reaching a height of 25 m. The date of La Blanca mound 1 remains problematic (*34*). Its monumental construction may predate those at Ceibal and La Venta or may be contemporaneous with them.

It is well documented in North and South America that monumental architecture could be built long before the emergence of centralized polities and marked social inequality (*35*). Critical issues in this study then are not only the sizes of buildings but also the social roles that buildings and spaces played in specific historical contexts. The data from Ceibal make it clear that the original emphasis was on the ceremonial complex as a stage for communal ritual performances. Pyramids resulted from a sequence of architectural renovations applied to original platforms and possibly provided spatial settings for more marked segregations among community members (*36*). The emergence of standardized ceremonial complexes exemplified by the E-Group assemblage and the MFC pattern were possibly associated with increasingly prescribed forms of interactions and shared notions of new social order (*37*). The sequential architectural development at Ceibal implies that this center was not a passive recipient of an idea established elsewhere, but it most likely participated actively in the process of this innovation. This development appears to have occurred through interregional interactions, primarily involving groups in the southwestern Maya lowlands, Chiapas, the Pacific Coast, and the southern Gulf Coast. Then around 800 to 400 BCE, plaza-pyramid complexes spread to other parts of southern Mesoamerica, including the central Maya lowlands, the Guatemalan highlands, El Salvador, and Honduras. The residents of highland Mexico, including the Basin of Mexico, Morelos, and Oaxaca, built substantial platforms during the Early Preclassic period, but they were slow to adopt pyramidal architecture (*38*–*40*). These observations indicate that the origins of lowland Maya civilization can be explained neither in terms of Gulf Coast Olmec influence nor independent development. One-directional influence from La Venta was probably not significant at the beginning of the Middle Preclassic period, but interactions with and inspirations from the area to the west were still critical for social changes in the Maya lowlands.

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Supplementary Materials
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Materials and Methods
Figs. S1 to S11
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References (*41–67*)

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PINK1-Phosphorylated Mitofusin 2 Is a Parkin Receptor for Culling Damaged Mitochondria

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Senescent and damaged mitochondria undergo selective mitophagic elimination through mechanisms requiring two Parkinson's disease factors, the mitochondrial kinase PINK1 (PTEN-induced putative kinase protein 1; PTEN is phosphatase and tensin homolog) and the cytosolic ubiquitin ligase Parkin. The nature of the PINK-Parkin interaction and the identity of key factors directing Parkin to damaged mitochondria are unknown. We show that the mitochondrial outer membrane guanosine triphosphatase mitofusin (Mfn) 2 mediates Parkin recruitment to damaged mitochondria. Parkin bound to Mfn2 in a PINK1-dependent manner; PINK1 phosphorylated Mfn2 and promoted its Parkin-mediated ubiqitination. Ablation of Mfn2 in mouse cardiac myocytes prevented depolarization-induced translocation of Parkin to the mitochondria and suppressed mitophagy. Accumulation of morphologically and functionally abnormal mitochondria induced respiratory dysfunction in Mfn2-deficient mouse embryonic fibroblasts and cardiomyocytes and in Parkin-deficient *Drosophila* heart tubes, causing dilated cardiomyopathy. Thus, Mfn2 functions as a mitochondrial receptor for Parkin and is required for quality control of cardiac mitochondria.

Mitochondria are endosymbiotic organelles derived from primitive aerobic bacteria. Healthy mitochondria are essential energy generators for most metazoan cell functions, whereas senescent or damaged mitochondria are sources of toxic reactive oxygen species. Thus, mitochondrial biogenesis and mitophagic elimination are carefully orchestrated, and their mutational disruption causes chronic degenerative diseases (*1*). Genetic studies have linked Parkinson's disease to mutations of two mitophagy genes, the E3 ubiquitin ligase Parkin and the serine-threonine protein kinase PINK1 (PTEN-induced putative kinase protein 1; PTEN is phosphatase and tensin homolog) (*2*). Loss of the mitochondrial inner membrane electrochemical gradient stabilizes PINK1 on damaged organelles, tagging them for Parkin binding, ubiquitination, and mitophagic elimination (*3*). The specific nature of the molecular interaction between PINK1 and Parkin is unclear, and Parkin receptor proteins on damaged mitochondria have not been identified.

Mitofusins (Mfn) 1 and 2 are mitochondrial outer-membrane fusion proteins and Parkin ubiquitination substrates (*4*, *5*). Combined genetic ablation of Mfn1 and Mfn2 in mouse hearts induces mitochondrial dysfunction and fragmentation that should stimulate mitophagic removal but instead results in proliferation of abnormal organelles (*6*). Because mitophagy is stimulated by Parkin-mediated ubiquitination of mitochondrial proteins (*7*, *8*), we tested whether Mfn1 or Mfn2 might mediate signaling activity of the PINK1-Parkin pathway. Parkin co-immunoprecipitated with Mfn2, but not Mfn1, from extracts of human embryonic kidney (HEK) cells transfected with tagged mitofusins and Parkin. The association of Mfn2 and Parkin was greatly enhanced in cells also transfected to overexpress PINK1 (Fig. 1, A and B, and fig. S1).

The oxidative phosphorylation inhibitor carbonyl cyanide 4-(trifluoromethoxy) phenylhydrazone (FCCP) depolarizes mitochondria and stimulates PINK1-mediated translocation of Parkin to mitochondria, thus targeting damaged organelles for mitophagy (*3*) (fig. S2). Consistent with a role

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