



## Review papers

## Holocene paleoagrostological impressions from the Eastern Chaco Region (Argentina)

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## ABSTRACT

The Chaco region is a sedimentary basin limited by the Andes and the Brazilian craton. This South American subtropical plain is defined as large alluvial fan sediments of the main rivers that were repeatedly deposited during the late Quaternary under diverse climatic conditions. The Eastern Chaco is characterized by semideciduous forests intermingled with extensive palm-savannas, with gallery forests being the common vegetation along the banks of the main rivers and their western tributaries. These vegetation patterns of the Chaco have been proposed to be the result of the Pleistocene–Holocene alluvial dynamics of the plain as well as of the intensive migration of fluvial belts of the main rivers.

Although no data are available on the paleoflora of the Chaco plain, plant fossil impressions are found in the banks of the low Bermejo River, which flows along the Eastern Chaco phytogeographic region. Here, we analyze paleoagrostological impressions recovered from two fossiliferous localities in order to provide insights into the environmental history of the Chaco region. Sixty complete Poaceae spikelet impressions were studied morphologically and compared with extant Chaco grass species. For each fossil spikelet, 11 morphological characters were described and statistically analyzed. All spikelets were found to belong to the Panicoideae subfamily, and some have consistent morphological features with this subfamily; hence, we assign them to the extant genera *Cenchrus*, *Echinochloa*, *Hymenachne*, and *Paspalum*. These impressions are the first floral remains found in the Eastern Chaco and collectively suggest that environmental and climatic conditions from these sediments corresponded to a subtropical humid climate and that vegetation was similar to the extant Eastern Chaco flora.

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## 1. Introduction

The Chaco region is a large South American subtropical plain that extends across northern, central, and eastern Argentina, southwestern Paraguay, and southeastern Bolivia. This low-lying region corresponds to an extremely large sedimentary basin limited by the Andes and the Brazilian region. The Paraguay and Paraná rivers flow along the eastern boundary, in association with four other principal rivers (Parapetí, Pilcomayo, Bermejo, and Juramento-Salado) that cross the Chaco plain from northwest to southeast (Iriondo, 1987).

Geologically, this area is included in the Chaco–Pampean Geological Province (SAGyP and CFA, 1995), and was defined as large alluvial fan sediments of the principal rivers (Iriondo, 1993; Argollo and Iriondo, 2008), which were repeatedly deposited over the Precambrian Brazilian shield (Prado, 1993) during the late Quaternary and under diverse climatic conditions (Iriondo, 1987). In some cases, these sediments were transported by wind (as in the southern Chaco plain) or by both wind and hydrological agents (as in the northern area of the Chaco plain); (Prado, 1993). In the latter case, aeolian deposits with suspended material originated in Andean mountainous regions were then transported by rivers, and, in some circumstances, were deposited in lacustrine environments (Molina, 2006). In the study area, two fluvial terraces appeared at the top of the sequences: the oldest one, probably in the Late Pleistocene, and the most recent one in postglacial times (Iriondo and Paira, 2007). Sedimentary sequences were generated following alternate humid climatic conditions (that favored the presence of stabilizing surfaces and pedogenesis) and dry climatic conditions (with more erosive and dispersal sedimentary elements; Iriondo and Paira, 2007). Stable surfaces with local characteristics related to wind and/or fluvial deposits can be observed (Molina, 2006).

In plain regions, hygrophilous and semideciduous forests coexist with savannas and dry shrublands. The forests are mainly composed of Amazonian species, whereas the other communities are composed of Chaco species. Thus, phytogeographic boundaries are uncertain and forests have been repeatedly included and excluded from the Chaco vegetation (Placci and Holz, 2004). These vegetation patterns have been proposed to be the result of the Pleistocene–Holocene alluvial dynamics of the plain and of the intensive migration of fluvial belts of the main rivers (Morello and Matteucci, 1999). In addition, climatic variations during the last 18,000 years would have had an effect on the floristic composition and structure of Chaco seasonal forests (Biani et al., 2004).

The Quaternary paleoflora of northern Argentina has been poorly studied, with no data being available for the paleoflora of the Chaco plain. The reconstruction of Quaternary paleoenvironments may contribute to the understanding of the role of the Quaternary episodes in shaping plant distributions and evolution in the Eastern Chaco. Here, we analyze paleoagrostological records found in the Bermejo river alluvial plains (Formosa, Argentina) and compare them to anatomical features of extant grasses from this region.

## 2. Study area

The study site is located in Villa Escolar (26° 36' S and 58° 40' W, Laishi department, Formosa province), in the lower Bermejo River Basin (Fig. 1). This site is included in the Eastern Chaco, which extends roughly up to the eastern half of Formosa province (Ginzburg and Adámoli, 2006). According to Iriondo (2010), two main geological

formations are found in the Bermejo River cliffs from the study area: the Río Bermejo Formation (Upper Pleistocene) and the La Fidelidad Formation (Holocene). The former, the flooded sector of the Bermejo River cliffs, developed during the dry and cold ages of the Last Glacial Maximum. This Formation correlates with the Tezanos Pinto, Urundel, and Fortín Tres Pozos formations. It is mainly composed of thin sediments that differ in the relative percentage of sand, lime, and clay (Iriondo, 2010), with absolute dating ( $C^{14}$  and optically stimulated luminescence (OSL)) that suggests an Upper Pleistocene–Lower Holocene age (Zurita et al., 2014). La Fidelidad Formation formed from old channels of the Bermejo River filled by avulsion of lime–clay sediments, from the Holocene until today (Iriondo, 2010).

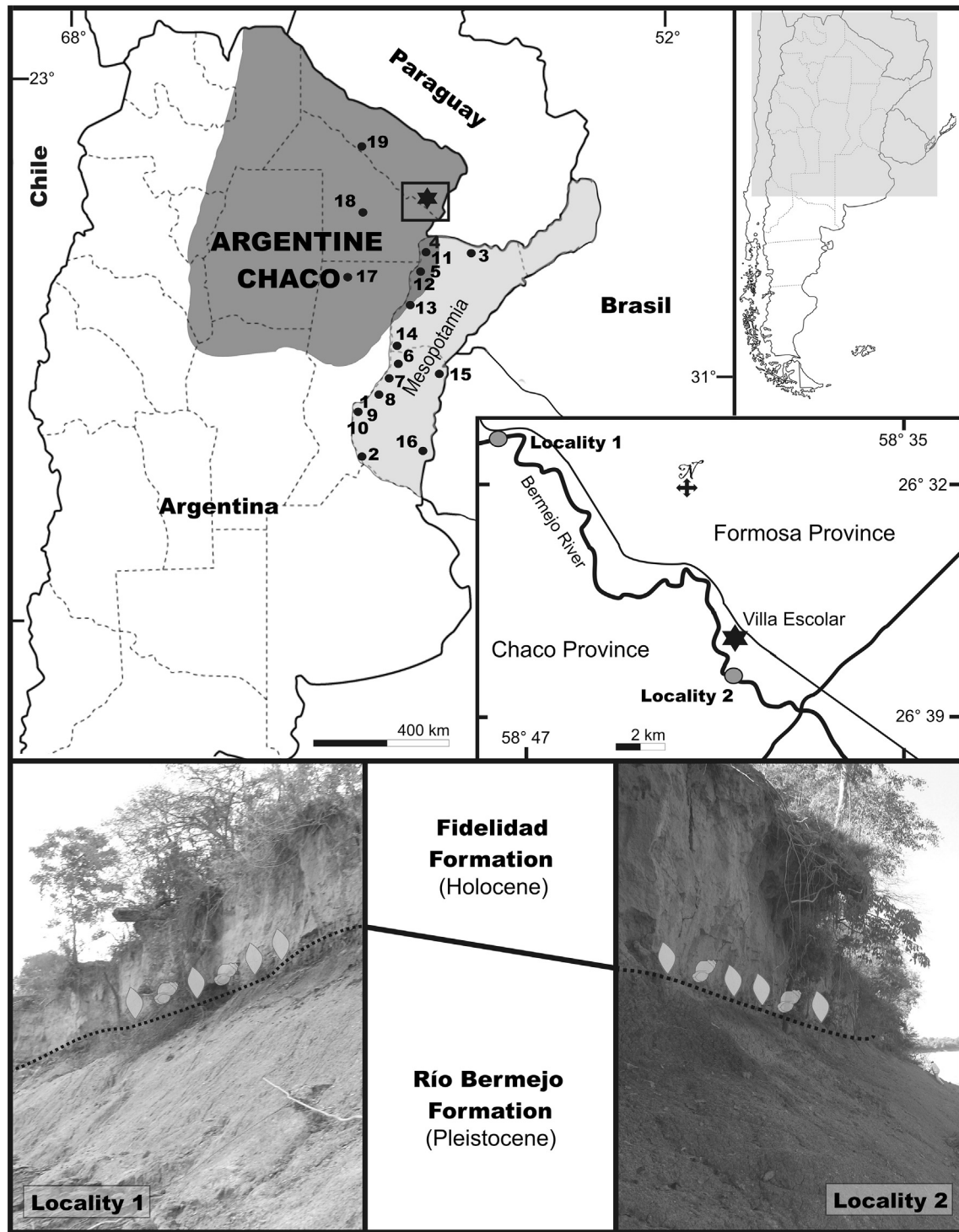
The Chacoan and Pampean regions are two of the most important arid areas of South America (along with Caatinga and Cerrado in Brazil). Their flora and fauna are closely related to the current Andean (in the west) and Amazon and Paraná (in the north and east) biotic components (*sensu* Cabrera, 1971; Cabrera and Willink, 1973; Morrone, 2001). Both regions could be considered mixed biotas that originated multiple times and adapted to xeric conditions, in a process that possibly began in the Miocene and continued during the Plio-Pleistocene (Iriondo, 1992).

The Eastern Chaco (Humid Chaco) consists of distal regions of alluvial fans of large rivers crossing the region. It is the largest district with periodic flooding rains and fluvial overflowing (Maturo et al., 2005), principally with swamp environments, crossed by old fluvial belts of rivers (Iriondo, 1992). The floods of the allochthonous rivers discharge large volumes of water across the landscape. Infiltration is scarce or null because the terrain is composed of thick silt-clays. The extremely low regional slope does not favor runoff of the excess water and, therefore, permanent and ephemeral swamps are densely covered by floating and paludal vegetation. A gallery forest usually occurs along banks of the main rivers and their western tributaries (Iriondo and Paira, 2007).

Grasslands and savannas are among the most important vegetation types in the Chaco. The grasslands developed on highlands, on sandy and wet, but rarely flooded soils. Dominant species are *Andropogon lateralis* Nees, *Schizachyrium spicatum* (Spreng.) Verter, and *Elionurus muticus* (Spreng.) Kuntze. The savanna occurs in topographically lower areas that are flooded during heavy rainfall periods. It has herbaceous vegetation alternated with woody species like *Prosopis affinis* Spreng., *Astronium balansae* Engl., and *Diplokeleba floribunda* N.E. Br.; thus, savanna takes on a rather open appearance between trees (Ginzburg and Adámoli, 2006).

## 3. Materials and methods

On recent paleontological fieldwork along the Bermejo River banks (Formosa Province, northeastern Argentina), we found large amounts of fossil impressions of plants as well as of mollusks and ostracods. Among the plant impressions, Poaceae spikelets were particularly abundant. Therefore, to provide insights into the environmental history of the region, we studied spikelet impressions found in two fossiliferous localities (Fig. 1), locality 1 (S 26° 28.21' W 58° 53.06') and locality 2 (S 26° 38.80' W 58° 39.82'). The study banks are approximately 10 m high and consist of six clearly defined levels. Locality 1 also has a thin black cap of approximately 4 cm, rich in organic matter. This level presents a high percentage of thin sediments and several impressions of leaves, stems, and caryopses, as well as pollen grains (Contreras,



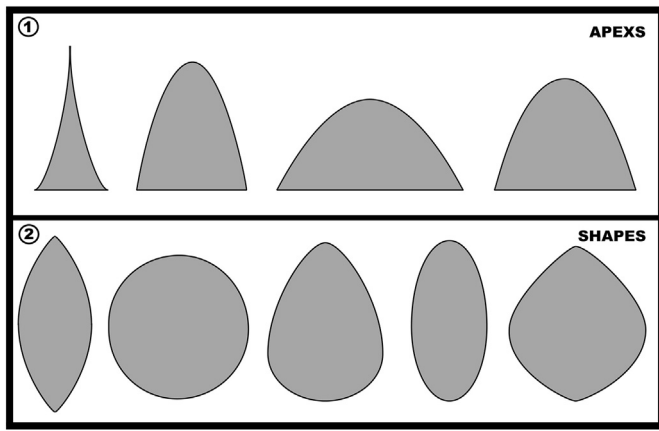
**Fig. 1.** Argentine Chaco Region and localities near the study area [Villa Escolar (Formosa)]. Some outcropping localities of the different Quaternary formations (Miño Boilini et al., 2006; Carlini et al., 2008; Iriondo, 2010; Brea and Zucol, 2011): Paraná (1, 2), Ituzaingó (3–8), Alvear (9), Tezanos Pinto (10), Toropí/Yupoi (11–14), Hernandarias (15–16), Fortín Tres Pozos (17), Urundel (18) and Fidelidad (19).

2010). Both localities belong to the Fidelidad Formation from the Holocene (Iriondo, 2010).

### 3.1. Description and analysis of spikelet impressions

Sixty complete grass spikelet impressions were described. Other kinds of grass impressions found (stems, leaves, and incomplete

inflorescences) were not included because they lack taxonomically useful characteristics. For each impression, 11 macroscopic quantitative and qualitative morphological features were analyzed using an Olympus stereomicroscope. Quantitative features include length, width, and number of observed structures (number of typical spikelet structures that can be recognized in each fossil, such as glume, lemma, and palea). Qualitative features include: spines/spiny-hairs, hairs, awns,



**Fig. 2.** 1. Apex shape (acuminate, acute, rounded and obtuse) considered follows [Carlton \(1961\)](#) and 2. Spikelet Shape (lanceolate, rounded, ovate, elliptical, and rounded-lanceolate) modified from [Lindley \(1951\)](#).

scabrous, bristles, prominent nerves, shapes and apices. Terminology of spikelet shapes (lanceolate, rounded, ovate, elliptical, and rounded-lanceolate) and of their respective apex types (acuminate, acute, obtuse, and rounded) follows [Lindley \(1951\)](#) and [Carlton \(1961\)](#) ([Fig. 2](#)). All spikelet impressions were deposited at the Museo de Ciencias Naturales de Villa Escolar (PBVE-F) with the following acronyms: Locality 1: PBVE-F 1–28, PBVE-F 32–46, PBVE-F 56–60; Locality 2: PBVE-F 29–31, PBVE-F 47–55.

### 3.2. Comparisons and taxonomy

Comparative species of extant grasses were chosen according to regional floras ([Molina, 2006](#)), and species distributed in the study area were primarily considered. Representative specimens for each of these species ([Table 1](#)) were selected from the herbarium of the Instituto de Botánica del Nordeste (CTES). Fifteen of them were further selected for morphological studies ([Table 1](#)). Three spikelets per specimen were measured in different positions. In spikelets with two florets, fertile anthoecia were considered. In diclinous species, with male and female/hermaphrodite florets, both of them or only the spikelet that reflected the studied variables was analyzed. Furthermore, both views (view 1 (mostly dorsal upper glume) and view 2 (mostly dorsal

lemma/lower glume), the principal views present in impression specimens) were measured in each spikelet, because differences between views depend on the structures on a spike side. However, six spikelets of *Cenchrus echinatus* were analyzed without specifying the view because they were enveloped by bristle involucre and, therefore, both views were similar ([Table 2](#)).

### 3.3. Statistical analyses

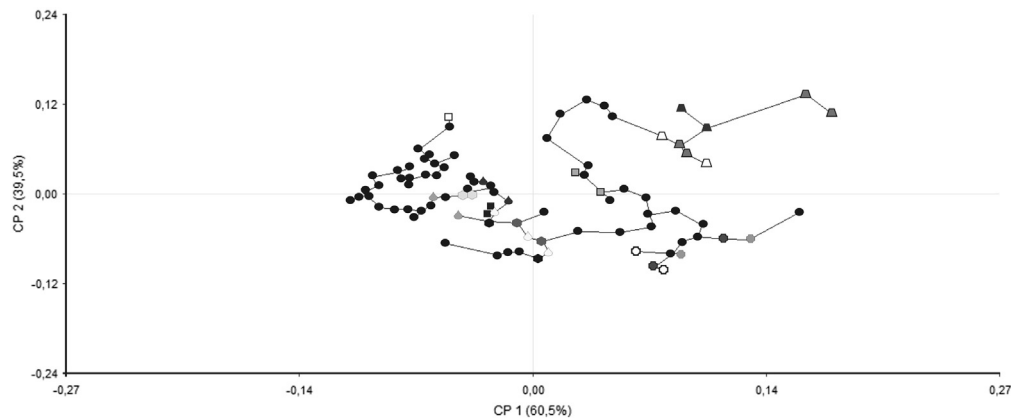
Statistical analyses to test our hypotheses about the taxonomic affinity of impressions was performed using Infostat software ([Infostat, 2012](#)). Eleven morphological characteristics of spikelet impressions and spikelets of extant species were analyzed. Quantitative characteristics were analyzed with a principal components analysis (PCA), which was calculated on the Euclidean matrix estimated from the resulting standardized data set. Qualitative characteristics were analyzed with a principal coordinates analysis (PCoA) using a simple matching similarity index. In addition, qualitative and quantitative characteristics were analyzed together using a generalized procrustes analysis (GPA) to obtain a consensus ([Gower, 1975](#)).

## 4. Results

Overall morphological similarity between fossils and herbarium spikelets of the Chacoan species indicates that the impressions belong to the Panicoideae subfamily, especially the Paniceae tribe.

### 4.1. Statistical analyses

GPA results showed a significant consensus (92%) between the ordinations based on qualitative and quantitative features measured on fossil imprints ([Fig. 3](#)). Principal component 1 (PC 1, 60.5%) and 2 (PC 2, 39.5%) accounted for 100% of the total variation. The first PC grouped all fossil specimens together with Paniceae species but not with Andropogoneae species. On the negative axis, spikelets showed rounded and rounded-lanceolate spikelets with a low number of structures. *Cenchrus echinatus*, *Lasiacis sorghoidea*, *Paspalum intermedium*, *Paspalum urvillei* and *Panicum mertensii* were grouped with some fossils (e. g. PBVE-F 17, PBVE-F 18, PBVE-F 19, PBVE-F 21, PBVE-F 30, PBVE-F 31, PBVE-F 47, PBVE-F 50 and PBVE-F 60). In contrast, spikelets scoring positively on PC 1 were lanceolate and had a high number of structures, and prominent and scabrous nerves. *Hymenachne amplexicaulis* fell close to some fossils (e. g. PBVE-F 1, PBVE-F 2, PBVE-F 3, PBVE-F 4, PBVE-F 6, PBVE-F 11, PBVE-F 36, PBVE-F 42 and PBVE-F 44), whereas *Echinochloa*



**Fig. 3.** Procrustes comparison of the qualitative and quantitative characteristics of the impressions and extant species: spikelet impressions (●), extant reference spikelets of *Andropogon lateralis* (▲), *Cenchrus echinatus* (□), *Echinochloa crus-galli* (■), *Echinochloa crus-pavonis* (●), *Elionurus muticus* (▲), *Erichloa punctata* (■), *Hymenachne amplexicaulis* (○), *Lasiacis sorghoidea* (○), *Panicum mertensii* (■), *Paspalum intermedium* (▲), *Paspalum urvillei* (▲), *Sacciolepis villoides* (△), *Setaria geniculata* (●), *Sorghastrum setosum* (△), and *Urochloa adspersa* (●).



*crus-galli* and *Echinochloa crus-pavonis* were similar to an awned fossil (PBVE-F 40). The other Paniceae species are grouped with the remaining fossils in the center of the plot. Along the second PC, Paniceae spikelets were grouped with all impressions, and Andropogoneae species were separated from fossils and other current grasses, as in PC 1.

#### 4.2. Systematic description

Fossil characteristics and statistical analyses were used to identify fossil specimens to genus and species levels. Twenty-eight fossils were assigned to the extant genera *Hymenachne*, *Cenchrus*, *Echinochloa* and *Paspalum*.

**Family** Poaceae

**Subfamily** Panicoideae Link

**Tribe** Paniceae R. Br.

**Genus** *Hymenachne* P. Beauv., Ess. Agrostogr: 48, 165. 1812.

**Species** *Hymenachne amplexicaulis* (Rudge) Nees, Fl. Bras. Enum. Pl. 2 (1): 276. 1829.

**Material** View 1: PBVE-F 1, PBVE-F 2. View 2: PBVE-F 3, PBVE-F 4, PBVE-F 5, PBVE-F 6, PBVE-F 11, PBVE-F 36, PBVE-F 42 and PBVE-F 44 (Plate I, 1–4).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Locality 1, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Impression lanceolate, with acuminate apices, prominent and scabrous along the nerves, and spiny-hair-like garments along the edge toward apex. Two different views present: upper glume (view 1) and lower glume and lower lemma (view 2). View 1, spikelets 5.4 mm (5.2–5.6 mm) long and 1.7 mm (1.6–1.9 mm) wide. Three spikelet structures present (upper glume and part of lower glume and lemma). Upper glume lanceolate, with acuminate apices, 3-nerved and scabrous. Nerve extension parallel all throughout glume surface. Lateral nerves slightly concave. Part of lower glume in basal position. A larger structure (lemma) behind the upper glume. Only lemma edges are observed. View 2, spikelets 5.3 mm (4–6.3 mm) long and 1.9 mm (1.3–2.5 mm) wide and with two structures (lemma and lower glume). Lemma lanceolate, with acuminate apices, 3–5 nerved, prominent and scabrous. Lower glume in basal position, less than or equal to half of the length of the lemma; lanceolate-ovate, acuminate apices, 3-nerved and scabrous.

**Comments** Based on the features of the structures, two spikelet views are distinguished, which facilitates characterization of the complete spikelet. These fossils have a close affinity with the extant species *Hymenachne amplexicaulis* because they have similar spikelet structures and arrangements. The extant genus *Hymenachne* is characterized by lanceolate, acuminate, and dorsiventrally compressed spikelets. The nerves of the spikelets are prominent and usually scabrous. It has two unequal glumes. The lower glume is 1–3-nerved and much shorter than the spikelet. The upper glume is lanceolate-acuminate, with 3–5 nerves, and slightly shorter than the lower lemma. The lower lemma is lanceolate-acuminate or tubulated, with five scabrous nerves (Molina, 2006). Three species of *Hymenachne* are present in the Chaco region (Molina, 2006), with *Hymenachne amplexicaulis* (Plate I, 11–12) being the most similar to the fossils. It is characterized by subequal, acuminate or caudate upper glume and lower lemma with scabrous nerves (Molina, 2006). The impressions have slight differences from extant spikelets in length and width, since they are somewhat larger than extant species.

**Genus** *Cenchrus* L., Sp. Pl. 2: 1049. 1753.

**Species** *Cenchrus echinatus* L., Sp. Pl. 2: 1050. 1753.

**Material** PBVE-F 14, PBVE-F 15, PBVE-F 16, PBVE-F 17, PBVE-F 18, PBVE-F 19, PBVE-F 20, PBVE-F 21, PBVE-F 50 and PBVE-F 60 (Plate I, 5–6).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Localities 1 and 2, near Villa Escolar town, Formosa, Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Spikelets with bristles rounded due to the involucre. Involucres with wide bristles and a basal ring of long, thin, bristle-like spines. In some cases the involucre enclose all the spikelets. Spikelets 2.6 mm (between 2–3.4 mm) long and 2.18 mm (2–2.6 mm) wide. There is only one structure, which cannot be determined due to the presence of involucre. Only the acute apex is observed. In some fossils (PBVE-F 17, PBVE-F 50, and PBVE-F 60), part of the pedicel is conserved. Above the pedicels, bristles inserted radially; length almost equal to or exceeding the spikelet length.

**Comments** The impressions have marked involucre with a ring of long spiny bristles that emerge from the spikelet base. Current specimens of *Cenchrus* have two florets, solitary or grouped in fascicles surrounded by an involucre of bristles. The bristles are welded into a disk at the involucre base or enclosed almost all along their length (Molina, 2006). The species *Cenchrus echinatus* (Plate I, 13) has an involucre with numerous erect spines, slightly wider at the base, and a basal ring of bristles. The involucre has 2–6 spikelets of 5–6 mm in length (Molina, 2006). Fossil involucre have some similarities to this current species; however, impressions show a spikelet shorter than extant spikelet due to the fossilization of the involucre, which spreads widely in current specimens. The morphological characteristics of the spikelets cannot be compared because this information was lost during the fossilization process.

**Genus** *Echinochloa* P. Beauv., Ess. Agrostogr. 53, 161, pl. 11 (2). 1812.

**Species** *Echinochloa crus-pavonis* (Kunth) Schultes, Mantissa 2, 269. 1824.

**Material** PBVE-F 40 (Plate I, 7).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Locality 1, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Spikelets lanceolate, with acuminate apex, scabrous nerves, spiny-hispid margins, awned (4 mm long). Spikelet 8 mm long including awn, 4 mm excluding awn, and 1.5 mm wide. Two spikelet structures present. Upper glume 5-nerved, prominent and scabrous. Three nerves run from the base toward the apex. The remaining two nerves cross toward the apex from the middle of the glume. The lemma has a straight awn and is behind the upper glume.

**Comments** Only the upper glume view of this species was observed. In the current genus *Echinochloa* sp. the spikelets are ovate, ellipsoid or lanceolate. This genus has a short pedicel and two glumes. Upper glume is ovate or lanceolate, awnless, mucronate, acuminate or awned. It is scabrous between the nerves (3–9). Spinules with or without papillose base (Molina, 2006). Spikelets of *Echinochloa crus-pavonis* are lanceolate and awned. They have unequal glumes. Upper glume is acuminate with five prominent nerves and two inconspicuous nerves from the middle to the apex. In addition, this glume has spinules on the ribs and hairs between them. It is

larger than lower glume. Lower lemma is similar to upper glume, with awn (2–15 mm long) (Molina, 2006). Comparing the living species with the impressions and taking into account the upper glume characteristics, the fossil specimen has more affinity with *Echinochloa crus-galli* than with the remaining species of genus (Plate I, 14).

**Genus** *Paspalum* L., Syst. Nat., ed. 10, 2: 855. 1759.

**Species** *Paspalum* Sp. (1)

**Material** PBVE-F 27, PBVE-F 29, PBVE-F 30 and PBVE-F 31 (Plate I, 8).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Localities 1 and 2, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Spikelets with wide elliptical outline, acute apexes and acute bases. Margins sometimes with thin and short hairs. All fossils with circular petioles. Length: 2.9 mm (2.2–3.4 mm) long and width: 2 mm (2–2.1 mm). Two subequal structures present. Upper glume elliptical, without central vein. Lemma behind the upper glume.

**Species** *Paspalum* Sp. (2)

**Material** PBVE-F 32 and PBVE-F 33 (Plate I, 9).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Locality 1, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Spikelets ovate-lanceolate, with acuminate apexes, margins with soft hairs. Length: 3–4 mm and width: 1.9–2.5 mm. Two subequal spikelet structures present. The first one, the lemma, with a prominent mid-rib and two submarginal nerves extending along the structure. The second structure may be upper glume and is behind the lemma.

**Species** *Paspalum* Sp. (3)

**Material** PBVE-F 47 (Plate I, 10).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Locality 2, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Spikelet ovate, acute apex; without hairs at edges; length: 4.2 mm and width: 3.8 mm. There are two subequal spikelet structures. Upper glume rounded-ovate, without middle vein or gross margins. Lemma behind the upper glume. There is a caryopsis between structures.

**Comments** Seven fossil impressions have similar characteristics to the extant genus *Paspalum* sp (Plate I, 15–16). Due to the wide diversity of the genus in the region, a credible species assignment can be a difficult challenge. However, these impressions have high similarity to the structures observed in this genus. *Paspalum* spikelets are orbicular, ellipsoid or obovoid, dorsiventrally compressed, flat-convex or concave-convex. Lower glume is absent, but when present, it is rudimentary. Upper glume is as long as the spikelet or shorter, sometimes absent. Lower lemma is present and as long as the spikelet. Lower palea is present or absent. Higher anthoecia with variable consistency. Lemma margins usually rolled on palea, with the back positioned against the rachis; palea of equal size and

consistency to lemma (Molina, 2006). Three types of fossils of this genus are found. They present only two distinct subequal structures. The bigger one is the lemma. Without lower glume. Fossils of *Paspalum* sp. (1) have thin hairs but it is not possible to elucidate the element where they come from. *Paspalum* sp. (2) differs from previously described *Paspalum* specimens in that the lemma in the latter has a prominent central vein and two convex submarginal veins, whereas *Paspalum* sp. (3) has no middle vein or hairs. The latter is similar to the other two impressions.

**Genus Incertae sedis** Morphotype A

**Material** View 1: PBVE-F 8, PBVE-F 9 and PBVE-F 10. View 2: PBVE-F 7 (Plate II, 1–2).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Locality 1, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Spikelets elliptical, acute apexes, scabrous nerves, long spiny-hair on the margin. View 1, 4.1 mm (4–4.3 mm) long and 2 mm wide. Three structure types are present. Upper glume elliptical, acute apexes apparently 3-nerved and scabrous. All fossils are badly preserved. Lemma behind the upper glume. Part of the lower glume is observed at the base of PBVE-F 8. View 2, 4.6 mm long and 1.9 mm wide. With two structure types. Lemma elliptical, acute apex, 3-nerved and scabrous. Smaller structure like lower glume at the base of the lemma, rounded-lanceolate, acute apex and 3-nerved.

**Comments** These spikelets are similar to several spikelets of genera in the Paniceae tribe, especially in the characteristics of their structures.

**Genus Incertae sedis** Morphotype B

**Material** PBVE-F 12, PBVE-F 13, PBVE-F 37, PBVE-F 46, PBVE-F 53 and PBVE-F 55 (Plate II, 3–4).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Localities 1 and 2, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Impressions lanceolate, with acuminate apexes and scabrous nerves, 5.05 mm (4.6–5.6 mm) long and 2.35 mm (1.8–3 mm) wide. These fossils did not conserve many characters of their spikelet structures, but scabrous and garments are distinguished.

**Comments** The incomplete set of characters for these spikelets hinders their systematic placement. Shape and venation are similar to those in several genera in the Paniceae tribe.

**Genus Incertae sedis** Morphotype C

**Material** PBVE-F 22, PBVE-F 23, PBVE-F 24, PBVE-F 25, PBVE-F 26 and PBVE-F 59 (Plate II, 5–6).

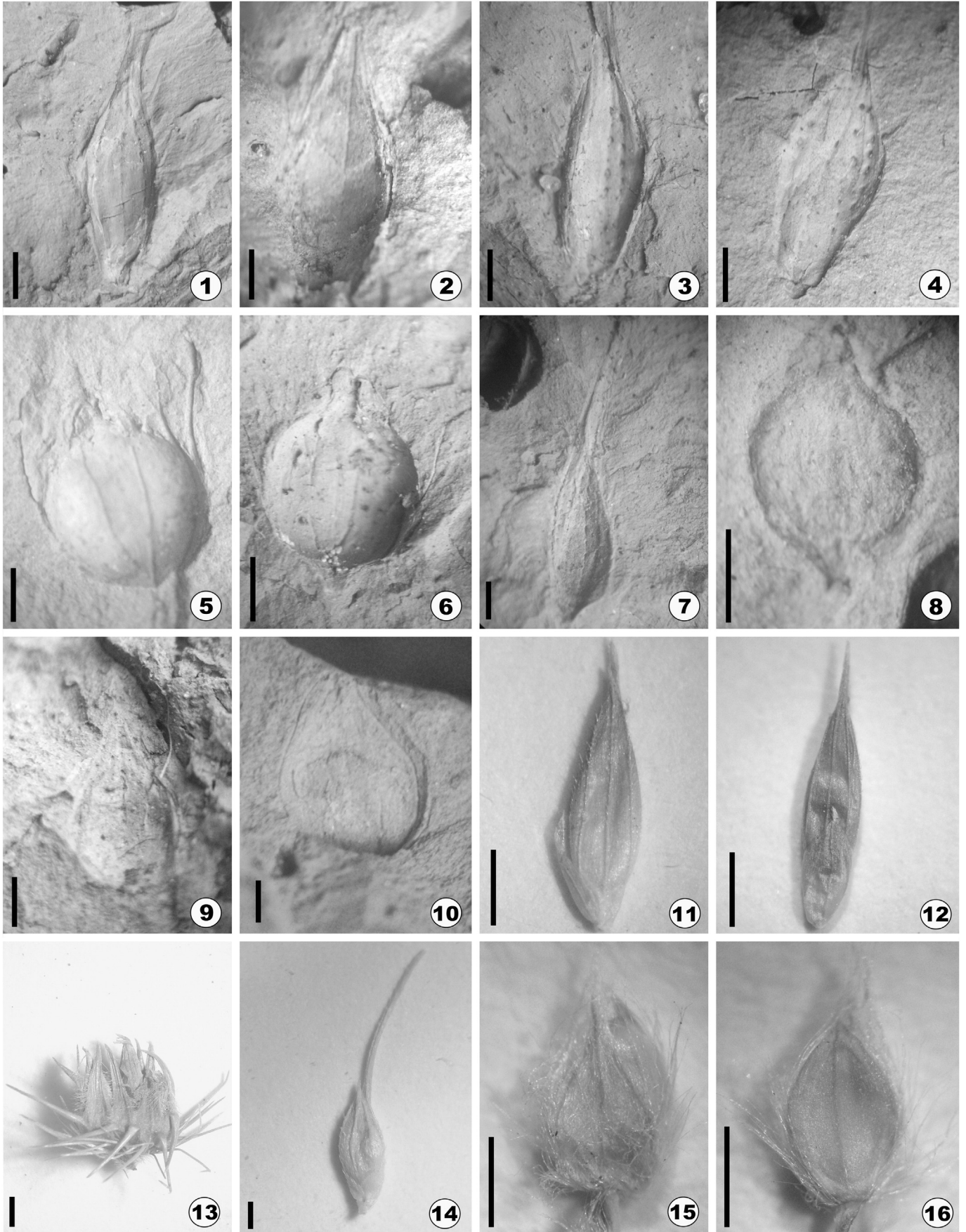
**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Locality 1, near Villa Escolar town, Formosa Argentina.

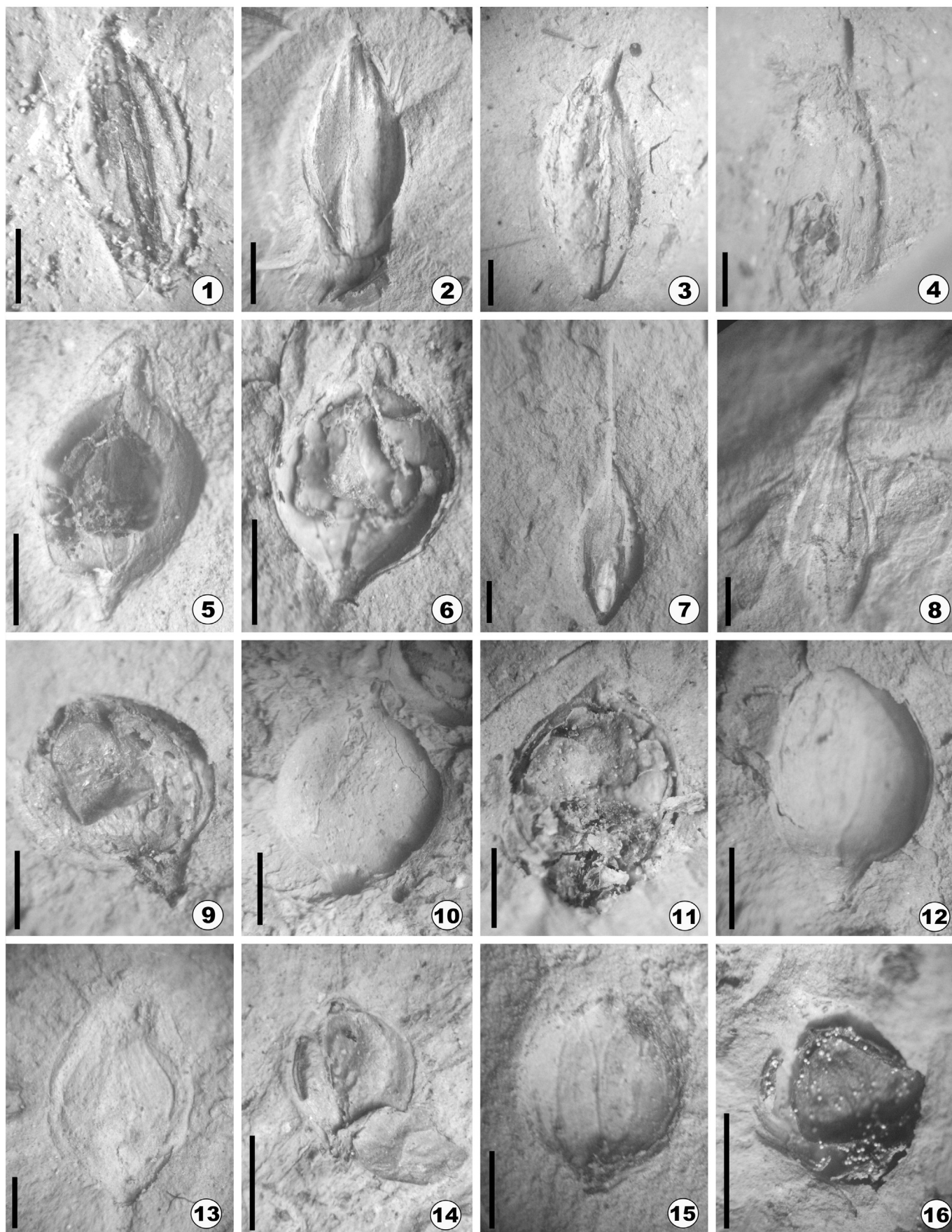
**Stratigraphy and age** Fidelidad Formation (Holocene).

**Plate I. Spikelet impressions:** impression of *Hymenachne amplexicaulis*: 1–2. Upper glume (PBVE-F 1 and PBVE-F 2). 3–4. Lower glume and lower lemma (PBVE-F 3 and PBVE-F 4). Impressions of *Cenchrus echinatus*: 5–6. Spikelets with involucre (PBVE-F 14 and PBVE-F 17). Impression of *Echinochloa crus-galli*: 7. Upper glume (PBVE-F 40). Impression of *Paspalum* sp.: 8. Upper glume of *Paspalum* sp. 1 (PBVE-F 29). 9. Lemma of *Paspalum* sp. 2 (PBVE-F 32). 10. Upper glume of *Paspalum* sp. 3 (PBVE-F 47). Extant spikelets: *Hymenachne amplexicaulis* (Rudge) Ness (Shinini, N° 9258): 11. Upper glume. 12. Lower glume and lower lemma. *Cenchrus echinatus* L. (Perez, N° 216): 13. Spikelet with bristles. *Echinochloa crus-galli* (Kunth) Hitchc (B. G. Piccinini and A. L. García, N° 1035): 14. Upper glume. *Paspalum urvillei* Steud. (Digiacomo, N° 9): 15. Lower Lemma 16. Upper Glume. Scale = 1 mm.









**Plate II.** Morphotype spikelet impressions. 1–2. Morphotype A (PBVE-F 7 and PBVE-F 8). 3–4. Morphotype B (PBVE-F 12 and PBVE-F 53). 5–6. Morphotype C (PBVE-F 22 and PBVE-F 24). 7–8. Morphotype D (PBVE-F 43 and PBVE-F 45). 9–10. Morphotype E (PBVE-F 57 and PBVE-F 58). 11. Morphotype F (PBVE-F 28). 12. Morphotype G (PBVE-F 48). 13. Morphotype H (PBVE-F 51). 14–15. Morphotype I (PBVE-F 35 and PBVE-F 34). 16. Morphotype J (PBVE-F 39). Scale = 1 mm.



**Description** Spikelets with bristles, rounded-lanceolate, with acute or obtuse apices, 2.98 mm (2.7–3 mm) long and 2 mm (1.7–2.2 mm) wide. There are two structures: a central structure shorter than the remaining spikelets, and the other structure behind the central one. The pedicels are preserved.

**Comments** The gross morphology of the spikelets is consistent with that of the Paniceae tribe, but it is not possible to assess relationships.

**Genus Incertae sedis** Morphotype D

**Material** PBVE-F 41, PBVE-F 43 and PBVE-F 45 (Plate II, 7–8).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Locality 1, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Elliptical, awned spikelets, 7.23 mm (7.1–7.4 mm) long and 2.86 mm (2.6–3 mm) wide. The characteristics of the structures were not clear enough for taxonomic identification.

**Comments** These spikelets are fragmentarily preserved and have only a few characters that are informative for genus placement. However, they are consistent with awned genera of the Paniceae tribe.

**Genus Incertae sedis** Morphotype E

**Material** PBVE-F 49 PBVE-F 52, PBVE-F 54, PBVE-F 57 and PBVE-F 58 (Plate II, 9–10).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Localities 1 and 2, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** La Fidelidad Formation (Holocene).

**Description** Spikelets rounded, obtuse or rounded apices, obtuse or rounded bases, with a small pointed termination as part of the petiole; 2.98 mm (2.8–3.1 mm) long and 2.28 mm (2–2.5 mm) wide. There is only one visible structure.

**Comments** It is difficult to make a reliable generic determination based on the partially preserved spikelets. However, overall shapes are similar to those of extant species of the subfamily Panicoideae, especially the tribe Paniceae.

**Genus Incertae sedis** Morphotype F

**Material** PBVE-F 28 (Plate II, 11).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Locality 1, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Spikelet ovate, acute at apex; slightly acute at the base; 3 mm long and 2 mm wide. There are two spikelet structures, one larger than the other. Nerves and other characteristics are not distinguished.

**Comments** The spikelet is partially observable, and is the only fossil impression with those traits. However, spikelet structures are similar to structures of genera of the Paniceae tribe.

**Tribe Incertae sedis**

**Genus Incertae sedis** Morphotype G

**Material** PBVE-F 48 and PBVE-F 56 (Plate II, 12).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Localities 1 and 2, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Specimens elliptical and ovate, with obtuse and acute apices; 3 and 2.5 mm long and 2.1 and 1.5 mm wide.

Structures not clearly distinguished, but elements like bristles and part of the pedicel are observed at the base.

**Comments** The lack of structure characteristics hinders assignment to any known species. However, the shapes of structures and bases of these fossils are similar to those of taxa of the subfamily Panicoideae.

**Genus Incertae sedis** Morphotype H

**Material** PBVE-F 51 (Plate II, 13).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Locality 2, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Spikelet elliptical, acute apex and thick margins; 4.1 mm long and 3 mm wide. Two spikelet structures of equal size are present.

**Comments** Details for taxonomic classification are insufficient, but both structures are consistent with descriptions for the subfamily Panicoideae.

**Genus Incertae sedis** Morphotype I

**Material** PBVE-F 34 and PBVE-F 35 (Plate II, 14–15).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Locality 1, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** Fidelidad Formation (Holocene).

**Description** Spikelets round-lanceolate, 3.2 and 2.7 mm long and 2 and 1.5 mm wide. There are two structures: the first structure is round-lanceolate, with acute and obtuse apices, without veins or other characteristics. In PBVE-F 34, the second structure is shorter than first one and covers part of the spikelet; with prominent veins. In PBVE-F 35, the second structure is displaced as a result of fossilization.

**Comments** These spikelets have characteristics common to several genera of the subfamily Panicoideae, but they cannot be assigned to a genus due to the conditions of their structures.

**Genus Incertae sedis** Morphotype J

**Material** PBVE-F 38 and PBVE-F 39 (Plate II, 16).

**Repository** Museo de Ciencias Naturales of Villa Escolar, Formosa, Argentina.

**Locality** Locality 1, near Villa Escolar town, Formosa Argentina.

**Stratigraphy and age** La Fidelidad Formation (Holocene).

**Description** Spikelets ovate or rounded-lanceolate, with obtuse or acute apices; 3 and 2.4 mm long and 2.1 and 1.9 mm wide. There are subequal structures. The first one is smaller than the second. They have no other visible features.

**Comments** The gross morphology of the spikelets is consistent with that of the Panicoideae subfamily, but there is insufficient information to determine them.

## 5. Discussion

### 5.1. Paleoflora remains of Eastern Chaco

The impressions of grass spikelets described here are the first floral remains found in the Eastern Chaco. These impressions were highly variable in morphology, but all of them can be assigned to the subfamily Panicoideae. This subfamily can be distinguished by spikelets that are usually paired, solitary or grouped in fascicles. They have two florets and equal glumes that are lower or higher than the florets. The lower glume is sometimes reduced or absent. The absence of both glumes is rare. The rachilla is articulated below the glumes that fall with the grain (Molina, 2006).

The Chaco Region is distributed in the subtropical zone of the continent, where Panicoideae and Chloridoideae are the best represented grass subfamilies (Molina, 2006). We found that 79 of 358 extant grass species mentioned for the Chaco region (Maturo et al., 2005; Molina, 2006) occur in the study area and mainly belong to the subfamily Panicoideae, demonstrating the high abundance of this subfamily in the region. In addition, our analysis shows that the impressions are highly similar to some extant Chacoan grass species, especially those of the subfamily Panicoideae. Twenty eight of the studied impressions were morphologically similar to spikelets of the extant genera *Cenchrus*, *Echinochloa*, *Hymenachne* and *Paspalum*. These results suggest that Panicoideae members may also have been abundant in the recent past.

Furthermore, these fossils increase our knowledge about the South American paleoagrostological records from the Quaternary. The few Poaceae records known to date are a petrified culm from Ituzaingó Formation (Brea and Zucol, 2007; Brea et al., 2013) and the pre-Holocene Poaceae thorny bamboo cf. *Guadua* from Peruvian Amazonia (Olivier et al., 2009). Therefore, the spikelet impressions here described not only represent the first paleofloristic information about the environmental history of the Eastern Chaco region but also contribute with new information to South American paleoagrostological records.

In the Chaco and neighboring Mesopotamian region, Quaternary fossils of plants, invertebrates, and vertebrates are found in different geological formations, and most of them are from the Pleistocene. The climate in the Mesopotamian region was different from that inferred for the Chaco region (Erra et al., 2013). In the Chaco-Pampean plains, the climate was relatively cold and arid during the Pleistocene, with a predominance of open environments, and mainly represented by southern faunal elements. By contrast, the Mesopotamian region was warmer and more humid, and characterized by the coexistence of Pampean fauna with intertropical and tropical fauna (Carlini et al., 2004; Erra et al., 2013).

In the Chaco region, Pleistocene megamammals were found in Fortín Tres Pozos and Río Bermejo formations located in southern-central Eastern Chaco (Tonni and Scillato-Yané, 1997; Prevosti et al., 2005; Zurita et al., 2009; Soibelzon et al., 2010). These mammals are representatives of the Pampa-Patagonian fauna and were probably adapted to open and relatively cold environments (Zurita et al., 2009). Holocene invertebrates were found together with plant impressions in La Fidelidad Formation: crustaceans (Crabs), bivalves (*Diplodon* spp.), gastropods (*Ampullaria* sp.), and ostracods (*Cytheridella*, *Cyprideis*, *Cypridopsis* and *Candona*) (Contreras, 2010; Zamudio, 2013). The ostracod association would indicate environments of continental influence and low-energy freshwater systems (Zamudio, 2013).

A detailed Neogene record has been described from the Mesopotamian region (Fig. 1), where the Paraná Formation is one of the best characterized formations. This formation includes the principal Neogene marine deposits (Middle Miocene–Lower Pliocene) of the Chaco–Paranaense region (Fernández Garrasino and Vrba, 2000). Indeed, it presents a continental sequence overlain by a marine sequence. The continental sequence is composed of floristic two elements belonging to the tropical and subtropical floristic elements (Zucol et al., 2004; Brea and Zucol, 2011).

The paleobotanical records of the Ituzaingó Formation (Pliocene–Pleistocene; Iriondo, 2010) are based on pollen, leaf impressions, and cuticle and wood petrifications (Zucol et al., 2004; Brea and Zucol, 2011; Franco and Brea, 2013). Toropí/Yupoí Formations underlie Ituzaingó Formation, both from the Lujanian s.s. (between 50 ka and 35 ka BP) faunal age. Their composition is a faunal mixture of Brazilian and typical Pampas elements (Miño Boilini et al., 2006). The only plant remains are stems of *Equisetum* L. found at the base of Yupoí Formation (Lutz and Gallego, 2001). Recent analyses of phytolith assemblages from both formations showed a predominance of grass phytoliths, with dominance of pooids,

chloridoids, and panicoids, and the presence of only a few morphotypes of forest indicator taxa (Erra et al., 2013). The Alvear Formation is another Mesopotamian unit (late Pliocene ca. 1.95 to 2.6 Ma; Candela et al., 2007). It is characterized by the presence of paleofaunas, indicating the dominance of semiarid and arid climates (Carlini et al., 2008). The only record of fossil plants described corresponds to phytolith assemblages, indicating the presence of a paleocommunity dominated by palms (Arecaceae) and grasses (Poaceae) (Zucol and Brea, 2005). The Hernandarias Formation is correlated with the Lujanense subfloor, and carries Pleistocene fossil vertebrates (Carlini et al., 2008). Phytolith assemblages from the Tezanos Pinto Formation (36 ka to 85 ka BP) are characterized by a cold to warm–temperate steppe with xeric conditions at the baseline and with humid temperate episodes mainly at the middle and upper sections (Erra et al., 2011).

Holocene impressions are scarce in Argentina. The only records are from the Pampas (Frenguelli, 1920; Gutiérrez Téllez et al., 2006) and Patagonian (Frenguelli and Parodi, 1941; Burry et al., 2006; Sottile et al., 2012) regions.

## 5.2. Comparison of composition and paleoenvironments between localities

The highest diversity of grass types occurs in Locality 1, where 80% of the spikelets (48 impressions) were found and identified as *Hymenachne*, *Cenchrus*, *Echinochloa*, *Paspalum* sp.1, *Paspalum* sp. 2 and morphotypes A–J. Of these, *Hymenachne*, *Echinochloa*, *Paspalum* sp. 2 and morphotypes A, C, D, F, I, and J occur only in Locality 1. The remaining 20% (12 spikelets) were found in Locality 2 and were identified as *Cenchrus*, *Paspalum* sp.1, *Paspalum* sp. 3, and morphotypes B, E, G, and H. *Paspalum* sp.3 and morphotype H are exclusive of locality 2. Furthermore, stems of *Equisetites* sp. similar to those of extant *Equisetum giganteum* were found in both localities (Contreras and Lutz, 2014). A larger number and diversity of eudicot leaves were found in Locality 2 (eight different leaves) than in Locality 1 (four leaves). They correspond to tree and herbaceous species but they remain undetermined (Contreras, 2010).

Differences between the two studied localities allow us to make inferences about the past plant communities in the region. The species composition inferred from both localities suggests a mosaic of grassland and humid savanna. In the present, the Eastern Chaco landscape is characterized by a high heterogeneity of environments (Maturo et al., 2005). Forests grow in higher and drier places of the Chaco landscape and are surrounded by marshes, humid savannas, grasslands, palm forests, and humid forests (Gómez and Kees, 2005). Grassland communities are mostly represented by species with the C<sub>4</sub> photosynthesis pathway (Molina, 2006). Both localities were dominated by panicoid grasses and these taxa generally prefer warm–temperate and humid climates. For example, *Hymenachne amplexicaulis* grows along rivers, streams, flooded places, and wetlands of the Eastern Chaco. *Echinochloa crus-galis* is hydrophilic and grows along rivers, wetlands, and muddy areas. Finally, *Cenchrus echinatus* and the genus *Paspalum* are typical of warm–temperate zones (Molina, 2006).

The fact that the studied impressions are mostly attributable to C<sub>4</sub>-grass genera suggests that environmental and climatic conditions in the recent past were similar to the present-day conditions in the Eastern Chaco. These results are in line with evidence from palynology (Contreras, 2010) and paleofauna (Zamudio, 2013) from both localities, which also indicate that the depositional paleoenvironment conditions of the Bermejo River sediments corresponded to a subtropical humid climate similar to the current conditions in the Eastern Chaco. Therefore, our results suggest that not only the paleoenvironmental conditions were similar to the current ones, but also the vegetation may have remained similar at least with respect to its dominant floristic elements.

## 6. Conclusions

Paleoagrostological impressions add new information about the environmental history of the Eastern Chaco. The species composition observed in both localities suggests that a mosaic of humid savanna and grassland occupied the landscape and that past recent climate was sub-tropical humid, comparable to the current climate in the region. Ongoing studies of sediments will contribute to our knowledge about the evolution of the vegetation from the Chaco phytogeographic region.

## Acknowledgments

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## Appendix A

**Table 1**

Species of the Chaco region selected for geographic distribution, including species from the study area and herbarium species selected for anatomical studies (\*).

Herbarium species	CTES-herbarium
Chloridoideae subfamily	
<i>Chloris cantherae</i> Arechav.	***
<i>Chloris halophila</i> Parodi var. <i>Humilis</i>	***
<i>Chloris pycnothrix</i> Trin.	***
<i>Cynodon dactylon</i> (L.) Pers. var. <i>Dactylon</i>	***
<i>Eragrostis lugens</i> Nees	***
<i>Eustachys distichophylla</i> (Lag.) Nees	***
<i>Leptochloa virgata</i> (L.) P. Beauv	***
<i>Sporobolus indicus</i> (L.) R. Br.	***
<i>Sporobolus pyramidatus</i> (Lam) Hitchc.	***
Panicoideae subfamily	
<i>Acroceras zizainoides</i> (Kunth) Dandy*	(Henkel, N°5288)
<i>Andropogon lateralis</i> Ness*	(Caponio and Sulekic., N° 112)
<i>Anthraenathia lanata</i> (Kunth) Benth.	***
<i>Axonopus fissifolius</i> (Raddi) Kulhm*	(Morrone, Deginani and Giraldo-Cañas, N° 1785)
<i>Cenchrus echinatus</i> L*	(Perez, N° 216)
<i>Cenchrus pilcomayensis</i> (Mez) Morrone*	(Bordon and Nicora, N° 91)
<i>Coleataenia priontis</i> (Nees) Soreng*	(Vergara, N°7)
<i>Digitaria phaeothrix</i> (Trin.) Parodi Var. <i>adusta</i> (Nees) Rúgolo*.	(Pedersen, N° 6972)
<i>Digitaria insulris</i> (L) Fedde*	(Deginani and Denham, N° 1974)
<i>Echinochloa crus-pavonis</i> (Kunth) Schult.*	(Piccinini and García, N° 1035)
<i>Echinochloa crus-galli</i> (L.) P. Beauv*.	(Lopez and Vanni. N°130)
<i>Eliunurus muticus</i> (Spreng.) Kuntze*	(Quarin, N° 3490)
<i>Eriochloa montevidensis</i> (Nees) Griseb.*	(Schulz, N° 10861)
<i>Eriochloa punctata</i> L. Desv. ex Ham.*	(Deginani and Denham, N° 1959)
<i>Hymenachne amplexicaulis</i> (Rudge) Ness*	(Shinini, N° 9258)
<i>Lasiacis sorghoidea</i> (Desv. ex Ham.) Hitchc. & Chase*	(Schulz, N° 16946)
<i>Paspalum alnum</i> Chase*	(Quarín, N° 577)
<i>Paspalum conjugatum</i> P. J. Bergius*	(Honfi, N° 4)
<i>Paspalum denticulatum</i> Trin.*	(Deginani and Denham, N° 1929)
<i>Paspalum inaequivalve</i> Raddi.	***
<i>Paspalum intermedium</i> Munro ex Morong & Britton*	(Martínez Crovetto, N° 29)
<i>Paspalum plicatulum</i> Michx	***
<i>Paspalum simplex</i> Morong ex Britton	***
<i>Paspalum stellatum</i> Humb. & Bonpl. Ex Flüggé.	***
<i>Paspalum urvillei</i> Steud.*	(Digiaco N° 9)
<i>Sacciolepis vilvoldes</i> (Trin.) Chase*	(Arbo, Schinini, Vanni and Pellegrini, N°6595)
<i>Schizachyrium microstachyum</i> (Desv. ex Ham.) Roseng. B. R. Arrill. & Izag.	***
<i>Setaria fiebrigii</i> R. A. W. Herm.	***
<i>Setaria hassleri</i> Hack.*	(Alisioni et al., N° 775)
<i>Setaria lachnea</i> (Nees) Kunth	***
<i>Setaria macrostachya</i> Kunth	***
<i>Setaria magna</i> Griseb.*	(Jiménez and Marín, N° 23)
<i>Setaria parviflora</i> (Poir.) Kerguelén*	(Schinini, N° 26272)
<i>Setaria vulpiseta</i> (Lam.) Roem. & Schult	***
<i>Sorghastrum setosum</i> (Griseb.) Hitchc*	(Digiaco, N° 18)
<i>Sporobolus indicus</i> (L.) R. Brown*	(Novara, N° 11422)
<i>Steinchisma laxa</i> (Sw.) Zuloaga	***
<i>Strophostachys mertensii</i> (Roth) Zuloaga & Morrone*	(Schulz, N° 7630)
<i>Urochloa adspersa</i> (Trin) R. D. Webster*	(Deginani and Denham. N° 1942)



**Table 2**

Analysis of spikelets of extant species. Measured characteristics are shown in both views. Length and width are expressed in means (mm). Length (Lg), width (Wt), number of structures (NE), shapes (Sh) (0 lanceolate, 1 ovate, 2 elliptical, 3 round, and 4 round-lanceolate), scabrous (Sc), awn (Aw), bristles (Bt), prominent nerves (PN), spines (Sp), apices (Ap) (0 acuminate, 1 acute, 2 obtuse, and 3 rounded) and hairs (Hr). Measured including awn (\*).

Species	Lg	Wt	NE	Sh	Sc	Aw	Bt	PN	Sp	Ap	Hr
<b>Tribe Andropogoneae</b>											
<i>Andropogon lateralis</i> female view 2	10*	0.9	2	0	0	1	0	0	0	0	1
<i>Andropogon lateralis</i> female view 1	10*	0.9	1	0	0	1	0	0	0	0	1
<i>Andropogon lateralis</i> male view 2	6	1	2	0	0	0	0	0	0	0	1
<i>Andropogon lateralis</i> male view 1	6	1	1	0	0	0	0	0	0	0	1
<i>Elionurus muticus</i> hermaphrodite view 1	7.23	1.6	2	0	0	0	0	0	0	0	1
<i>Elionurus muticus</i> hermaphrodite view 2	7.23	1.6	1	0	0	0	0	0	0	0	1
<i>Sorghastrum setosum</i> view 2	6.58*	0.9	1	0	0	1	0	0	0	0	1
<i>Sorghastrum setosum</i> view 1	6.58*	0.9	2	0	0	1	0	0	0	0	1
<b>Tribe Paniceae</b>											
<i>Cenchrus echinatus</i>	5.8	4.2	1	4	0	0	1	0	0	0	0
<i>Echinochloa crus-galli</i> view 2	5.7*	1.33	3	0	1	1	0	1	1	0	0
<i>Echinochloa crus-galli</i> view 1	4	1.33	3	0	1	1	0	1	1	0	0
<i>Echinochloa crus-pavonis</i> view 2	6.33*	1.1	3	0	1	1	0	1	1	0	0
<i>Echinochloa crus-pavonis</i> view 1	3.2	1.1	3	0	1	1	0	1	1	0	0
<i>Erichloa punctata</i> view 1	3.97	1	2	0	0	0	0	0	0	0	0
<i>Erichloa punctata</i> view 2	4	1	1	0	0	0	0	0	0	0	0
<i>Hymenachne amplexicaulis</i> view 2	4.13	1	2	0	1	0	0	1	1	0	0
<i>Hymenachne amplexicaulis</i> view 1	4.13	1	3	0	1	0	0	1	1	0	0
<i>Lasiacis sorghoidea</i> view 2	4	1.97	3	2	0	0	0	0	0	2	0
<i>Lasiacis sorghoidea</i> view 1	4	1.97	2	2	0	0	0	0	0	2	0
<i>Paspalum intermedium</i> view 1	2.1	1	1	2	0	0	0	0	0	2	1
<i>Paspalum intermedium</i> view 2	2.1	1	2	2	0	0	0	0	0	2	1
<i>Paspalum urvillei</i> view 2	2	1.1	2	1	0	0	0	0	0	1	1
<i>Paspalum urvillei</i> view 1	2	1.1	1	1	0	0	0	0	0	1	1
<i>Sacciolepis vilvoidea</i> view 2	3	1	2	0	0	0	0	1	0	1	0
<i>Sacciolepis vilvoidea</i> view 1	3	1	2	0	0	0	0	1	0	1	0
<i>Sacciolepis vilvoidea</i> lateral view	3	1.17	3	1	0	0	0	1	0	1	0
<i>Setaria parviflora</i> view 2	2.1	1.1	2	1	0	0	0	0	0	1	0
<i>Setaria parviflora</i> view 1	2.1	1.1	4	1	0	0	0	0	0	1	0
<i>Stephostachys mertensii</i> view 2	4	2	3	2	0	0	0	0	0	1	0
<i>Stephostachys mertensii</i> view 1	3.97	2	3	2	0	0	0	0	0	1	0
<i>Urochloa adspersa</i> view 2	3.13	1.43	3	2	0	0	0	1	0	0	0
<i>Urochloa adspersa</i> view 1	3.13	1.43	2	2	0	0	0	1	0	0	0

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