## Late Pleistocene and Holocene environmental history of the Iguala Valley, Central Balsas Watershed of Mexico

D. R. Piperno\*<sup>†‡</sup>, J. E. Moreno\*, J. Iriarte<sup>§</sup>, I. Holst\*, M. Lachniet<sup>¶</sup>, J. G. Jones<sup>|</sup>, A. J. Ranere\*\*, and R. Castanzo<sup>†</sup>

\*Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Balboa, Republic of Panama; <sup>†</sup>Archaeobiology Program, Department of Anthropology, National Museum of Natural History, Washington, DC 20560; <sup>§</sup>Department of Archaeology, School of Geography, Archaeology, and Earth Resources, University of Exeter, Exeter EX4 4QJ, United Kingdom; <sup>¶</sup>Department of Geoscience, University of Nevada, Las Vegas, NV 89154; <sup>¶</sup>Department of Anthropology, Washington State University, Pullman, WA 99164; and \*\*Department of Anthropology, Temple University, Philadelphia, PA 19122

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The origin of agriculture was a signal development in human affairs and as such has occupied the attention of scholars from the natural and social sciences for well over a century. Historical studies of climate and vegetation are closely associated with crop plant evolution because they can reveal the ecological contexts of plant domestication together with the antiquity and effects of agricultural practices on the environment. In this article, we present paleoecological evidence from three lakes and a swamp located in the Central Balsas watershed of tropical southwestern Mexico that date from 14,000 B.P. to the modern era. [Dates expressed in B.P. years are radiocarbon ages. Calibrated (calendar) ages, expressed as cal B.P., are provided for dates in the text.] Previous molecular studies suggest that maize (Zea mays L.) and other important crops such as squashes (Cucurbita spp.) were domesticated in the region. Our combined pollen, phytolith, charcoal, and sedimentary studies indicate that during the late glacial period (14,000-10,000 B.P.), lake beds were dry, the climate was cooler and drier, and open vegetational communities were more widespread than after the Pleistocene ended. Zea was a continuous part of the vegetation since at least the terminal Pleistocene. During the Holocene, lakes became important foci of human activity, and cultural interference with a species-diverse tropical forest is indicated. Maize and squash were grown at lake edges starting between 10,000 and 5,000 B.P., most likely sometime during the first half of that period. Significant episodes of climatic drying evidenced between 1,800 B.P. and 900 B.P. appear to be coeval with those documented in the Classic Maya region and elsewhere, showing widespread instability in the late Holocene

 $agricultural\ origins\ |\ ecological\ contexts\ |\ microfossils\ |\ paleoecology$ 

Paleoecological records from Guatemala to the Amazon Basin demonstrate that lowland Neotropical environments were not stable in the past (e.g., refs. 1-3). Shifts in climate and vegetation associated with the last phases of tropical deglaciation were particularly strong as the Pleistocene was ending at  $\approx 12,000-10,000$  B.P. ( $\approx 14,000-11,200$  cal B.P.), †† when temperature and precipitation rose considerably and lowland tropical forest replaced the herbaceous and cool-adapted flora that dominated the ice age vegetation of many regions. Such dramatic ecological changes have been linked to the origins of agriculture in a number of areas of the world, including the Americas (2, 4). Mexico was one of the world's great centers of plant domestication, and among the many crops it contributed, none is of longer or more intense interest to investigators than the premier cereal crop of the Americas, maize. Molecular research indicates that the wild ancestor of maize is an annual species of teosinte, Zea mays ssp. parviglumis (Iltis and Doebley) (the race Balsas) presently found at elevations between 500 and 1,800 m in the

central parts of the Río Balsas drainage in tropical southwestern Mexico (5, 6) (Fig. 1). Other major crops may have been domesticated there; for example, the "silverseeded squash," *Cucurbita argyrosperma* Huber (7). The natural vegetation of much of the region is, or was before intensive human disturbance, species-diverse tropical deciduous forest. Extant forests are considered centers of diversification for important genera of trees such as *Bursera* and *Leucaena*, contain many endemic species, and are of high conservation interest (8).

Despite its importance, no data relating to early agricultural evolution and associated environmental history are available from the Balsas drainage. Evidence from Guilá Naquitz Cave, located in the semiarid highlands of Oaxaca, indicates that plant domestication in Mexico (*C. pepo* L. squash) occurred by 9,000 B.P. (10,000 cal B.P.) (9). Currently, however, the earliest evidence for Mexican maize consists of cobs recovered from Guilá Naquitz dated to 5,400 B.P. (6,200 cal B.P.) (10), and pollen and phytoliths from San Andrés, Tabasco, with an age of 6,200 B.P. (7,300 cal B.P.) (11, 12). Both sites are outside of the present distributional range of wild maize, and neither provided evidence for a premaize use of teosinte.

This article presents the results of paleoecological studies carried out on three lakes and a swamp located in the central Balsas watershed that provide information on the natural- and human-induced changes in vegetation and climate since the late Pleistocene. The sites, called Ixtacyola, Ixtapa, Tuxpan, and Chaucles, are situated in and near the Iguala Valley in northern Guerrero state (Fig. 1). The work is part of a large initiative combining paleoecological and archaeological studies in the Central Balsas drainage. During six field seasons undertaken from 1999 to 2005, we carried out reconnaissance, testing, and coring of the sites reported on here.

## Results

**The Iguala Area and Its Physical and Ecological Characteristics.** The floor of the Iguala Valley lies at 720 m above sea level and has an average annual temperature of 27°C. A consecutive 34-yr record of

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<sup>&</sup>lt;sup>‡</sup>To whom correspondence should be addressed. E-mail: pipernod@si.edu.

<sup>&</sup>lt;sup>††</sup>Dates expressed in B.P. years are radiocarbon ages. Calibrated (calendar) ages, expressed as cal B.P., are also provided.



**Fig. 1.** Map of Mexico showing the location of the Iguala region and sites mentioned in the text.

annual precipitation from 1953 to 1987 averages 1,078 mm (www. worldclimate.com). Rainfall is distributed on a highly seasonal basis, with >80% falling between June and October; thus, the area has a marked 7- to 8-month dry season. The northwest and northern sides of the valley are bordered by high limestone hills with  $\approx$ 1 km of relief above the valley bottom. The local bedrock consists predominantly of limestone (>95%) with minor amounts of conglomerate and sandstone (<5%). The potential vegetation of the area is a tropical deciduous forest (8, 13), much of which has been cut. Small, disturbed remnants grow on the lower parts of hills surrounding the lake beds, and larger areas of possibly more mature formations occur further upslope on these and larger hills at elevations of between 800 and 1,200 m. In our vegetation surveys of these areas, we observed a variety of native tree taxa typical of lowland tropical formations [a list of these taxa can be found under Field Work in supporting information (SI) Materials and Methods]. On the upper slopes of mountains ringing the Valley at elevations >1,200 m can be found forests rich in oaks. We did not observe *Podocarpus* or pine, and we did not see *Quercus* growing below 1,200 m. Today, the nearest pines occur 50 km to the west near the town of Teloloapan.

With regard to crop plant ancestors, neither teosinte nor wild species of Cucurbita appear to grow in the Iguala area today, based on information provided by local people and our own field surveys. Collections made previously by other investigators (14) and our surveys indicate that the nearest populations of teosinte (race Balsas) occur near the town of Teloloapan, ≈50 km west of Iguala. The Iguala area provides suitable habitats for Balsas teosinte, and it may once have occurred there. Local people who were well acquainted with Cucurbita argyrosperma Huber ssp. sororia (L. H. Bailey) Merrick and Bates, the wild progenitor of *C. argyrosperma*, took us to what they considered to be the populations growing closest to Iguala. They also occur near Teloloapan, ≈45 km west of Iguala, but unlike teosinte are found in moist soil settings along and near small streams. Balsas teosinte, in contrast, is a plant of well drained soils. During our searches for lakes and swamps that covered a wide area of Guerrero and parts of Michoacán, we located several large Balsas teosinte populations but never saw associated C. sororia. Local people emphasized to us that the two species do not grow together because their ecological preferences are different.

Laguna Ixtacyola: Sedimentary, Climatic, and Vegetational History. Laguna Ixtacyola ( $18^{\circ}20'N$ ,  $99^{\circ}35'W$ ) is a flat-bottomed, now-dry lake bed, 1.5 km long and 1 km wide, located a few kilometers west of the town of Iguala. It was drained by local people  $\approx 35$  years ago to make land for cultivation. Ixtacyola lies at an elevation of 720 m

and had a natural outlet at its western end. In the memory of the people, the lake was not deep, reaching a depth of  $\approx 2$  m. The central portions where we sampled retained water throughout the year. We obtained two long sedimentary sequences, called Core 1 and Core 2, from the center by hand excavation (Fig. 2). Core 1 was dug to a depth of 7.45 m when it had to be abandoned before reaching bedrock because of the danger of wall cave-in. We successfully reached bedrock at a depth of 7.8 m in Core 2, placed near Core 1, by using an AMS Inc.-brand soil corer attached to a closed sampling barrel. The two sequences are very similar, and in Core 2 we used only the bottom-most meter to better establish when early and significant water level changes occurred in the basin. As explained below, the basal deposits in Core 2 probably date to at least the terminal Pleistocene.

The Ixtacyola sequence can be divided into two main sedimentary horizons (Fig. 2). From the bottom at 7.8 m in Core 2 to a depth of 7.1 m in Core 2 and 6.5 m in Core 1, sediments are organic-poor, light gray, sandy clays with evidence of oxidation near the Core 2 base. During this interval the lake bed contained little water, and it was completely dry when the basal-most Core 2 sediments were deposited. Above this zone, sediments are compact, black clays with silt indicative of deposition under permanent standing water. The biogenic silica content of the sediments is generally poor, but the diatom Aulacoseira is present beginning at 6.5 m, indicating that an open water body had developed. Ten radiocarbon dates on sediment plus two on preparations of pollen sampled from the same or adjacent levels were carried out on Core 1 (Fig. 2; SI Table 1 contains all of the radiocarbon dates and their calendar-year equivalents). Comparison of the dates indicates an offset and possible hard water error of ≈1,000-2,000 years (because of sediment similarities, the 6.0- to 6.1-m level is a better comparison than the 6.4- to 6.5-m level for the pollen dated from 6.2 to 6.3 m).

The oxidized sediments at the base of Ixtacyola, represented in Core 2, could not be dated, but a number of factors allow an estimation of their age. The earliest sediment date of 11,110  $\pm$  80 B.P. is from the base of Core 1 at 7.2–7.4 m below the surface. Because an additional 43 cm of sediment that marks the beginning of deposition at the site was retrieved from the base of Core 2, and 1,250 radiocarbon years elapsed for the formation of the same type of sediment within a 40- to 60-cm interval in Core 1, the beginning of the sedimentary record at Ixtacyola probably would date to at least 12,000 B.P. Allowing for a maximum hard water error of 2,000 years, the true age would be at least 10,000 B.P. ( $\approx$ 11,200 cal B.P.), keeping in mind that this basal sediment, derived from a dry lake bed, was probably not as affected by hard water error as the sediment at 6.5 m and above formed underneath water, from where our estimates for hard water error actually derive. This likelihood is supported by the modern <sup>14</sup>C age on sediment from 0–10 cm below the surface of the modern dry lake bed (SI Table 1). The dramatic sediment change indicative of substantially rising water levels leading to permanent ponding occurs at 6.5 cm of Core 1, dated to  $9,770 \pm 50$ . This change occurred at a depth of 7.1 cm in Core 2, which was probably located in a deeper part of the basin where ponding started somewhat earlier. Taking into account hard water error, the formation of the lake, which was almost certainly brought about by rising regional precipitation, occurred by at least 9,000-8,000 B.P. ( $\approx 10,000-8,800$  cal B.P.). The earlier of these estimates is supported by data from Ixtapa where phytolith records were directly dated, eliminating any hard water or other errors (below). Two sedimentary sequences called Pozo Norte-1 and Pozo Sur recovered, respectively, 75 and 50 m from the north and south lake edge provide additional data supporting these reconstructed lake level changes (see notes to SI Table 1).

The oldest sediments from the base of Core 2 are oxidized and lack pollen, and phytoliths are rare in both cores. However, pollen occurred in analyzable quantities in all of Core 1. Pollen concentrations are generally not very high, and robust pollen types may be overrepresented while some of the more fragile types may not have

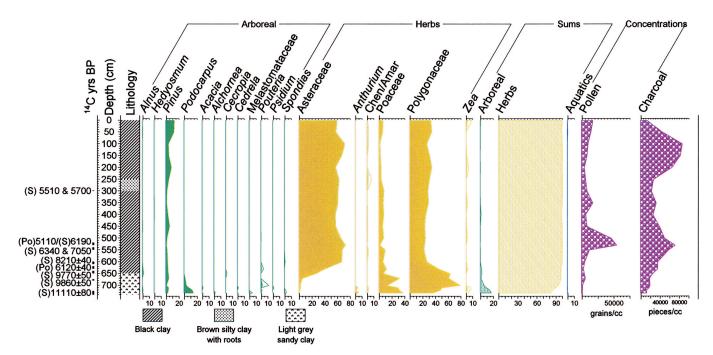


Fig. 2. Pollen diagram showing the percentage of taxa identified in Core 2 at Ixtacyola. In this and other diagrams, (Po) and (S) before radiocarbon determinations indicate that the material dated was pollen and sediment, respectively. A few grains of Quercus were found between 5.3 and 1.5 m. Fern percentages generally range from 2% to 11%, including in basal levels, with a maximum of 35% at 5.3 m. The Pozo Sur edge hole also contains a good pollen record above 4.5 m. Arboreal taxa not recorded in the center hole and present in the Pozo Sur edge sediments are Moraceae, Sapotaceae, Anacardiaceae, Prosopis, Ilex, and Liquidambar.

survived. Nonetheless, important changes in climate and vegetation can be identified (Fig. 2). From the base of Core 1 at 7.45 m to a depth of 7 m, pollen concentrations are lowest, increasing at 6.7 m. Podocarpus is present in the basal deposits, declines in frequency at 7 m, and disappears at 6.5 m, when the sedimentary change indicating water rise in the basin occurs. *Podocarpus* is a conifer whose modern distribution in Mexico is in cloud forests at elevations mainly between 1,500 and 2,800 m (National Herbarium collection sheets, Smithsonian Institution National Museum of Natural History). We did not observe the tree growing in the study area (local people agreed that it was absent), and it is not recorded in our modern pollen samples, including those from the top of Cerro Jumil at elevations of 1,300–1,600 m (SI Fig. 5). The nearest modern recorded occurrence we can find is ≈90 km south of Iguala in the Sierra Madre del Sur at an elevation of 2,430 m (National Herbarium sheets).

Podocarpus in the Ixtacyola pollen record thus indicates a cooler late Pleistocene climate that caused it to expand its range considerably and descend into lower elevations. Its disappearance at 6.5 m probably resulted from a retreat of the tree upon an early Holocene temperature increase. Associated with *Podo*carpus below 6.5 m are high frequencies of the Poaceae and Polygonaceae. Charcoal is persistently present. Poaceae percentages approach 40, a sign that grasses were common in the terrestrial vegetation (15). The Polygonaceae can be common both in open, herb-dominated vegetation and on dry lake beds. Therefore, both pollen data and associated sediment characteristics indicate that the late Pleistocene climate was drier and cooler than today's. The vegetation cover appears to have been sparse, and it contained a considerable herbaceous component and trees tolerant of lower temperatures. Arboreal taxa of lowland tropical forest also recorded at this time are *Pouteria*, Psidium, Cedrela, and Spondias. They may have formed pockets of trees in favorable locations, such as along rivers and streams. Collection localities commonly listed for *Podocarpus* today are riverbanks and edges of arroyos, habitats it may have shared with tropical trees to form species associations without modern analog.

The Holocene pollen records from Core 2 (above 6.5 m in Fig. 2) and Pozo Sur (not graphed) contain a variety of tropical trees, including Alchornea, Bursera, Pouteria and other Sapotaceae, Spondias, Cecropia and other Moraceae, Psidium, Anacardiaceae, Ilex, Hedyosmum, Liquidambar, and various Fabaceae, including Prosopis. Here and at other sites, Pinus and Alnus are a result of long distance transport. Pollen data indicate that the natural vegetation was a diverse tropical forest.

Laguna Ixtacyola: Human Impacts. We emphasize at the outset that we do not identify any Zea pollen as maize because neither grain size nor morphology allow teosinte and maize to be distinguished. Pollen size and especially morphology allow the genus to be separated from all non-Zea grasses, including Tripsacum (11) (for further details, see Pollen and Phytolith Identification in SI Materials and Methods and SI Fig. 6). Zea pollen first occurs near the bottom of Core 1 at 7.15–7.25 m, where four grains measuring from 47 to 59  $\mu$ m in maximum diameter and one fragment 40  $\mu$ m in size were found (the 59-\mu m grain was extremely folded; its actual size would be considerably larger). At 7.05–7.15 m, two Zea grains 66  $\mu$ m and 89 µm long and one fragment 40 µm in size occurred. Zea pollen, usually a few grains per level, occurred throughout the rest of the Core 1 sequence (size range of 47–75 µm). Zea was also identified from the bottom to near the top of the pollen-bearing sediments at Pozo Sur. A date of 6,290  $\pm$  40 B.P. (7,240 cal B.P.) was obtained on a pollen isolate at 4.2–4.3 m there, 20 cm above the lowest zone with Zea pollen (sediments below 4.5 m were devoid of pollen). It is clear that Zea has been a continuous part of the vegetation of the Iguala region probably since the end of the last ice age.

A significant transition in the Ixtacyola record occurs between 6 and 6.5 m of Core 1 when a large increase of pollen from the herbaceous family Asteraceae and charcoal takes place. More than 90% of the Asteraceae grains in these and other levels are *Ambro*sia-types, which are weeds strongly associated with agricultural

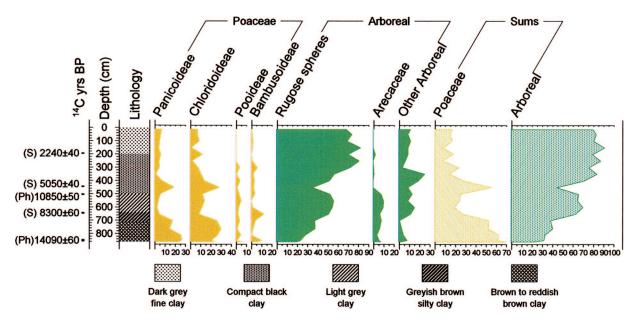


Fig. 3. Phytolith diagram from Ixtapa showing the percentage of taxa present. In this and other diagrams, (Ph) before radiocarbon determinations indicates that the material dated was phytoliths.

practices. A pollen isolate from 6.2–6.3 m returned an age of 6,120  $\pm$  40 B.P. (6,990 cal B.P.). The Asteraceae also increase greatly at 4.2–4.3 m in the Pozo Sur record. The pollen isolate from this level dated to 6,290  $\pm$  40 B.P. provides good agreement with the date from the lake's center. The remainder of the Holocene period is characterized by persistently high Asteraceae frequencies. Pollen from several tree taxa (e.g., *Pouteria*, *Alchornea*, Anacardiaceae, and Sapotaceae) disappears from the center and edge records by  $\approx$ 4,500 B.P. An interval of charcoal decline occurs between 5 and 2.5 m; however, charcoal frequencies remain twice as high as in pre-6,200 B.P. levels.

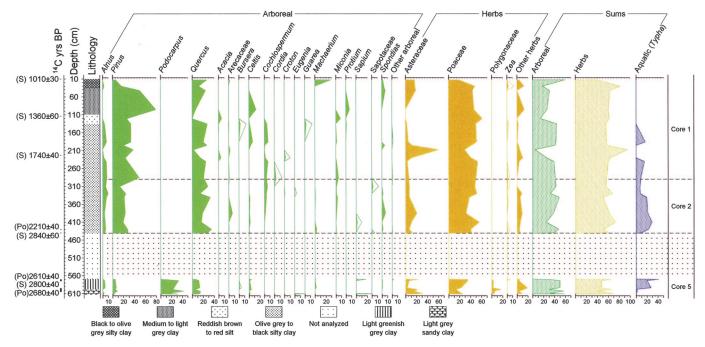
The data indicate human vegetational disturbance with frequent fires and forest clearing beginning at 6,300 B.P. There is no pollen or sedimentary evidence for a drier climate at this time that might have led to an increase of natural fires; to the contrary, the charcoal rise occurs against a gradient of increasing water level across the basin. Zea pollen associated with the vegetational disturbance is more likely to be from maize than not, but phytoliths are not available to confirm maize presence. Artifacts recovered from near the lake edge provide direct evidence that human populations were exploiting the immediate lake environment during the major period of charcoal rise and later. In every edge excavation, we recovered small pottery sherds and chipped stone of quartz and chalcedony, raw materials that do not occur in the terrain surrounding the lakes. Sherds occurred to a depth of 2.8 m in Pozo Sur. The lithic artifacts included a chalcedony scraper and graver. Sediment associated with the graver from 2.9 to 3.0 m at Pozo Norte-1 returned a date of  $5,450 \pm 50$  B.P. The deepest chipped stone occurred at Pozo Sur at 4.3–4.4 m. The 6,290  $\pm$  40 date on pollen from this unit is from 10 cm above the stone (SI Table 1).

Ixtapa: Sedimentary, Vegetational, and Climatic History. Ixtapa is a closed limestone basin  $\approx$ 1 km long and 0.25 km wide located 9 km east of the Iguala Valley (18°21′N, 99°26′W) at an elevation of 900 m. Currently, it holds a few meters of water during the wettest portions of the year and dries seasonally. We retrieved a long sedimentary record, reaching bedrock at 8.5 m. The sequence spans 14,000 radiocarbon years, making it the oldest in the area. Pollen is not well preserved, but phytoliths are abundant. The <sup>14</sup>C dates that we have confidence in were determined directly on phytoliths isolated from the site's sediments. Dates on the sediments, including

those associated with major water level and vegetational changes early in the sequence that appear to be related to the same events recorded at Ixtacyola, appear to be too young and are rejected.

Sediments from the base at 8.3 m to a depth of 5 m are organic-poor, light gray to reddish brown silty clays (Fig. 3). Two phytolith dates, which are not affected by hard water or other potential errors, indicate that deposition of this zone took place between 14,090 and 10,850 B.P. (16,890-12,910 cal B.P.). The oxidized sediments that occur between 8.3 and 7.2 m indicate that the basin was dry during this interval. A dramatic sedimentary change from a light gray to a compact, black silty clay occurs at 10,850 B.P. It marks significantly rising water levels, probably a response to increasing precipitation. A less dramatic change from a brown to a light gray sediment occurs earlier at a depth of 6.4 m, probably marking a water table rise more subtle than that which occurred at 10,850 B.P. The date for the major water level rise at Ixtapa at 10,850 B.P. is earlier than that estimated at Ixtacyola, which was sometime in the  $\approx$ 9,000- to 8,000-B.P. period. Either the Ixtacyola estimate is too young or Ixtapa, a smaller basin with no outlet, pooled water more efficiently and earlier. The remainder of the sequence at Ixtapa from 5 m to the surface is composed of compact black to dark gray, fine clay representative of continuing moist conditions in the swamp.

The Ixtapa phytolith record indicates that late Pleistocene vegetation around the swamp contained considerably more grasses and fewer trees than at present, and that a change from herb- to arboreal-dominated vegetation began at 6.5 m when the initial water table rise is inferred (Fig. 3). A reasonable estimated date for this vegetational transition based on sedimentation rate is 11,800 B.P. (≈13,600 cal B.P.). High frequencies of grass phytoliths from the Chloridoideae and Panicoideae subfamilies before ≈11,800 B.P. indicate that C<sub>4</sub> grasses, which are better adapted to dry climates and low atmospheric concentrations of CO<sub>2</sub> than C<sub>3</sub> species, were common in the vegetation. Arboreal species present before 10,850 B.P. include palms and phytoliths (rugose spheres) that can be characteristic of an ecologically wide range of trees and shrubs. Palm phytoliths are of the type produced in arid-landadapted species. The vegetation on the low hills surrounding the swamp may have been a low, grassy woodland. Palms decrease to low levels after 10,850 B.P. At ≈11,800 B.P., arboreal species begin to increase in frequency and diversity. Present for the first time are



Pollen diagram from Tuxpan showing the percentage of taxa present. The "Other Arboreal" class includes Alchornea and Bunchosia. The pollen sum does not include aquatic taxa, which are almost entirely from Typha. Fern percentages generally range from 1% to 8%. Sediments between 5.7 and 4.4 m from Core 5 were not analyzed because, due to Core 5 having a more extended sediment record, they represent deposits of the same age as at the base of Core 2. Hence, a continuous sequence is displayed.

sclereids, a class of phytoliths produced by a range of tropical trees (e.g., Moraceae, Flacourtiaceae, Fabaceae, and Annonaceae). From this point on, phytoliths associated with forests continue to increase in number and diversity. For example, beginning at 4.1 m, the Marantaceae and/or Zingiberaceae, understory herbs of tropical forest, are continuously present.

Because of poor pollen preservation, only the presence of taxa in the sequence can be used. There are nonetheless informative trends (not graphed) that are concordant with the phytolith data. *Podo*carpus occurs only at the base of the sequence, and the Polygonaceae are much more common before 10,850 B.P. As at Ixtacyola, Podocarpus indicates cooler temperatures, and Polygonaceae reflect drier land conditions on and around the swamp before the Pleistocene ended. Woody taxa represented at this time include Acacia, Euphorbia, Pouteria, and Pterocarpus. Beginning 10,850 B.P., when the marked sedimentary change indicating increasing precipitation occurs, trees with higher moisture requirements such as Trichilia and Myrtaceae appear. The trees Sapium, Spondias, Didymopanax, and Cecropia are also recorded during the Holocene.

**Ixtapa: Human Impacts.** Plants associated with human disturbance do not attain significant frequencies during the Holocene at Ixtapa as they do at the other sites investigated (Fig. 3). Charcoal frequencies (not graphed) are also low throughout the sequence. If the Holocene vegetation fires documented at Ixtacvola and other sites (below) had been caused by natural factors, a similar pattern of charcoal frequency at Ixtapa would be expected. Despite the richness of the phytolith record, no teosinte, maize, or Cucurbita were found. A fragmented pollen grain from Zea (60 μm in size, observed at 5.0–5.1 m, and associated with a date of 10, 850 B.P.) is the only evidence of this taxon with the exception of grains found in surface sediment. Concordant with this picture is the absence of human artifacts. We carried out a foot survey of a sizeable area west of the swamp where the ground is exposed and also dug "shovel tests" to a depth of 45 cm below the surface, passing the soil through 1/4-inch mesh screen. No ceramics, exotic stone, or stone tools were encountered, making Ixtapa the only site without these materials. Therefore, all of the available evidence indicates that little pre-Columbian human activity took place around this locality.

Laguna Tuxpan: Sedimentary, Vegetational, and Climatic History. Tuxpan is a large (2.5 km  $\times$  1.75 km) lake located 4 km east of the town of Iguala (18°21'N, 99°29'W) at an elevation of 740 m in the small pueblo of Tuxpan. It has several feeder streams entering from its eastern side and no natural outflow. Tuxpan is the largest lake in the region but formed at ≈3,000 B.P., much more recently than Ixtacyola and Ixtapa. It is possible that tectonic activity or other factors caused a former outflow on the western end that we tentatively identified to be blocked. We raised three parallel cores from the deepest part of the lake in from 5.5 to 5.8 m of water. They demonstrate closely parallel records, and we used the sections from each core that provided the most complete sedimentary sequence (Fig. 4 and SI Figs. 7 and 8). We also retrieved deep sediments terminating in bedrock from near the northwestern edge of the lake (discussed below). Overlying the lacustrine deposits in the lake's center is 4.8-6 m of sediment that was diverted into Tuxpan 50 years ago from the construction of an artificial reservoir east of the lake. Local people told us that previous to this event, Tuxpan was 15 m deep in the center and supported many native fish and crustaceans. The modern sediment, recognizable by its orange color and sticky, unconsolidated characteristics, intermingled with and disturbed the uppermost ancient deposits, resulting in the loss of the most recent 800–1,000 years of the record.

The ancient sediments have good pollen and phytolith records. Dates on paired sediment and pollen isolates indicate that hard water error in this system is not more than a few hundred years (SI Table 1). The basal material of the lake was reached in Core 5. Occurring at a depth of between 6.0 and 6.2 m, it is a horizon of sandy, reddish to light gray clay with pinkish red laminations (four to five laminations per centimeter) that represents the initial filling of the basin (Fig. 4). The sediment characteristics are indicative of a shallow water body that dried frequently, perhaps seasonally. The distinct pink-red laminae represent eroded sediment that may have

been exposed at the lake edge and then washed into the lake with the onset of the wet season.

Above this zone in Core 5 between a depth of 6 and 5.6 m is a mostly light greenish gray and laminated clay that represents a deepening and permanent water body. A variety of diatoms are abundant, adding to this picture. A date of 2,680  $\pm$  40 B.P. (2,770 cal B.P.) was obtained on a pollen isolate from 5.95-6.05 m, encompassing the bottom of this zone and the top of the underlying sandy clay. Because pollen is rare in the latter, the date mainly refers to pollen from the greenish gray clay. Another pollen date of  $2,610 \pm 40 \ (2,750 \ \text{cal B.P.})$  from  $5.70-5.75 \ \text{cm}$  of this zone is stratigraphically consistent with the date below it and in good agreement with a sediment age of 2,800  $\pm$  40 (2,880 cal B.P.) from the same interval. Therefore, it appears that ponding at Tuxpan began at  $\approx$ 3,000 B.P. For the remainder of the record, we used two cores, called 1 and 2, that we raised and analyzed before carrying out the Core 5 work, which was successfully undertaken to reach the basal deposits. The bottom-most sediments at 4.4–4.5 m of Core 2 with a date of  $2,840 \pm 60$  B.P. (2,945 cal B.P.) represent deposits immediately overlying the greenish gray clay recovered in Core 5. A pollen sample from 4.3 m has an age of 2,210  $\pm$  40 (2,200 cal B.P.). The sediments in Cores 1 and 2 are for the most part characterized by laminated olive gray to black silty clays indicative of a permanent water body. The open water diatom Aulacoseira is common.

The Tuxpan sediments generally have excellent pollen preservation. Although by the beginning of the record human interference with vegetation was substantial (below), a range of tropical trees is recorded (e.g., *Bursera*, *Cordia*, *Eugenia*, *Protium*, Sapotaceae, *Spondias*, *Eugenia*, and a variety of palms, including the American oil palm *Elaeis*) (Fig. 4). The oak probably derives in large part from the upper (>1,200 m) slopes of Cerro Jumil and Tuxpan that rise directly above the north side of the lake, where we observed forests rich in *Quercus* spp. The phytolith record (SI Fig. 8) documents palms and other arboreal taxa (e.g., Flacourtiaceae, Fabaceae, Annonaceae, and Moraceae), bamboos, the Marantaceae (e.g., *Calathea*), and the Podostemaceae. The latter are tropical plants that grow attached to rocks in rivers and streams. Their presence indicates that streams entering Tuxpan transported many phytoliths from source areas in the lake's watershed.

The ecological preference of the suite of represented taxa is seasonally dry tropical forest. Interestingly, high amounts of *Podocarpus* occur in the greenish gray clay horizon immediately above the base of the sequence. It disappears from the record after 2,600 B.P., much later than at Ixtacyola and Ixtapa. Tuxpan is closer to, and more immediately downwind from, the highest peaks surrounding the valley, and it was probably more sensitive to receiving *Podocarpus* pollen for a protracted period as the tree retreated and likely persisted for a time on the highest peaks. High oak percentages found at Tuxpan but not at other lakes despite the abundance of oak on the upper parts of hills support this scenario.

Sediment changes that occur during the later Holocene appear to document significant fluctuations in regional precipitation. A 26to 40-cm-thick horizon of reddish brown to red clayey silt occurs at the same stratigraphic interval in every core (in Core 1 displayed in Fig. 4 it is at 1.1–1.36 m). It indicates a period when the lake bed had no standing water and sediments were exposed to oxidation. A drier climate is thus indicated. Two <sup>14</sup>C determinations on sediment from 5 cm above the top of the oxidized zone in Core 1 and Core 5 yielded overlapping ages of 1,360  $\pm$  60 B.P. (1,285 cal B.P. or cal A.D. 665) and 1,400  $\pm$  40 B.P. (1,300 cal B.P. or cal. A.D. 650), respectively. There are a few shorter, 1- to 12-cm wide, intervals of oxidized sediment that date from  $\approx$ 2,200 to 1,600 B.P., based on <sup>14</sup>C ages from sediments and sedimentation rates. They appear to record briefer or less intense drying events. Such horizons do not occur above 1.1 m. However, the zone of medium to light gray clay between 1.1 and 0.3 m suggests lower lake levels and possibly reduced precipitation compared with the pre-2,000 B.P. period, a scenario supported by the disappearance of *Typha*, which had probably grown in marsh fringing the shallower western end of the basin, not presently underwater, when lake levels were higher. Furthermore, starting shortly before 1,750 B.P. and continuing to the end of the sequence, phytoliths are rare, suggesting substantially reduced stream flow into the lake.

The drier times at Tuxpan overlap dry periods recorded elsewhere in lowland Mesoamerica between  $\approx 1,800$  and 900 B.P (16, 17). If a hard water error of a few hundred years is assumed, the most intense drying at Tuxpan, recorded between 1.1 and 1.36 m, encompassed the ninth century A.D. In other regions of Mesoamerica, severe drying documented at this time is associated with the Classic Maya collapse (16, 17).

Laguna Tuxpan: Human Impacts. Pollen and phytolith results indicate that by the beginning of the sequence, the forest in Tuxpan's watershed was heavily affected by agricultural activity. There are high frequencies of pollen from grasses and other weedy plants and very large amounts of charcoal. *Cochlospermum*, an early secondary tree of highly disturbed lowland tropical landscapes, is present in frequencies indicating that it was common in the vegetation. *Zea* pollen occurs in many levels (size range:  $58-83~\mu m$  in diameter). In the phytolith record, grasses, including those typical of agricultural field weeds such as the Panicoideae and Chloridoideae, predominate (many of them are burned), and there is low representation from arboreal species throughout. Maize cob and leaf phytoliths occur at the bottom of the sequence (see SI Table 2 and its notes). There is no sign of teosinte phytoliths.

We collected numerous pre-Columbian pottery sherds and ground stone tools (e.g., manos, metates, and edge ground cobbles) from the surface of a maize field  $\approx 50$  m from the lake edge. The pottery probably dates from  $\approx 2,800-1,200$  B.P. ( $\approx 2,900-1,100$  cal B.P.) based on our studies of the same types of ceramics we recovered from archaeological sites near the lake.

Laguna Tuxpan: Excavations at the Lake Edge. Earlier human impacts, including the remains of cultivated plants, are recorded at the northwestern edge of the lake, where we excavated a 3.2-m-deep hole to bedrock 20 m upslope from the water. The sediment sequence consists of 33 cm of topsoil underlain by a zone of rocks between 33 and 56 cm. Beneath 56 cm to a depth of 1.5 m is a zone of dark clay that represents lacustrine sediment and a past extension of the lake beyond today's limits. From 1.5 m to 3.2 m is a zone of organic-poor sandy clays that become sandier and lighter in color with depth and are nearly pure sand with gravel at the bottom. This horizon is the basal sedimentary unit, the uppermost part of which occurred at the bottom of Core 5 at the lake's center. We recovered all of the horizon to bedrock at the edge hole because hand excavation allowed us to penetrate through the sands. Sediments from 1.5–1.6 m just below the beginning of the lacustrine deposits have an age of  $3,820 \pm 40$  (4,230 cal B.P.).

Pollen is poorly preserved in the sediments but phytoliths are common below a depth of 2.7 m (SI Fig. 9). Two <sup>14</sup>C determinations run directly on phytoliths recovered from 3.0-3.1 and 2.8-2.9 m yielded ages of 8,860  $\pm$  250 B.P. ( $\approx$ 10,000 cal B.P.) and 10,630  $\pm$ 300 B.P. ( $\approx$ 12,700 cal B.P.), respectively (SI Table 1). The inverted phytolith dates may be due to shoreline erosion and sediment slumping at the edge as the water table rose. Sediment from 3.1–3.2 m provided an age of 5,110  $\pm$  40 B.P. (5,900 cal B.P.), much younger than phytoliths from immediately above. There are two possible interpretations of the depositional history. One is that an initial water table rise with sedimentation occurred during the early Holocene and the phytolith <sup>14</sup>C dates record that event, in which case the organic-poor basal sands are contaminated with younger carbon (e.g., from percolating humic acids), a common problem with sediments of this type (see SI Materials and Methods). The other is that water table rise occurred at 5,100 B.P., and the older phytoliths are derived from erosion and influx of preexisting dry land, near-edge sediment. Both phytolith and sediment ages suggest a shallow and probably ephemeral water body existed for a time before the lake formed.

In any case, as at Ixtapa, dates determined directly from phytoliths provide more accurate ages for vegetational reconstructions based on phytolith records than do those determined from other components of the sediment matrix. Phytoliths between 2.8 and 3.2 m could date to anywhere in the 10,630  $\pm$  300 to 8,860  $\pm$  250 period, and each level may contain a mixture of phytoliths from that broad time, especially if shoreline erosion and slumping occurred. Phytoliths are rare above 2.7 m, including in the lacustrine sediment, thus these ages are well constrained. If the sediment date of 5,100 B.P. is accurate, phytoliths of that age may be present, but in light of the phytolith dates, the significant majority of phytoliths between 2.8 and 3.2 m must be considerably older.

Despite poor pollen preservation, a Zea grain 87  $\mu$ m long was recovered at 3.1–3.2 m. About a half of a Zea grain 38  $\mu$ m in size occurred at 2.6–2.7 m. When complete, the grain would have been at least 75  $\mu$ m long. Maize cob phytoliths occur at 3.1–3.2 and 2.9–3.0 m, and probable maize leaf phytoliths are present at 3.1–3.2 and 2.8–2.9 m. Phytoliths commonly found in the fruitcases and leaves of teosinte are absent. Phytoliths from the fruit rinds of *Cucurbita* continuously occur between 3.2 and 2.7 m. Size and morphological characteristics indicate that the phytoliths are from domesticated fruits (SI Table 3 and SI Fig. 10). Unlike phytoliths from the lake's center, which were transported from the wider watershed in stream-flow, a local source area is probably represented through erosional processes described above and/or run-off from the adjacent dry land surface.

Other aspects of the phytolith record indicate that the vegetation near the lake shore was disturbed by human activity (SI Fig. 9). Between 3.2 and 2.7 m there are high frequencies of grasses, and many grass and arboreal phytoliths are burned. In soils sampled from underneath modern forest near the shore, burned phytoliths of any kind are absent and frequencies of weedy grass phytoliths such as from the Panicoideae are considerably lower (SI Fig. 11). Large (>200 μm) pieces of burned grass leaf epidermis with articulated phytoliths occur, further indicating a nearby source for the phytoliths and fires. The evidence indicates human use and alteration of the near shore environment through frequent fire and some vegetation clearing. Cucurbita and maize appear to have been planted in the fertile soils near the edge sometime during the  $\approx$ 10,000 B.P.- to 5,000-B.P. period. Given the  $^{14}$ C phytolith determinations and the fact that the dated collections of phytoliths contain many indicative of human disturbance, it is likely that the maize and squash were deposited sometime during the first half of that time span along with the disturbance taxa.

**Chaucles.** The final record we discuss is from Chaucles, a now-dry lake bed that occupied part of a small ( $\approx$ 2 km  $\times$  2 km) closed valley a few kilometers northwest of Ixtapa. We retrieved 2.5 m of sediment that dates to somewhat before 3,500 B.P. ( $\approx$ 3,800 cal B.P.). Phytolith, pollen, and charcoal data indicate substantial human interference with the vegetation and cultivation of maize and squash throughout the lake's history (SI Figs. 12 and 13 and SI Table 3). We collected a rich pre-Columbian ceramic and stone tool assemblage, including manos and metates, from the surface of the southwestern edge of the system.

## Discussion

Our data have implications for understanding a number of issues concerning environmental and agricultural history in Mexico. As has been demonstrated in other areas of the lowland Neotropics (1–3, 15), the end of the Pleistocene brought significant shifts in climate and vegetation (and probably plant and animal resources available for human exploitation) to the Iguala region. Upon what appear to have been substantial increases in temperature and

precipitation between ≈11,000 and 9,000 B.P. (13,000–10,000 cal B.P.), lowland tropical forest expanded on the landscape, and once-dry lake beds filled with water. The newly developed lakes with their rich natural resources started to become magnets for human populations. The chronology suggested for the transition to modern climatic conditions at Iguala is in accord with that demonstrated elsewhere in the lowland tropics and in the central Mexican highlands (1–3, 18). Inferences for Pleistocene cooling are based on pollen from the tree *Podocarpus*, which is present early in the Ixtacyola and Ixtapa sequences. In light of the modern distribution of this genus, an elevational descent of at least 700-900 m and temperatures 4–5°C cooler than today (based on a moist-air lapse rate of 0.6°C 100 m<sup>-1</sup>) during the late glacial period can be estimated. The lower limit of annual precipitation required to support tropical deciduous forest in Mexico today is ≈800-1,000 mm (2). Hence, reasonable estimates for precipitation reduction during the late and terminal Pleistocene seem to be on the order of 10-30%. As elsewhere, Pleistocene to Holocene precipitation changes were probably driven by the effects of ocean surface temperatures on moisture availability over land masses and shifts in the position of the Intertropical Convergence Zone (1, 2, 15, 18).

During the Holocene, a diverse tropical broadleaf forest is documented in the Iguala area. The suite of trees identified bears close similarities to extant arboreal associations in Iguala and elsewhere in the Balsas drainage adapted to warm temperatures, annual precipitation of between 1,000 and 1,600 mm, and seasonally dry annual cycles (8, 13). Evidence for significantly drier periods at Tuxpan between ≈2,000 and 1,100 B.P. supports views that dry episodes recorded in a number of places at this time, including the one associated with the collapse of the Classic Maya civilization, reflect hemisphere-wide, perhaps global climatic perturbations (17, 19), and that against a backdrop of a mostly stable Holocene climate, severe, short-term oscillations occurred that may have had considerable importance for social change.

What do our records say about the evolution of agriculture? Teosinte does not presently occur in the Iguala area, located on the eastern edge of the Central Balsas drainage. However, the pollen record at one of the oldest sites studied, Ixtacyola, indicates initial Zea presence immediately above a sediment level dated to 11,110 B.P. If we are correct that hard water error in these sediments formed on a dry lake bed is either not a factor or limited to 1,000 yr, then the pollen is probably from teosinte because maize domestication before the Pleistocene ended would not be expected. A Zea pollen grain recovered from Ixtapa at 10,850 B.P. lends support to this scenario, especially because Zea is absent afterward and no other evidence for agriculture or human activity in general is recorded at the site.

It should be emphasized that the downslope movement of vegetation during the late to terminal Pleistocene indicated by our data may well have involved various types of teosinte, including the race Chalco, which presently grows in semiarid habitats at elevations >1,600 m in Central Mexico (14). Similarly, Balsas teosinte, largely absent below 400–500 m today, could have descended into lower-lying tropical areas that cover much of Guerrero and other similar regions of Mexico. As research into the geography and chronology of maize domestication continues, investigators should consider that at the end of the Pleistocene, probably continuing into the early Holocene when vegetation was resorting and in all likelihood the plant was taken under cultivation and domesticated (see below), Balsas teosinte may have been common in lower elevation areas where it does not now occur.

At Tuxpan, phytoliths from maize and domesticated *Cucurbita* occur with *Zea* pollen in sediments formed at the site's edge some time between 10,000 and 5,000 B.P. <sup>14</sup>C studies on the phytoliths themselves indicate that the cultivars were probably deposited earlier rather than later in that interval. The same association of phytoliths and pollen is found in basal deposits at Chaucles dating to 3,500 B.P. Because pollen from maize and teosinte cannot be

distinguished, the pollen record is equivocal as to which taxa contributed the *Zea* grains, which are continuously present in Holocene pollen records at most of the sites. However, teosinte would not be expected to grow at the moist margins of lakes, and phytolith records from Tuxpan and elsewhere lack any sign of the plant. Along with data for maize and squash cultivation at Tuxpan and Chaucles, there is evidence for human burning and vegetational modification. *C. argyrosperma*, whose closest wild relatives are native to the Central Balsas region (7), is probably the species present at these sites. Because teosinte and *C. argyrosperma*'s wild ancestor do not grow naturally together today, humans paired these elements of the maize–squash–bean triad during their early days as farmers.

In the Ixtacyola watershed, signs of significant forest clearing by humans with frequent burning occur in association with Zea pollen at 6,300 B.P. (7,200 cal B.P.), and an association of charcoal and Zea pollen is persistently present from the beginning of the record there. By the time a permanent lake formed at Tuxpan at 3,000 B.P., its large watershed had been substantially altered by agricultural practices. Paleoecological data are also available from a region of the Central Balsas located 120 km west of Iguala showing that at the base of a sequence dated to 4,100 B.P. (4,500 cal B.P.), maize was present and the vegetation was already dominated by herbaceous disturbance taxa indicative of agriculture (20). As in many other Neotropical regions (e.g., see refs. 2, 11, 12, 21, and 22), the Balsas forests were subjected to frequent burning and clearing during the pre-Columbian era.

An early development of agriculture in the Central Balsas region with a focus on maize and Cucurbita is not surprising. Molecular data suggest that maize was domesticated there at  $\approx 9,000$  cal B.P (2), and a large body of archaeological and paleoecological data indicates that maize was dispersed southward out of Mexico before 7,000 B.P. (7,800 cal B.P.) and well established in northern South America by 5,500 B.P. (6,300 cal B.P.) (e.g., see refs. 2, 12, 23, and 24). Our archaeological investigations of rock shelters near the lakes provide mutually supporting information on human settlement of the Iguala area and plant use and domestication during the early and middle Holocene (unpublished work). Our paleoecological data make it clear that these developments took place within a lowland tropical forest context.

Seasonally dry tropical forest appears to have supported early human occupation and the development and spread of agriculture,

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both seed and root cropping, elsewhere in Central and South America (e.g., see refs. 2 and 25). These formations, which do not carry the prestige enjoyed by their rain forest relatives, once covered much larger areas of the Neotropics before they were cut for agriculture or converted into pasture. Their flora and fauna experienced dramatic changes as the Pleistocene was drawing to a close, and as we and others have argued, these ecological cascades created new selective pressures on human populations and their subsistence pursuits, leading to novel and ultimately successful strategies that included the cultivation and domestication of plants (2, 4, 26, 27). It increasingly appears that seasonal tropical forests were of greater prominence in New World cultural development than once imagined.

## **Materials and Methods**

Tuxpan was cored from a raft of rubber boats by using a modified Colinvaux-Vohnout locking piston corer. Sediments were removed from dry lake beds by hand excavations. Pollen (J.E.M. and J.G.J.), phytolith (J.I. and D.R.P.), and charcoal (J.I. and D.R.P.) studies were carried out by using standard methods of analysis. Pollen and phytolith identifications were made on the basis of modern reference collections in possession of the authors and published references. To provide controls on potential errors associated with carbon-14 studies of the sites' sediments, including hard water and humic acid effects, we dated pollen and phytolith preparations and compared the results with those from associated sediments. Additional descriptions of field and laboratory methods along with criteria used for microfossil identification can be found in *SI Materials and Methods*.

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