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Diversity of cultivars and other plant resources used at habitation sites in the Llanos de Mojos, Beni, Bolivia: evidence from macrobotanical remains, starch grains, and phytoliths

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ABSTRACT

Although sparsely populated today, the Llanos de Mojos, Bolivia, sustained large sedentary societies in the Late Holocene (ca. 500 to 1400 AD). In order to gain insight into the subsistence of these people, we undertook macrobotanical and phytolith analyses of sediment samples, and starch grain and phytolith analyses of artifact residues, from four large habitation sites within this region. Macrobotanical remains show the presence of maize (*Zea mays*), squash (*Cucurbita* sp.), peanut (*Arachis hypogaea*), cotton (*Gossypium* sp.), and palm fruits (Arecaceae). Microbotanical results confirm the widespread use of maize at all sites, along with manioc (*Manihot esculenta*), squash, and yam (*Dioscorea* sp.). These integrated results present the first comprehensive archaeobotanical evidence of the diversity of plants cultivated, processed, and consumed, by the pre-Hispanic inhabitants of the Amazonian lowlands of Bolivia.

1. Introduction

The Llanos de Mojos, in the Beni department of Bolivia, are a mosaic of seasonally-flooded savannah, gallery forests, and patches of forest called 'forest islands'. Poor drainage of the heavy Quaternary lacustrine clays and a strongly seasonal pattern of rainfall result in annual cycles of widespread inundation followed by dry conditions and a scarcity of surface water in many areas. Archaeologically, the area is well known for its extensive complex of raised fields, canals, causeways, mounds, and other earthworks. Survey and mapping of these earthworks since the 1960s has revealed pre-Hispanic hydraulic engineering on an enormous scale and innovative mitigation of the challenges presented by the landscape (Denevan, 1963, 1966; Dougherty and Calandra, 1981, 1981-82, 1983, 1984, 1984-85; Erickson, 1980, 1995, 2000, 2006; Erickson and Balée, 2006; Lee, 1979, 1996; Lombardo et al., 2011; Lombardo and Prümers, 2010; Plafker, 1963; Walker, 2004, 2008a). However, the Llanos de Mojos were by no means a culturally homogeneous area in pre-Hispanic times. At least four regions can be discerned by marked differences in the ceramic inventories, settlement patterns, and earthworks (Denevan, 1966, 2001; Jaimes Bentancourt, 2010; Lombardo and Prümers, 2010; Walker, 2008a: 930, Fig. 46.3). To the northwest is an area dominated by extensive areas of raised fields and evidence of large villages (Lombardo et al., 2011; Walker, 2004, 2008b). In the southwest is a complex landscape of several types of raised and ditched fields, along with causeways, mounds, and canals (Erickson, 2000). East of the Mamoré River in the Iténez region is an area of ring-ditch enclosures and causeways (Erickson et al., 2008; Prümers et al., 2006; Saunaluoma, 2010). In the southeast there exists numerous habitation mounds (*lomas*), some monumentally large in scale (Erickson and Balée, 2006; Nordenskiöld, 1913; Prümers, 2004a, b, 2006).

Our knowledge about the time depth and evolution of the pre-Hispanic cultures which occupied the Llanos de Mojos is still sketchy. To address this, Prümers and his team have undertaken large-scale excavations of habitation sites in two of the above mentioned sub-regions of the Llanos de Mojos over the past two

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decades (Fig. 1): the mounds of Salvatierra and Mendoza in the southeastern region near the village of Casarabe (Prümers, 2003, 2004a, b, 2006, 2008, 2009a, 2009c), and two ringed-ditch sites, Granja del Padre and BV-3, in the Iténez region (northeast) near the village of Bella Vista (Prümers, 2010). In this paper we present the results of archaeobotanical analyses on artifacts and sediments from these sites.

The earliest Jesuit accounts from the area mention the consumption of manioc (*Manihot esculenta* Crantz), maize (*Zea mays* L.), and peanuts (*Arachis hypogaea* L.) as dietary staples, along with beans (*Phaseolus* spp. and *Canavalia* spp.), sweet potato (*Ipomoea batatas* [L.] Lam.), arracacha (*Arracacia xanthorrhiza* Bancr.), avocado (*Persea americana* Mill.), papaya (*Carica papaya* L.), pineapple (*Ananas comosus* [L.] Mer.), chili peppers (*Capsicum* spp.), tobacco (*Nicotiana tabacum* L.), cacao (*Theobroma cacao* L.), Brasil nuts (*Bertholletia excelsa* Bonpl.), and palm nuts (Arecaceae), and the cultivation of cotton (*Gossypium* sp.) for cloth (Castillo, 1906 [1670]; Eder, 1985 [1791]; Eguiliz, 1884 [1696]; Marbán, 1898; Métraux, 1948: 57). There has been little archaeobotanical analysis within the region, however, to provide hard evidence of which plants were cultivated and consumed prior to the arrival of Europeans. In a preliminary study of raised field contexts at the sites of El Villar and Santa Fe, Jones (in Erickson, 1995: 91-92) recovered pollen from *Xanthosoma*, *Bixa*, and *Ilex*, in addition to a wide range of grass, tree, and aquatic plants. South of the Llanos de Mojos, within the Chiquitano Dry Forest zone, a carbonized mass of maize kernels was recovered from the site of Pailón, 60 km east of the city of Santa Cruz, dating to 1129 ± 35 BP (cal AD 895–925, cal AD 935–985) (Chevalier, 2002; Prümers, 2002: 111; Prümers and Winkler, 1998).

We employed multiple lines of archaeobotanical inquiry in order to recover a more complete perspective on plant use: macrobotanical analysis, starch grain analysis, and phytolith analysis. Each particular botanical fossil type has strengths and weaknesses

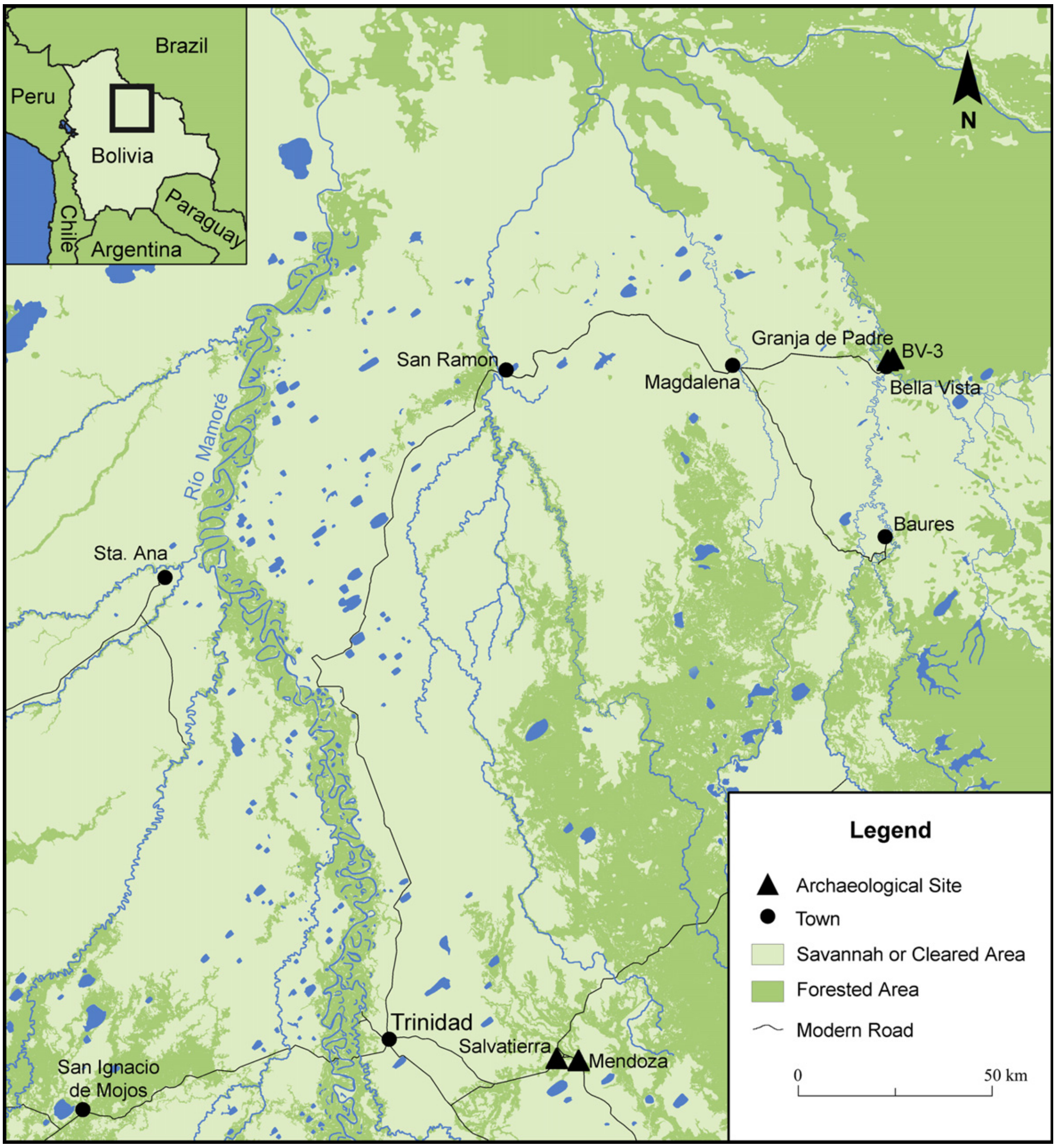

Fig. 1. Map of the Llanos de Mojos, Bolivia, showing site locations.

in terms of deposition, plant parts represented, taphonomy and preservation, and level of taxonomic identification. Results from multiple techniques of analysis therefore compliment and reinforce one another, and significantly improve the chances of reconstructing a more inclusive history of pre-Hispanic plant use (Dickau, 2010; Iriarte et al., 2010, 2004; Pearsall, 1995, 2000; Piperno, 1995, 1998, 2006; Piperno and Holst, 2004).

2. Archaeological contexts

2.1. Mendoza

Mendoza (20 L 343930 m E, 8354050 m S) is a large habitation mound located approximately 50 km east of the modern town of Trinidad and 3 km south of the village of Casarabe. The construction of the road connecting Trinidad with Santa Cruz de la Sierra in the late 1970s cut through the centre of the site (see site map in Prümers, 2004a: 57, Abb. 6). On the western side of the road, part of the original mound was left intact as a 5 m high embankment. Two sections of this embankment were straightened, the resulting profiles cleaned, and the archaeological contexts documented (Prümers, 2004a, b). Excavation pits 2 m wide and up to 34 m long were dug into the profile. A series of 38 radiocarbon dates indicated that the occupation of the site started around 500 cal AD and ended about 1400 cal AD.

The mound was formed by the successive construction, elevation, and modification of platforms. The first platform, only 1 m high, was constructed in the southern part of the site. From this nucleus the mound progressively developed to the north, and probably west and east as well. Refuse layers, rich in archaeological materials, accumulated at the flanks of the platforms. Thousands of ceramic sherds were found in these refuse layers, as well as animal bones, some modified to serve as tools. Stone tools were uncommon; only 5 fragmented axes, 2 hammers, and 1 polisher were recovered. Several burials, including children, were found within the sequence of platform constructions.

2.2. Salvatierra

Salvatierra (20 L 340060 m E, 8354070 m S) is located 3 km west of the Mendoza mound. The site has escaped any major modern modifications and mapping permitted, for the first time, a glimpse at the complex structure and planned outline of this kind of habitation site (Prümers, 2006, 2008, 2009a). The centre was occupied by a large artificial platform, 1.5 m high and 2 ha in area, situated on the inner bank of the curving channel of a paleo-river (see site map in Lombardo and Prümers, 2010: 1881, Fig. 7). On this platform were located various building platforms. The largest of these massive earthen buildings, Mound 1, was located to the northeast. On its top were three platforms arranged in a 'U' shape, delimiting a plaza-like space that opened to the northwest. Approximately 50 m to the south of Mound 1 lay the much smaller Mound 2, an L-shaped, 3 m high structure that seems to have served as a cemetery. The outer limits of the site proper were marked by a polygonal rampart, approximately 120 m from the artificial platform, and enclosing an area of 21 ha. Other earthworks, including canals, ponds, and causeways located immediately to the south of the platform and rampart, were part of the site as well.

The artifacts selected for archaeobotanical analysis came from stratigraphic excavations in Mounds 1 and 2 and from Pit 2, located southeast of Mound 1 on the artificial platform. Abundant archaeological material was recovered in each of these excavation units, mainly from refuse layers. More than 30,000 diagnostic ceramic sherds were recovered and analyzed by Jaimes Bentancourt (2010). The results of her study, as well as a series of radiocarbon dates, confirm that Salvatierra had much the same occupation history as Mendoza.

2.3. Bella Vista

The modern village of Bella Vista is located 200 km to the northeast of Mendoza and Salvatierra, at the border of the Brazilian Shield. The two ring-ditched sites investigated are located north of the village approximately 1 km apart. They are connected by a long semi-circular ditch that encloses an area of more than 150 ha on the eastern levee of a paleo-river (see site map in Prümers, 2009b). The function of the ditch is difficult to interpret, but most likely served defensive purposes.

Granja del Padre (20 L 423408 m E, 8533700 m S) is located at the southwestern end of the larger semi-circular ditch. The ring-ditch encircling the site measures 300 m in diameter and, as excavations showed, was more than 2 m deep at the time of construction. An area of approximately 400 m^2 was excavated within the ring. A single, thin, occupation layer of dark-grayish soil was found, indicating that the occupation was rather short in duration. No evidence of houses (post-holes) or fire-pits were found, but an occupation surface was evidenced in several spots by a mosaic-like layer of ceramic sherds from large, poorly-fired vessels. Radiocarbon dates on soot from ceramic sherds date the occupation to about 1200–1400 cal AD. A series of urn burials were found at the site (Prümers et al., 2006).

The other ring-ditched site, BV-3 (20 L 424700 m E, 8534470 m S), had many of the same characteristics as Granja del Padre. A very thin occupation layer, normally 20 cm thick, but up to 50 cm thick in parts, was encountered directly below the surface. No urn burials were found within the 150 m^2 area excavated at this site. Two radiocarbon dates on soot from ceramic sherds date BV-3 to 1400–1500 cal AD, indicating that the occupation of BV-3 was somewhat later than at the Granja del Padre site. However, the ceramic inventory at both sites is almost identical.

3. Artifact description

A total of 28 artifacts from the four sites were analyzed for starch and phytoliths (Table 1). Eight ceramic artifacts from Mendoza were examined, including two flat grater fragments (Fig. 2a and b) and two colander or sieve fragments (Fig. 2h). Graters are typically large flattish or slightly curved vessels with deep parallel grooves incised on the interior surface. They are thought to have been used as rough surfaces for grating manioc and other foods (Jaimes Bentancourt, 2010; Nordenskiöld, 1913; Rydén, 1964). Colanders are bowl shaped vessels with multiple holes in the bottom, probably used for straining or sieving different foods or substances (Jaimes Bentancourt, 2010). Jesuit accounts describe the use of colanders in the production of *chicha*, a drink of fermented maize or manioc mash (Castillo, 1906 [1670]: 328–329). A partial ceramic *mano* with longitudinal parallel grooves was tested (Fig. 2e), along with a heavily used artifact that presumably originated as a similar grooved *mano* (Fig. 2d); remnants of grooves are visible on part of the artifact, but the *mano* either broke, or was completely ground down from use, creating a narrow edge. Carbonized residues from the interiors of two ceramic body sherds were sampled (Fig. 2m and n).

Ten ceramic artifacts from Salvatierra were analyzed: eight colander fragments, one grater fragment, and a solid clay *mano*. The grater and colanders are similar to those found at Mendoza (Fig. 2c and i–l), although one colander (SAL 06-2-796) appeared to have only one large hole rather than the usual multiple smaller holes (Fig. 2g). The clay *mano* looks like stone *manos* found in other parts

Table 1
Tools and sediments analyzed and their contexts.

Catalogue #	Site	Cut	Feature	Quadrant	Level (cm b.d.)	Sample type
LM 99-1864	Mendoza	1	5	28/B	190–200	Ceramic grater frag
LM 99-1865	Mendoza	1	5	32/A	160–170	Ceramic grater frag
LM 99-1866	Mendoza	1	5	31/A	170–180	Grooved clay mano
LM 99-1867	Mendoza	1	5	31/A	170–180	Flat clay mano or chopper
LM 01-4189	Mendoza	3	325	29/111	150–160	Ceramic colander frag
LM 01-5307	Mendoza	3	–	29/108	60–70	Ceramic colander frag
LM 02-291	Mendoza	5	514B	7/A	430–440	Sherd with burnt residue
LM 02-294	Mendoza	5	514B	7/A	430–440	Sherd with burnt residue
Soil sample 1	Mendoza	5	542	62/A	470–480	Sediment
Soil sample 2	Mendoza	5	569	61/B	490–500	Sediment
Soil sample 3	Mendoza	6	619	57-58/A-B	480–490	Sediment
Soil sample 4	Mendoza	6	638	55/A	480–490	Sediment
SAL 04-2-2698	Salvatierra	2	229	3/B	190–200	Ceramic colander frag
SAL 04-2-7447	Salvatierra	2	227	5/D	200–210	Ceramic colander frag
SAL 04-4-3597	Salvatierra	4	437	18/D	210–220	Ceramic colander frag
SAL 05-4-2743	Salvatierra	4	4084	A/16	330–340	Ceramic colander frag
SAL 05-4-2745	Salvatierra	4	4084	E/16	330–340	Ceramic colander frag
SAL 06-2-796	Salvatierra	2	2051	Z/3	330–340	Ceramic colander frag
SAL 06-2-1658	Salvatierra	2	202	Z/6	110–120	Ceramic colander frag
SAL 06-2-1671	Salvatierra	2	–	–	330–350	Ceramic mano
SAL 06-4-2750	Salvatierra	4	4188	Y/18	220–230	Ceramic colander frag
SAL 06-10-1642	Salvatierra	10	1136	209/113	220–230	Ceramic grater frag
BV2 08-2-939	Granja del Padre	2	212	196/82	80–90	Quartz wedge
BV2 08-2-940	Granja del Padre	2	213	196/81	80–90	Granitic axe
BV2 08-4-286	Granja del Padre	4	402	183/81	90–100	Handstone
BV2 08-4-287	Granja del Padre	4	402	186/80	90–100	Handstone
BV2 08-4-288	Granja del Padre	4	402	190/82	170–180	Dioritic axe
BV2 08-4-289	Granja del Padre	4	401	182/84	70–80	Quartz wedge
BV2 08-5-374	Granja del Padre	5	502	186/85	80–90	Quartz flake
BV2 08-5-375	Granja del Padre	5	506	187/88	90–100	Quartz flake
BV3 09-L-49	BV-3	2	202	391/271	10–20	Handstone

of South and Central America (Fig. 2f). The lack of easily accessible stone near Salvatierra likely prompted the inhabitants to come up with alternatives for tools. Over 1100 clay *manos* or fragments were found at Salvatierra, many with grooves or punctuations on the surface (Jaimes Bentancourt, 2010: 61), similar to those from Mendoza.

Nine stone tools from the sites of Granja de Padre and BV-3 near Bella Vista were selected for analysis: four small quartz flakes or wedges, two small polished axes, and three handstones (Fig. 3). The quartz artifacts (Fig. 3a–d) were analyzed in order to test the hypothesis that they were used as grater-board chips for grating manioc and other foods, especially since grooved ceramic graters like those found at Mendoza and Salvatierra were not recovered at the Bella Vista sites. The smaller of the two polished stone axes (BV2 08-4-288) was made from a dark dioritic stone (Fig. 3g). The larger (BV2 08-2-940) was made from a light-colored granitic material, and was quite worn and dull (Fig. 3h). The handstones were granitic or felsic stones that had been modified to greater or lesser degrees by intentional shaping. Generally, they had flattened sides and a working surface around the outer perimeter (Fig. 3e, f and i).

4. Methods

4.1. Macrobotanical analysis

A flotation program to recover macrobotanical remains and other small finds was initiated in 2005 at Salvatierra and was very productive. Remains were recovered from bulk sediment samples processed using a modified SMAP flotation machine (Terceros Céspedes, 2007; Watson, 1976), and later analyzed by Bruno (2010) following protocols based on Pearsall (2000). For details, see Supplementary Information and Bruno (2010). Data were summarized and quantified in terms of ubiquity (percent of samples that contained a particular taxon or remain type) and density (count per litre of sediment and grams per litre [g/L] of sediment). Identifications were made using comparative material from ethnobotanical fieldwork conducted in Bella Vista in 2009, complemented by the aid of available seed guides (Lentz and Dickau, 2005; Martin and Barkley, 1961; USDA/ARS, 2011).

A series of flotation samples were collected at Mendoza, but await analysis. Several flotation samples were collected at Granja del Padre, but none produced any carbonized plant remains. The preservation conditions at this site were very different than those at Salvatierra; even bone did not preserve. This may be due to the fact that it was a relatively shallow, single-occupation site, in contrast to the deep, anthropogenically constructed site of Salvatierra.

4.2. Microbotanical analysis

Artifacts were processed to recover starch grains and phytoliths, and bulk sediment samples were processed to recover phytoliths, based on standard protocols (Loy, 1994; Pearsall, 2000; Pearsall et al., 2004; Piperno, 1988, 2006; Piperno and Holst, 1998; Torrence and Barton, 2006; Zarrillo et al., 2008). For details, please see Supplementary Information. After obtaining adhering residues from artifacts via sonication, starch was extracted first since it is more fragile and susceptible to damage from the acids and heat processes used in phytolith analysis (Chandler-Ezell and Pearsall, 2003; Coil et al., 2003; Horrocks, 2005; Pearsall et al., 2004). Phytolith extraction then followed on the remaining residue.

Starch was identified using a comparative collection of 235 Neotropical species including material obtained from the 'Herbario Regional del Oriente Boliviano' of the 'Noel Kempff Mercado' Natural History Museum, Santa Cruz, Bolivia. Phytoliths were

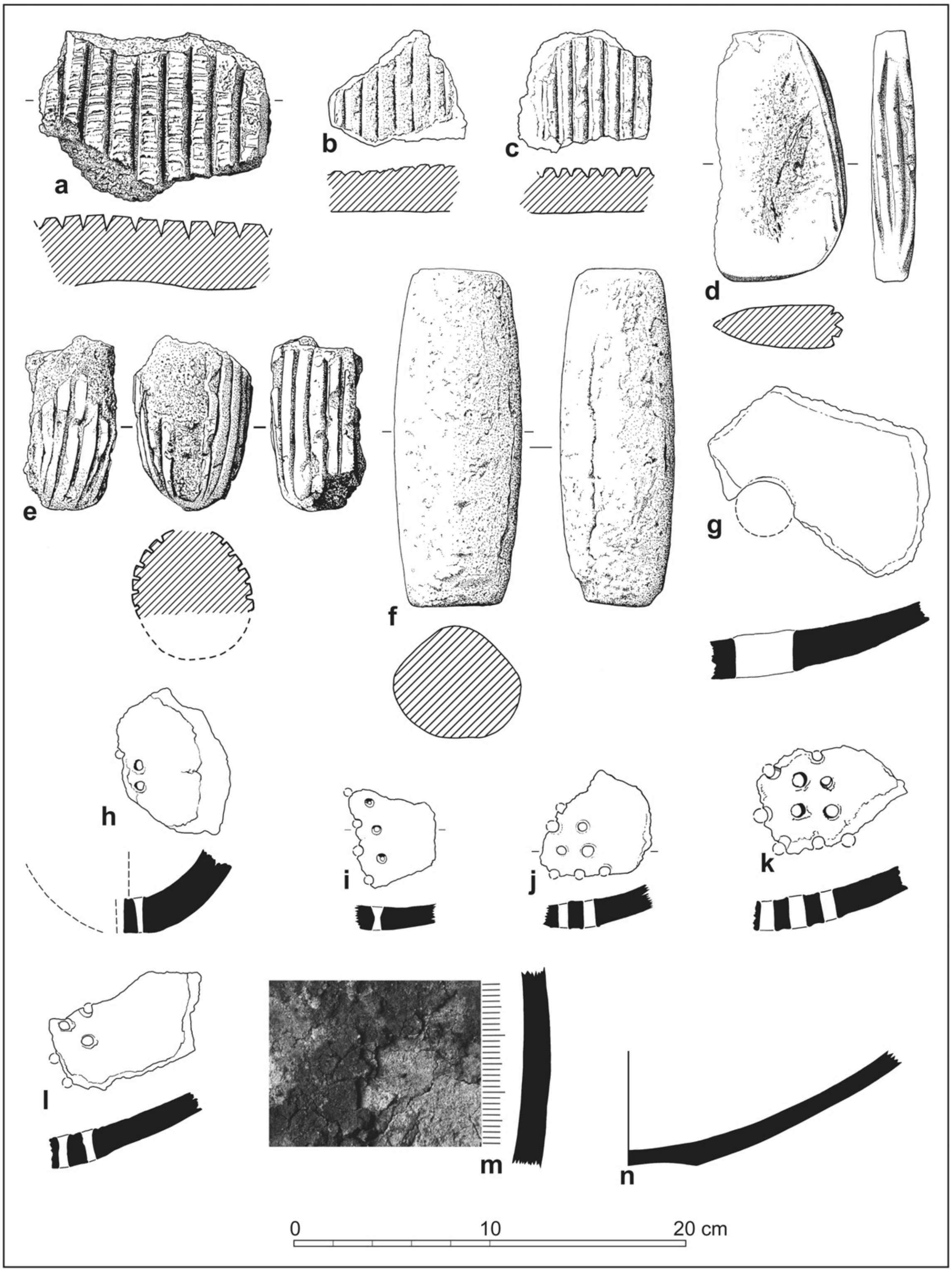

Fig. 2. Ceramic artifacts analyzed for microbotanical remains. a) Grater fragment LM 99-1865, b) Grater fragment LM 99-1864, c) Grater fragment SAL 06-10-1642, d) Flat clay *mano* or chopper LM 99-1866, e) Grooved clay *mano* LM 99-1866, f) Clay *mano* SAL 06-2-1671, g) Colander fragment with large hole SAL 06-2-796, h) Ceramic colander fragment LM 01-4189, i) Colander fragment SAL 04-2-7447, j) Colander fragment SAL 05-4-2743, k) Colander fragment SAL 06-4-2750, l) Colander fragment SAL 04-4-3597, m) Sherd with burnt residue on the interior LM 02-294, n) Sherd with burnt residue on the interior LM 02-291.

identified using a comparative collection of over 500 tropical and subtropical species from South America, housed at the University of Exeter Archaeobotany Laboratory. An additional 265 taxa from Bolivia have been obtained from the 'Herbario Regional del Oriente Boliviano' and are currently being processed to enlarge the comparative collection.

Two of the sediment samples from Mendoza were tested for starch, but none was recovered. We therefore infer that the starch

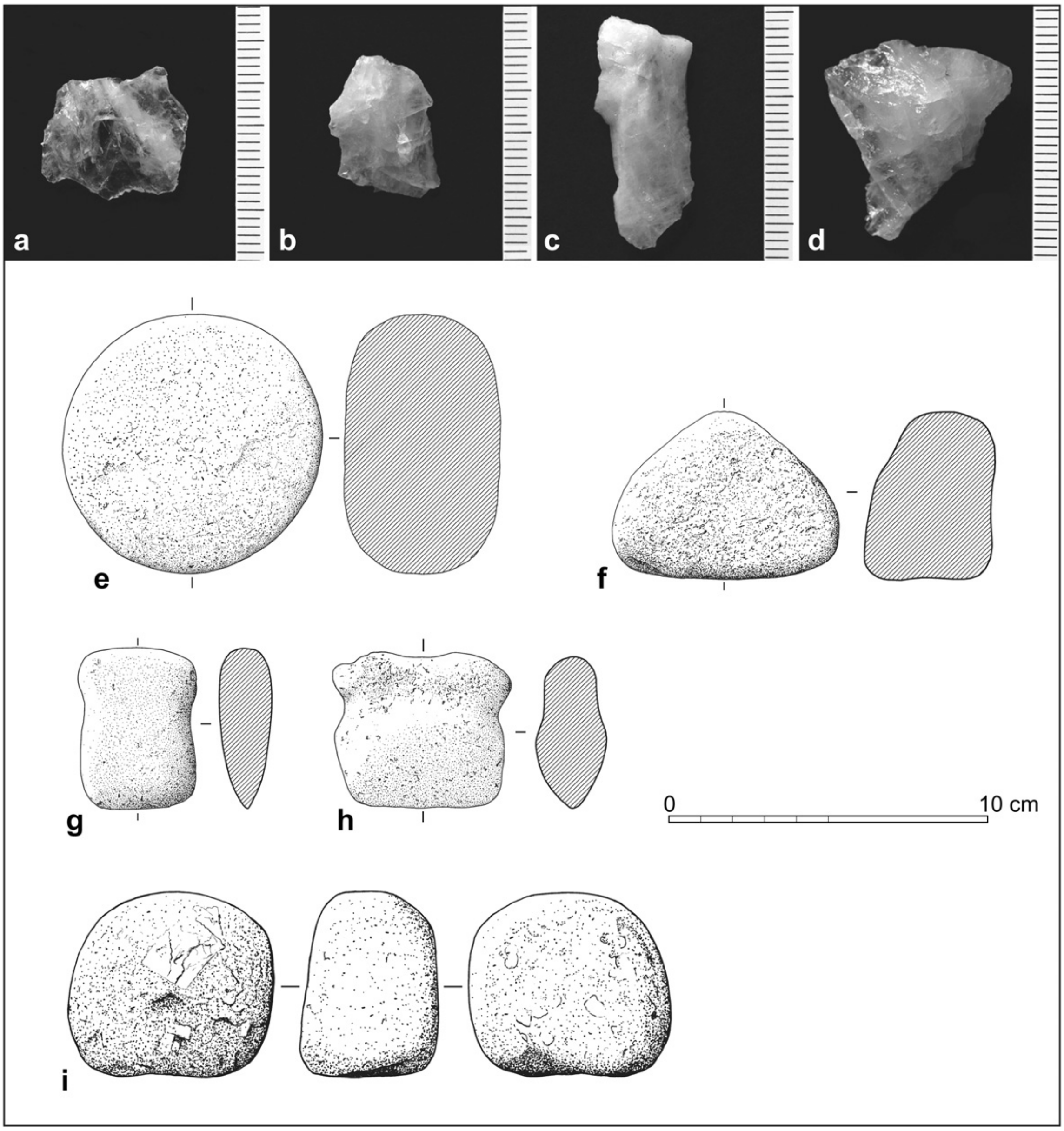

Fig. 3. Lithic artifacts analyzed for microbotanical remains. a) Quartz wedge BV2 08-2-939, b) Quartz wedge BV2 08-4-289, c) Quartz flake BV2 08-5-374, d) Quartz flake BV2 08-5-375, e) Handstone BV2 08-4-286, f) Handstone BV2 08-4-287, g) dioritic axe BV2 08-4-288, h) Granitic axe BV2 08-2-940, i) Handstone BV3 09-L-49.

grains recovered from the artifacts represent actual residue preserved on the tool surfaces, and the result of tool use, rather than background starch from the surrounding sediment.

5. Results

5.1. Macrobotanical remains

Lowland tropical regions are well known for being problematic environments for the preservation and recovery of macrobotanical remains (Pearsall, 1995; Piperno and Pearsall, 1998). We found, however, that preservation of carbonized plant remains was very good at Salvatierra (Bruno, 2010). The total weight of the identified items (including wood) was 422.78 g, or 0.61 g per litre of soil. A broad range of taxa and plant parts were identified (Table 2).

The most common cultivated species in the samples was maize. It was present in almost all samples and fairly abundant. Fragments of cobs, individual cupules (some with glumes still attached), and kernels or kernel fragments were present (Fig. 4a).

Evidence of several other crops was also recovered. Peanut was identified based on diagnostic shell fragments with a distinctive alveolate pattern on the outer surface like that observed in comparative material (Fig. 4b). Fragments of squash (*Cucurbita* sp.) rind were identified in several samples. In cross-section, these fragments show the characteristic small, dense cells of the epidermis overlying a layer of larger, thick-walled stone cells (Cutler and Whitaker, 1961). A few fragments also appeared to have small, round silica bodies at the interface of the epidermis and the stone cells, the scalloped phytoliths diagnostic of *Cucurbita* rind (Bozarth, 1987; Piperno et al., 2000, 2002). Although these rind fragments have not yet been tested for phytoliths, squash phytoliths were identified in other contexts at the site, as discussed below.

Many samples contained both testa and kernel fragments of cotton seeds. Testa fragments with a diagnostic attachment scar

Table 2
Summary of macrobotanical remains identified at Salvatierra.

Taxa	No. of samples*	Ubiquity	Volume (L)	Count	Weight (g)	Density (count/L)	Density (weight/L)
Amaranthaceae/Caryophyllaceae seed	8	19%	174.5	41	0.060	0.23	0.0003
Arachis sp. shell	4	9%	84.5	130	0.155	1.54	0.0018
Arecaceae endocarp	40	93%	626.0	2233	8.195	3.57	0.0130
Cyperaceae seed	2	5%	70.0	2	0.010	0.03	0.0001
Cucurbita sp. rind	5	12%	79.5	24	0.090	0.30	0.0011
Fabaceae seed (small, wild)	2	5%	22.0	2	0.005	0.09	0.0002
Malvaceae type 1 seed	1	2%	55.0	6	0.015	0.11	0.0003
Malvaceae type 2 seed	4	9%	87.0	14	0.030	0.16	0.0003
Gossypium sp. seed	23	53%	432.8	152	0.260	0.35	0.0006
Poaceae seed	17	40%	398.8	225	0.260	0.56	0.0007
Zea mays cob fragment	10	23%	213.8	59	0.230	0.28	0.0011
Zea mays cupule	41	95%	678.5	2258	2.300	0.32	0.0033
Zea mays glume	21	49%	398.5	560	0.560	1.41	0.0014
Zea mays kernel fragment	38	88%	670.0	930	5.515	1.39	0.0080
Zea mays embryo	13	30%	220.8	110	0.195	0.50	0.0009
Zea mays poss. embryo	5	12%	118.0	8	0.035	0.07	0.0003
***Zea mays* total**	**41**	**95%**	**678.5**	**3925**	**8.835**	**5.78**	**0.0130**
Solanaceae seed	10	23%	245.0	40	0.110	0.16	0.0004
Verbena sp. seed	1	2%	12.0	1	0.005	0.08	0.0004
Wood	43	100%	690.4		369.760		0.5356
Parenchyma	43	100%	690.4	15884	28.555	24.02	0.0447
Thin Pericarp/Testa	38	88%	645.5	1350	1.260	2.09	0.0020

* Total number of samples analyzed = 43.

(Fig. 4c) were quite common, and there were also several nearly complete kernels (seeds without testa). We cannot verify whether these remains come from domesticated or wild stands of cotton, but it is very likely they were from domesticated crops.

Several seeds typical of the Solanoideae subfamily (Olmstead and Sweere, 1994) were identified. A few of the seeds have traits typical of chili peppers (*Capsicum* spp.), such as a beaked hilum and parallel cells along the seed margin (Minnis and Whalen, 2010: 246–247). The diversity of the Solanaceae family in the region is high, however, and until more comparative work is conducted, our identifications remain tentative.

Numerous fragments of endocarp and/or testa were recovered. There were two general size categories of these fragments. The most common and abundant were 1–3 mm thick and had a very dense cell structure, characteristic of palm (Arecaceae) endocarps. Unfortunately they lacked any obviously diagnostic attributes that would permit species identification. The other category, <1 mm thick, was fairly common but less abundant. These might be the testa from some type of large seed or other fruit.

Numerous seeds of non-domesticated taxa were identified including Amaranthaceae/Caryophyllaceae, Poaceae, Cyperaceae, Polygonaceae, Fabaceae, Malvaceae, Plantaginaceae, Solanaceae, and Verbanaceae. Wood charcoal was present in all the samples and comprised 77% of the total weight density of the entire analyzed assemblage. Future studies aim to identify the woody taxa represented.

5.2. Microbotanical remains from artifacts

5.2.1. Mendoza

Starch consistent with maize was recovered from both ceramic grater fragments, one of the colander fragments, and from the burnt sherd (Table 3). Mean size of these grains was 18.3 μm along the longest axis (Fig. 5a). This falls within the range of comparative maize starch, which is larger than any other Poaceae species with similar morphological characteristics (Holst et al., 2007). The identification of maize was confirmed by the recovery of wavy-top rondels and *Zea*-type IRP (irregular with short projections) phytoliths diagnostic of cob and glume structures (Pearsall et al., 2003; Piperno and Pearsall, 1993). We identified wavy-top rondels based on the following established criteria: a) a flat, circular to oval base that is longer than the height of the rondel, b) a top that is a single, complete wave equal to or less than the length of the rondel, without acute or sharply angled edges, and c) lateral ends that are concave (Bozarth, 1993; Mulholland, 1993; Pearsall et al., 2003; Piperno and Pearsall, 1993) (Fig. 5j and k).

The colander also yielded a significant assemblage of unidentified root starch grains ($n = 27$). These grains were generally ovoid to elongate, with eccentric hila and visible lamellae (Fig. 5d). Some had a slightly cunate or truncate distal end, a trait seen among some species of yam (Dioscoreaceae). Several of the starch grains from this artifact exhibited alteration consistent with grinding damage, including enlarged hila, radial fissures, poor bifringence, and split, torn, or partial grains (Babot, 2001; Chandler-Ezell et al., 2006; Perry et al., 2006).

Phytoliths from the artifact sediment residue include grasses (Poaceae), sedges (Cyperaceae), palms (Arecaceae), and arboreal types (Table 4). The taxonomic assemblage is similar to that seen from analysis of bulk sediment samples from the site (Section 5.3). For this reason, the phytoliths, including maize rondels, likely represent background vegetation rather than direct artifact residue from plant processing.

One exception to this was sherd LM 02-294, where the thick layer of carbonized residue from the interior was directly sampled. No starch was observed from this residue, either because its extraction and visibility were inhibited by the carbon particles, or because it was destroyed during the cooking process that formed the carbon. The residue did yield abundant phytoliths, however. The assemblage was completely dominated by *Heliconia* (82%) with the remainder comprised mainly of palm (Arecaceae) (17%) and the occasional Marantaceae seed phytolith (1%). While it is possible that small amounts of sediment may have been adhering to the sampled carbonized residue, the high percentage of *Heliconia* phytoliths suggests that the majority of phytoliths came directly from the residue. *Heliconia* is uncommon in other contexts from the site (ranging between only 2–3% of identifiable phytoliths, see Fig. 6). The abundance of *Heliconia* phytoliths in the pot residue suggests that either the leaves were being used in the cooking process and accidently carbonized, or the rhizomes were a targeted food source. Both structures produce the characteristic trough-like

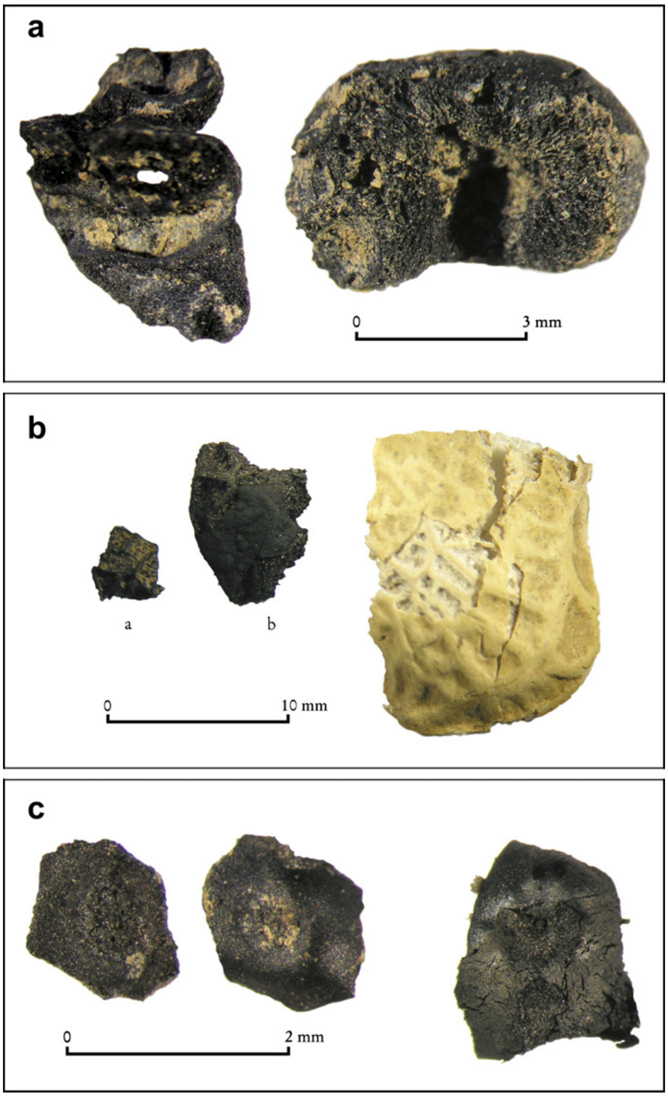

Fig. 4. Selected macrobotanical remains from Salvatierra. a) *Zea mays* cupule (left) and kernel (right), b) *Arachis hypogaea* archaeological shell fragment (left), modern carbonized shell fragment for comparison (centre), modern uncarbonized shell fragment for comparison (right), c) *Gossypium barbadense* carbonized testa from modern wild specimen for comparison (left and centre), exterior view of archaeological fragment (right). From Bruno (2010).

phytoliths found in members of the genus (Piperno, 2006: 38) (Fig. 5n).

5.2.2. Salvatierra

Starch analysis of the colander fragments from Salvatierra show that they were used in the processing of a variety of plant foods. Maize was identified on five of the colanders, and manioc was present on three. Diagnostic granules of manioc were identified by their smooth surface, round bell-shape with multiple concave pressure-facets at the base, and a centric hilum with a stellate fissure, mean length of 20.2 μm (Fig. 5b). The majority of these grains showed the pronounced stellate fissure, open hilum, and 'inflated' bell-shape characteristic of lowland Amazonian races of manioc, compared to the non-stellate fissures and more hemi-spherical shape of Peruvian races (Perry, 2002: see also Duncan et al., 2009) A large (50.0 μm) cunate-shaped starch with lamellae, consistent with *Dioscorea* sp., was recovered from SAL 04-2-7447 (Fig. 5c). Unidentified root starch grains were found on three colander fragments.

Both the ceramic grater and the clay *mano* appear to have been used primarily for processing maize. They were also likely used to process chili peppers, based on the recovery of lenticular-shaped grains with slightly depressed centers and a longitudinal line in profile (Fig. 5f). Mean diameter was 26.2 μm, within the range of domesticated *Capsicum* spp. (Perry et al., 2007). Comparative work on the Solanaceae from the region is not yet complete, but thus far, no other species demonstrate these features. Some of the starch from two colander fragments and from the clay *mano* showed evidence of grinding damage (Fig. 5g and h). There was also evidence of heat damage (gelatinization) on a few unidentified grains from the *mano*, suggesting some food may have been cooked prior to being ground (Henry et al., 2009).

Phytoliths of maize cobs and squash rinds were among the taxa recovered in the sediments, confirming macrobotanical evidence for these crops at the site.

5.2.3. Bella Vista

The quartz chips from Bella Vista yielded few starch grains; maize was identified on one of these tools. Results from the stone axes were also rather sparse. The handstones, however, provided much more information on plant use and processing. Starch granules consistent with maize were found on all three, and manioc was processed with at least one of them. One of the handstones was also used to process some sort of tuberous root or rhizome, based on the recovery of ovoid starch grains with eccentric hila and lamellae (Fig. 5e). This starch morphotype has only been seen in underground storage organs, such as those produced by many members of the Zingiberales. Several starch grains from this tool showed evidence of grinding damage.

Phytoliths obtained from the artifact residues show the presence of maize cobs, along with grasses, sedges, *Heliconia*, palms, and other arboreal taxa.

5.3. Microbotanical remains from sediments

Four bulk sediment samples from Mendoza were analyzed for phytoliths (Fig. 6). Sediment Samples 2–4 come from refuse layers, presumably of domestic debris, that had accumulated on the flanks of the first platform constructed at the site, around 500 cal AD. Sample 1 was taken from the refuse layer formed during subsequent enlargement of the platform at the beginning of Occupation Phase 2.

A large range of plants were documented in the samples from the initial occupation of the site, either growing at the site, or brought to the platform mound by the people living there. Grasses and Asteraceae (Fig. 5i and r) dominate, but there is also evidence for arboreal taxa in the area. Palm phytoliths are abundant (Fig. 5q), particularly in Samples 2 and 3. Small amounts of sedges (Cyperaceae) (Fig. 5s) and *Heliconia* are present. Marantaceae seed phytoliths are very abundant in all three samples, and at least two different species were observed (Fig. 5o and p). In terms of domesticated species, maize cobs were among debris of the initial occupation of the site, documented by the recovery of wavy-top and/or ruffle-top rondels and IRP phytoliths (Fig. 5j–l). Interestingly, discriminant function analysis of cross bodies from these samples does not show evidence of maize leaves in these contexts. It is possible that harvested maize cobs were brought into the site, but the rest of the plant was left out in the field. Scalloped spheres from squash rinds were also found in the initial occupation level (Fig. 5m). Their dimensions are clearly within the range of domesticated squash.

The phytolith assemblage from Sample 1 shows some significant differences from the other samples. Grasses are still dominant, but

Table 3
Starch grains recovered from artifacts.

Site/cat #	Tool	*Capsicum* sp.	*Dioscorea* sp.	*Manihot esculenta*	*Zea mays*	Unidentified root[a]	Unidentified	Total	Notes
Mendoza									
LM 99-1864	Grater frag.			(2)	3 (2)		5	**12**	PC
LM 99-1865	Grater frag.				2			**2**	
LM 99-1866	Grooved clay mano							**0**	
LM 99-1867	Flat clay mano							**0**	
LM 01-4189	Colander frag.			(2)	4	27	34	**67**	GD, PC
LM 01-5307	Colander frag.							**0**	
LM 02-291	Burnt residue				1			**1**	
LM 02-294	Burnt residue							**0**[b]	
Salvatierra									
SAL 04-2-2698	Colander frag.				3			**3**	
SAL 04-2-7447	Colander frag.		1		1		8	**10**	
SAL 04-4-3597	Colander frag.	(2)		2 (2)	16 (2)	2	55	**81**	
SAL 05-4-2743	Colander frag.						24	**24**	
SAL 05-4-2745	Colander frag.	(1)			(1)	2	6	**10**	GD, PC
SAL 06-2-796	Colander frag.			1 (2)	5 (1)		4	**13**	
SAL 06-2-1658	Colander frag.			1		3	68	**72**	GD, PC
SAL 06-2-1671	Clay mano	(2)			13 (7)		29	**51**	GD, HD, PC
SAL 06-4-2750	Colander frag.						7	**7**	PC
SAL 06-10-1642	Grater frag.	(1)			22 (5)		17	**45**	PC
Bella Vista									
BV2 08-2-939	Quartz wedge				1		1	**2**	
BV2 08-2-940	Granitic axe						8	**8**	
BV2 08-4-286	Handstone				1 (2)		4	**7**	PC
BV2 08-4-287	Handstone			(1)	15 (1)		16	**33**	
BV2 08-4-288	Dioritic axe				(1)		9	**10**	
BV2 08-4-289	Quartz wedge				(1)		4	**5**	
BV2 08-5-374	Quartz flake							**0**	
BV2 08-5-375	Quartz flake						1	**1**	
BV3 09-L-49	Handstone			2 (1)	28 (5)	6	62	**104**	GD, PC

Table Notes: Numbers are total number of starch grains identified to a particular taxon. Numbers in parentheses indicate tentative identifications. Under Notes: GD = evidence of grinding damage, HD = evidence of heat damage, PC = presence of particulate charcoal.
[a] Starch grains that are longer than they are wide (generally oval or elongate), with eccentric hila. This morphotype has only been seen in root tissues.
[b] High amounts of charcoal inhibited starch extraction.

Asteraceae declines markedly and Marantaceae seed phytoliths virtually disappear. Palms are still abundant. Only a few maize cob phytoliths were detected, but analysis of cross bodies shows the presence of maize leaves. Squash phytoliths were not observed.

All four samples contain numerous burnt phytoliths, suggesting the regular occurrence of fire on or near the mound.

6. Discussion

Archaeobotanical evidence shows that a range of cultivars were being used by the pre-Hispanic inhabitants of the southern and eastern Llanos de Mojos. Maize stands out as a major contributor to the diet based on its ubiquity. It was identified at all four sites in multiple contexts through starch grains and phytoliths, and by abundant macrobotanical remains at Salvatierra. Although not as ubiquitous, manioc was also present in multiple contexts. These two staples were likely the cornerstones of daily subsistence, but they were supplemented by numerous other crops.

Squash was identified from both carbonized rind fragments and phytoliths. The particular species represented is unknown. Some of the phytoliths show a granular surface that so far has only been seen in *Cucurbita maxima*, but more specimens of *C. moschata* need to be studied before a positive identification is possible (Piperno, personal communication, 2010). Evidence of peanuts, a crop likely native to the region (Piperno and Pearsall, 1998), was found at Salvatierra. Peanuts would have provided an important source of protein to complement starch-rich maize and manioc. Other crops included a variety of yam (*Dioscorea* sp.) and several other unidentified tuberous species. The dominance of *Heliconia* phytoliths within carbonized residue from the interior of a ceramic vessel may be from harvesting and cooking of rhizomes. We were unable to find any records for the consumption of *Heliconia* rhizomes among the indigenous groups of Bolivia; however, they are an occasional source of food elsewhere in the Neotropics (Brussell, 2004; Clement, 1999; García-Serrano and Del Monte, 2004; Schultes and Raffauf, 1990). Alternatively, the phytoliths may also be the result of leaves used as pot liners or food wrappers.

Palm nuts were consumed based on the abundance of endocarp fragments at Salvatierra. The fragmented state of the endocarps may be in part the result of smashing of nuts to get at the kernel. Palm phytoliths were also ubiquitous at all sites in multiple contexts. The characteristic phytoliths, however, are not exclusive to fruits but produced in all parts of the plant, including the leaves and the stem (Piperno, 1988; Tomlinson, 1961). Therefore they may reflect use of palms for construction of structures (especially roof thatching), craft manufacture, fiber, fuel, and medicine (Balick, 1984, 1988). Palms were often left during clearing because of their high economic status (Balée, 1988).

In addition to food crops, we also have evidence for the use of cotton. The seed fragments found at Salvatierra likely represent domesticated cotton, cultivated in the fields alongside maize, manioc, peanuts, and other crops. Jesuit accounts describe the Mojo and Baures Indians wearing cotton clothing and using woven cotton hammocks (Métraux, 1948). They traded cotton cloth to the Spanish in Santa Cruz for metal goods (Marbán, 1898), which suggests they grew enough to provide a surplus. The recovery of 62 spindle whorls at Salvatierra (Jaimes Bentancourt, 2010) lends support to the importance of cotton in the economy.

Our analysis also provides some insight into food preparation methods. At the Bella Vista sites, access to stone allowed the manufacture of grinding implements. Not surprisingly, results

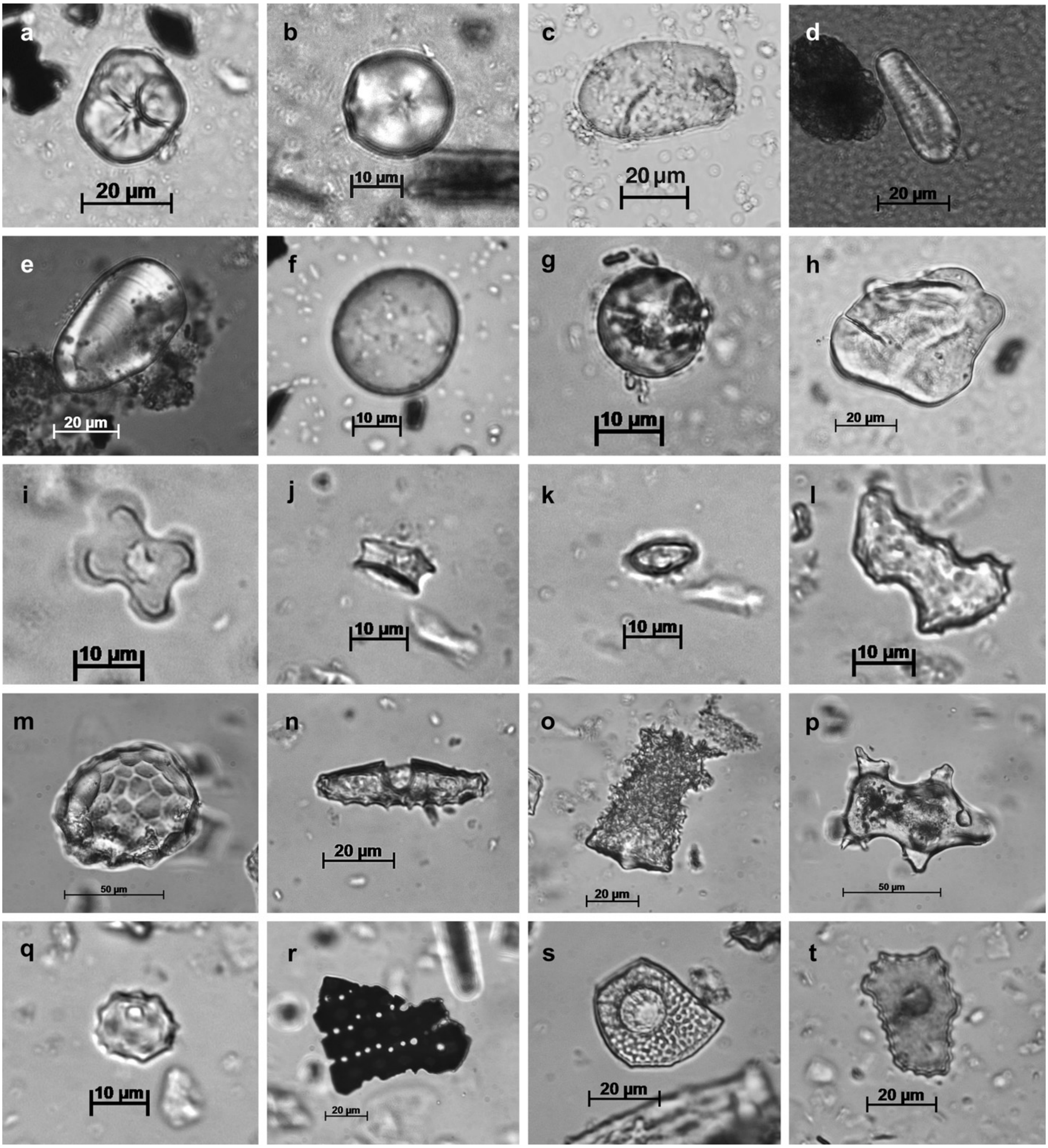

Fig. 5. Selected microbotanical remains. Starch grains: a) *Zea mays* (SAL 06-10-1642), b) *Manihot esculenta* (SAL 04-4-3597), c) *Dioscorea* sp. (SAL 04-2-7447), d) Unidentified root starch, possibly Dioscoreaceae, under cross-polarized light (LM 01-4189), e) Unidentified root starch (BV3-09-L-49), under cross-polarized light, f) cf. *Capsicum* sp. (SAL 06-2-1671), g) Unidentified species with processing damage (SAL 06-2-1671), h) Large unidentified root starch with processing and possible cooking damage (SAL 05-4-2745). Phytoliths: i) Panicoideae cross-shape (Sed. Sample 2), j) *Z. mays* cob wavy-top rondel, profile view (Sed. Sample 4), k) The same phytolith, rotated to top view, l) *Z. mays* cob IRP (Sed. Sample 3), m) *Cucurbita* sp. rind scalloped sphere (Sed. Sample 3), n) *Heliconia* troughed phytolith (LM 02-2014), o) Marantaceae 1 seed (Sed. Sample 4), p) Marantaceae 2 seed (Sed. Sample 3), q) Arecaceae globular echinate (Sed. Sample 3), r) Asteraceae opaque perforated plate (Sed. Sample 3), s) *Cyperus*/*Kyllinga* achene (Sed. Sample 3), t) *Scirpus* achene (LM 99-1864).

show that the handstones were multipurpose tools, used for processing numerous different plants. At Salvatierra and Mendoza, however, where stone was a precious commodity, the inhabitants used locally available resources and made grinding implements from clay. Some of these yielded large amounts of starch from plant processing, while others yielded no starch at all. A more thorough investigation of form and function as revealed by residues may prove an interesting future project.

Table 4
Phytoliths observed from artifact residues.

Site/cat. #	Tool	*Zea mays* cob[a]	*Cucurbita* sp. rind[b]	Panicoideae	Chloroideae	Oryzoideae	Bambusoideae	Cyperaceae	*Heliconia*	Asteraceae	Marantacae seed	Arecaceae	*Celtis*	Arboreal	Notes
Mendoza															
LM 99-1864	Grater frag.	x		x	x	x	x	x	x		x	x	x	x	
LM 99-1865	Grater frag.	x									x				Burnt phytoliths, limited data[c]
LM 99-1866	Grooved clay mano	x									x				Burnt phytoliths, limited data[c]
LM 99-1867	Flat clay mano	x									x				Burnt phytoliths, limited data[c]
LM 01-4189	Colander frag.	x		x	x	x		x	x		x	x		x	
LM 01-5307	Colander frag.	x													Few phytoliths
LM 02-291	Burnt residue														Limited data[c]
LM 02-294	Burnt residue								x		x	x			*Heliconia* dominates, most burnt
Salvatierra															
SAL 04-2-2698	Colander frag.														Limited data[c]
SAL 04-2-7447	Colander frag.														Limited data[c]
SAL 04-4-3597	Colander frag.			x	x					x		x		x	
SAL 05-4-2743	Colander frag.														Limited data[c]
SAL 05-4-2745	Colander frag.														No data
SAL 06-2-796	Colander frag.														No data
SAL 06-2-1658	Colander frag.	x		x	x	x		x		x	x	x		x	
SAL 06-2-1671	Clay mano	x	x	x				x			x	x	x	x	Burnt phytoliths
SAL 06-4-2750	Colander frag.	x		x	x	x	x	x	x	x		x		x	
SAL 06-10-1642	Grater frag.	x		x	x			x	x	x	x	x		x	Burnt phytoliths
Bella Vista															
BV2 08-2-939	Quartz wedge														No phytoliths recovered
BV2 08-2-940	Granitic axe											x		x	Few phytoliths
BV2 08-4-286	Handstone														No data
BV2 08-4-287	Handstone	x		x	x	x		x	x			x	x	x	Burnt phytoliths
BV2 08-4-288	Dioritic axe			x		x		x				x	x	x	
BV2 08-4-289	Quartz wedge														No phytoliths recovered
BV2 08-5-374	Quartz flake			x								x		x	Few phytoliths, some burnt
BV2 08-5-375	Quartz flake					x						x		x	Few phytoliths, some burnt
BV3 09-L-49	Handstone	x		x								x	x	x	

[a] Cob bodies: wavy-top rondels, ruffle-top rondels, and IRPs (irregular with projections).
[b] Scalloped spheres.
[c] No phytolith data on taxa other than *Zea mays*, *Cucurbita*, or Marantaceae.

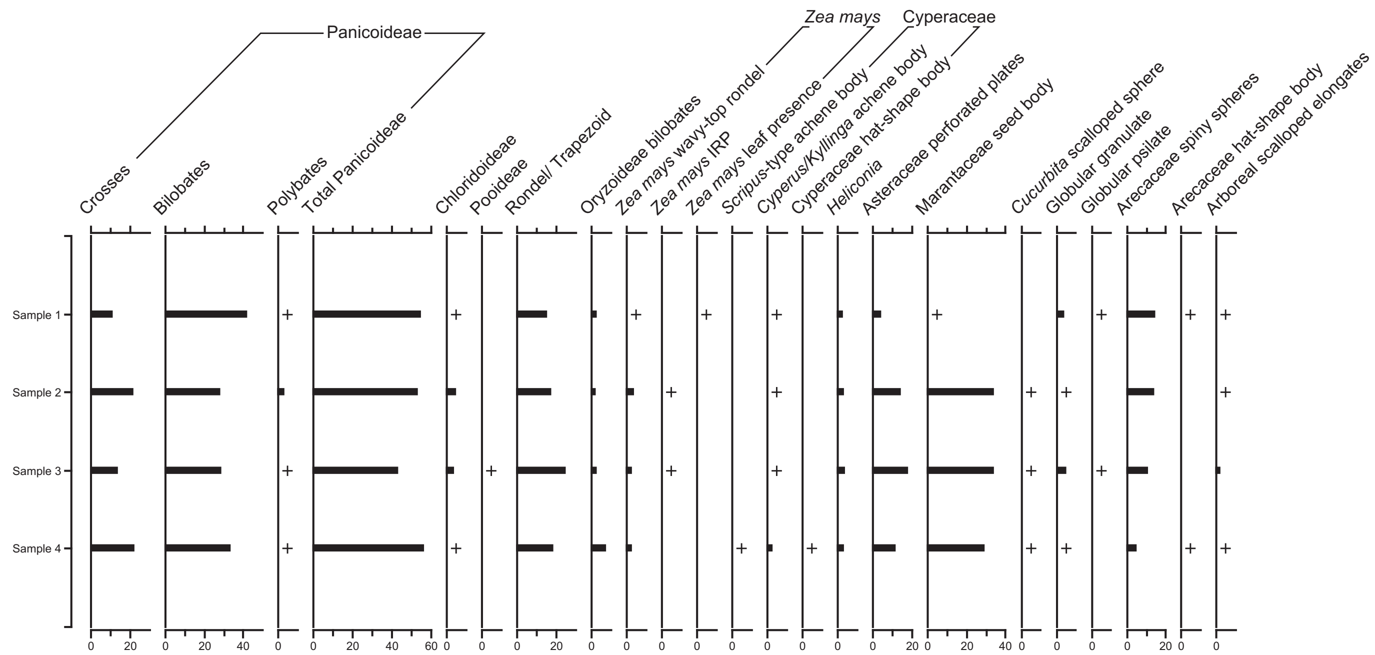

Fig. 6. Summary diagram of phytolith types for each sediment sample from Loma Mendoza. Samples along the Y axis represent different contexts, not stratigraphic order. Abundance of small phytoliths (Fraction A, <50 μm: all Poaceae including *Zea mays*, Cyperaceae, *Heliconia*, globular granulate and psilate, and Arecaceae) was calculated as the percentage of the Fraction A sum (200 grains). Abundance of large phytoliths (Fraction C, >50 μm: Asteraceae, Marantaceae, *Cucurbita*, and arboreal faceted elongates) was calculated as the percentage of the sum of Fraction A plus Fraction C. Where phytoliths are present but in low abundance (less than 2%) they are indicated by '+'. Diagram created using C2 software (Juggins, 2010).

Ceramic graters have been proposed as processing tools for grating manioc, essentially fulfilling the roll of grater-boards (Jaimes Bentancourt, 2010; Nordenskiöld, 1913; Rydén, 1964). Manioc was tentatively identified on two of the graters from Mendoza, but maize was much more commonly encountered. Chili pepper was another possible item processed on the rough surface. In comparison, the four quartz chips from Granja de Padre, thought to be grater-board chips, yielded limited results: a starch grain of maize, several other unidentified starch grains, but no evidence of manioc. Elsewhere in the Neotropics, starch analyses of proposed grater-board chips have resulted in a similar lack of expected manioc starch (Berman and Pearsall, 2008; Perry, 2004, 2005). But as these and other researchers (DeBoer, 1975; Dole, 1994) have noted, ethnographic literature shows that grater-boards were made from many materials other than stone chips, such as palm spines, animal teeth, shell, and ceramic, as noted above, and they were often used for many things other than manioc.

Colanders were by far the most productive class of artifact tested in terms of taxonomic variety. They are most often associated with the production of *chicha*, made from fermented maize or manioc. For example, Castillo (1906 [1670]: 328) observed that the Mojo Indians: "covered their beer jars with a perforated dish, and that they placed on sticks vessels with holes which they filled with chewed yuca. They poured over it water which trickled drop by drop." (translation Métraux, 1948:74). We did find maize and manioc on these artifacts, but we also recovered yam and other taxa. It is clear that these artifacts were used in the preparation of many different foods.

The diversity of species recovered demonstrates the benefits of using multiple types of analyses. Certain taxa visible in one data set were completely absent from another. When data sets overlapped, they provided not only supporting evidence, but often different perspectives on plant processing and use.

7. Summary and conclusions

This study provides the first hard evidence for the use of numerous domesticates and other plants at habitation sites in the southern and eastern Llanos de Mojos in the Bolivian Amazon. The use of multiple methods allowed us to identify a wide range of crops, including maize, manioc, squash, peanuts, cotton, yams, and palms. The ubiquity of maize, and to a smaller extent, manioc, indicate that these crops provided the bulk of carbohydrates for the inhabitants. These staples were supplemented by many other taxa, both cultivated and collected. These plants not only added variety to the diet, but also provided various essential nutrients, and served as risk insurance against one or more crops failing. Other botanical remains, such as those from cotton, provide evidence for craft production activities.

Settlement data indicates that the population density in southern and eastern Llanos de Mojos was much higher in the past than it is today (Lombardo and Prümers, 2010). Our archaeobotanical data show that the pre-Hispanic inhabitants made use of a well-developed and diverse suite of cultivars and other plant resources to sustain their populations and support a significant level of social complexity. The Llanos de Mojos is among several areas within the Amazon Basin in which recent archaeological research is revealing significant population density and a high degree of complex social organization (Balée and Erickson, 2006; Heckenberger and Neves, 2009; Heckenberger et al., 2008; McEwan et al., 2001; Parssinen et al., 2009; Rebellato et al., 2009; Roosevelt, 1999; Schaan, 2000). Archaeobotanical studies such as this provide the foundation for reconstructing the economic basis of these societies.

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Appendix. Supplementary data

Supplementary data related to this article can be found online at doi:10.1016/j.jas.2011.09.021

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