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Guadua zuloagae sp. nov., the First Petrified Bamboo Culm Record from the Ituzaingó Formation (Pliocene), Paraná Basin, Argentina

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• *Background and Aims* The anatomical characterization and morphology of *Guadua zuloagae* nov. sp. (Poaceae–Bambusoideae) culm was determined. This material was collected at the Toma Vieja fossil locality, Paraná basin, Argentina. This fossil culm is the first record of Bambusoideae in sediments of the Pliocene from the Ituzaingó Formation. The studied specimen was compared with the taxa of the Bambusoideae sub-family, especially with the American woody bamboos and others taxa that have woody culms, including *Arundo*, *Thysalonaena* and *Gynerium*.
• *Methods* The material was preserved by siliceous cellular permineralization, and it was prepared for microscopic examination by surface polishing and thin sections. The morphology and anatomy of this new species were described. The estimated height, critical buckling height and safety factor were calculated on the basis of the fossil bamboo diameter using the formula of Niklas. The relationship and comparison with the nearest living relatives (NLRs) are discussed.
• *Key Results* Well-preserved petrified culm with internodes and nodes from the Pliocene of Argentina provides the basis for the description of a new fossil bamboo, *Guadua zuloagae*. The results of the anatomical analysis of the fossil bamboo showed a great affinity with the extant species *Guadua angustifolia* and constitute the first evidence of petrified bamboo culm.
• *Conclusions* The new fossil bamboo culm constitutes the only fossil record, preserved as permineralized by silicification, in the world. This fossil record indicates that the genus *Guadua* was more widespread in the past than today. Discovery of *G. zuloagae* allows the presence of a Bambusoideae understorey in the mixed forests described for the Ituzaingó Formation to be inferred. The climatic conditions inferred from fossil bamboo and sedimentary deposits indicate a temperate-warm, humid climate.

Key words: Paleobotany, petrified culm, morpho-anatomical description, Poaceae, Bambusoideae, Bamboo, *Guadua zuloagae*, Pliocene, Argentina.

INTRODUCTION

The description and systematic assignment of petrified bamboo culm to Bambusoideae are discussed. This fossil culm is the first record of Bambusoideae in sediments of the Pliocene from the Ituzaingó Formation, Paraná basin, Argentina (Figs 1 and 2).

The Paraná River basin has been the object of several geological and vertebrate fossil studies (Frenguelli, 1920; Iriondo and Rodriguez, 1973; Aceñolaza and Sayago, 1980; Iriondo, 1998; Cione *et al.*, 2000; Herbst, 2000; Aceñolaza, 2004). The vertebrate records correspond to diverse taxa with marine, continental, aquatic and terrestrial habitats (Cione *et al.*, 2000).

The paleobotanical records of the Ituzaingó Formation are extremely scarce, and are based on studies of palynomorphs, fossil leaves, cuticles and fossil woods (Anzótegui, 1974, 1980; Lutz, 1979, 1991, 1993; Anzótegui and Lutz, 1987; Caccavari and Anzótegui, 1987; Anzótegui and Acevedo, 1995; Brea and Zucol, 2000; Zucol *et al.*, 2004; Zucol and Brea, 2005).

The identification of the extant woody bamboos is based principally on vegetative characters since most of them

have long vegetative periods with a short reproductive stage (Judziewicz *et al.*, 1999). Furthermore, studies referring to the anatomy of extant bamboo culms are known (Metcalfe, 1960; Liese 1980, 1998; Sekar and Balasubramanian, 1994; Liese and Grosser, 2000; Londoño *et al.*, 2002; Rúgolo de Agrasar and Rodríguez, 2003). To date, the fossil record of the Bambusoideae sub-family is based on pollen grains, leaf impressions and phytoliths (Berry, 1929; Strömberg, 2005; Worobiec and Worobiec, 2005).

A new fossil species of Bambusoideae based on culm fragments is herein described. This description is based on morphological and anatomical features of a permineralized culm of 21·10 cm in length and 3·00–3·50 cm in diameter. The morphology and anatomy of this fossil specimen present a combination of diagnostic features and allow recognition of a new species from the Pliocene in the Paraná Basin, *Guadua zuloagae* sp. nov. This fossil was assigned to the Bambusoideae sub-family and shares a great number of characters with the extant species *Guadua angustifolia*.

Taking into account ecological and distribution characteristics of the nearest living relatives (NLRs), paleogeographic and paleoecological characteristics of its distribution were analysed.

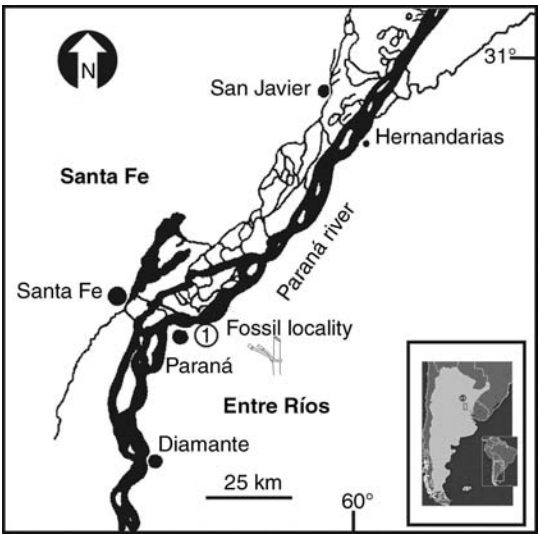* For correspondence. E-mail cidmbrea@infoaire.com.ar

FIG. 1. Location map showing the fossil locality (1), Entre Ríos province, Argentina.

Stratigraphic and sedimentological setting of the fossil flora

The fossil bamboo was collected from the lower part of the Ituzaingó Formation (Fig. 2). This sedimentary unit of fluvial origin was formally recognized by D'Orbigny (1842) as one of the Tertiary Guarani horizons ('*Tertiare Guaranien*'). This term was defined by De Alba (1953), accepted and subsequently used. However, it was Herbst (1971) and Herbst *et al.* (1976) who characterized it lithologically, giving its vertical and horizontal extension, and who defined it as Formation.

This deposit appears in the western riverside cliff of the Paraná River, from the north of Corrientes province in the city of Ituzaingó to the city of Goya, and from there to the south until the north-west of the city of Paraná, Entre Ríos province (Herbst, 2000; Anis *et al.*, 2005). In the Argentine sub-soil, it extends over the west of Corrientes and Entre Ríos up to the latitude of the city of Paraná, to the east of Chaco and almost all of Santa Fé, to the east of Córdoba and to the north of Buenos Aires provinces (Herbst, 2000).

This formation is composed of sands and sandstones with different indurations, with a granulometry that ranges from fine to coarse sands, occasionally whitish, yellowish conglomerates and, sometimes, brown-reddish and dark brownish conglomerates. Dark grey and greenish silty lens intercalations are frequent among the sands (Iriondo and Rodríguez, 1973; Aceñolaza and Sayago, 1980; Herbst and Santa Cruz, 1985; Iriondo, 1998; Herbst, 2000). The main sedimentary structure is tangential cross-bedding.
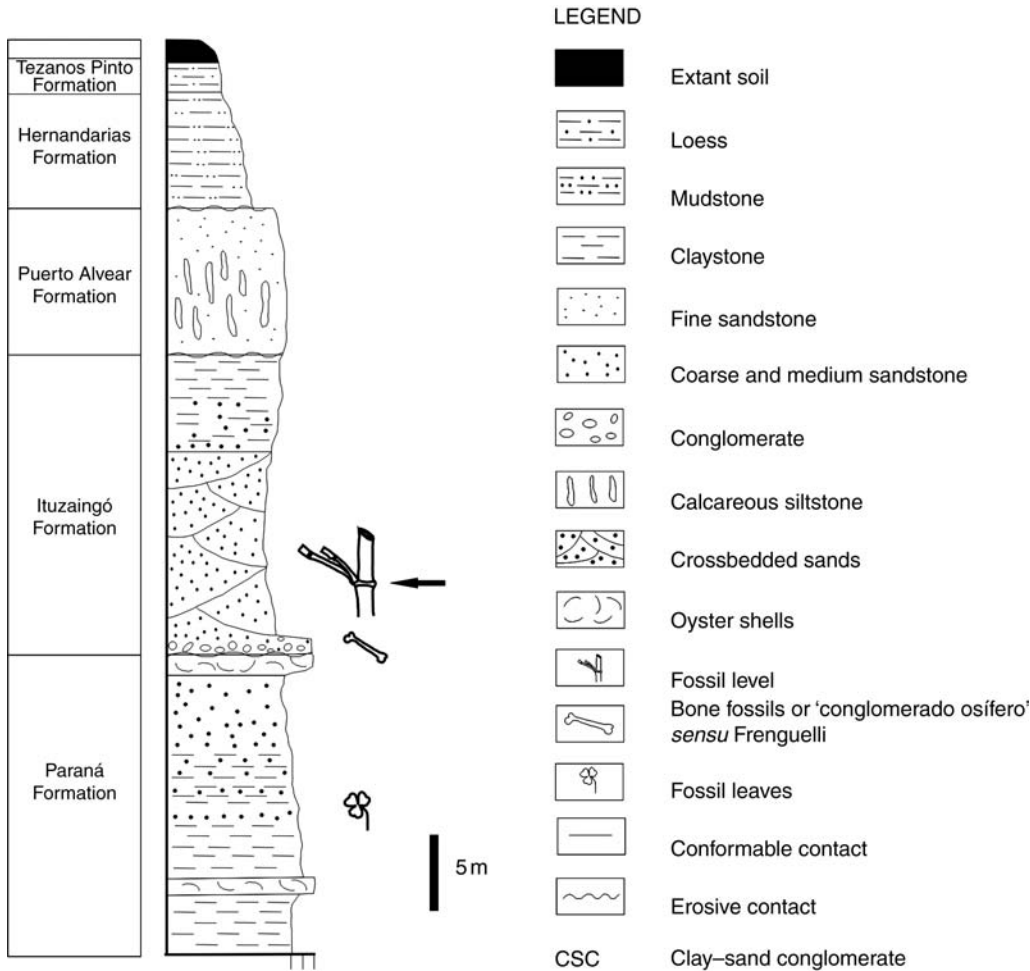

FIG. 2. Schematic profile of the Late Cenozoic in the riverside cliffs by the Paraná River, in the region of Toma Vieja. The arrow indicates the fossil level in the Ituzaingó Formation (modified from Aceñolaza, 1976).

Troughs and planar bedding are also found, and low-angle ripple cross-laminations of fluvial origin are recognized towards the top of each stratum (Anis *et al.*, 2005).

In the Entre Ríos province, the Paraná Formation (Middle–lower Upper Miocene) lies disconformably upon the bone fossils or '*conglomerado osífero*'. The most conspicuous feature of this formation is the abundant and diverse molluscan assemblages (Fig. 2). This is overlain by Frenguelli's (1920: 80–89) conglomerate with bones ('*conglomerado osífero*') characterized by abundant marine, continental, aquatic and terrestrial vertebrate remains. This stratum is the uppermost unit of the Paraná Formation (Fig. 2). Upon this, the Ituzaingó Formation rests disconformably, with the typical ochre, white and red fine sands intercalated with silt (Fig. 2). Cione *et al.* (2000) deduced that most of the fauna present in the '*conglomerado osífero*' have affinity for the Chasicoan and/or Huayquerian mammal age (SALMA – South American Land Mammals). They concluded that the fauna may be as young as Early Pliocene or as old as Late Miocene, or that the Ituzaingó Formation base may be as old as the Tortonian–Messinian (Late Miocene) (Cione *et al.*, 2000).

The sand of the Ituzaingó Formation is recycled from Mesozoic Gondwanan aeolian deposits; it is composed almost exclusively of quartz (Iriondo, 1998; Herbst, 2000). This fluvial unit was deposited by the divagation of the Paleoparaná River under warm and humid climatic conditions (Iriondo, 1996).

The Ituzaingó Formation has a fossil floral record in the form of palynomorphs, leaf impressions, cuticles and fossil woods. The fossil woods have been assigned principally to the Anacardiaceae (Lutz, 1979) and Mimosaceae families (Lutz, 1991). The palynological record shows the presence of the Sapotaceae, Winteraceae, Aquifoliaceae, Fabaceae, Myrtaceae, Euphorbiaceae, Ulmaceae, Malpighiaceae, Anacardiaceae, Arecaceae, Halogracaeae, Polygonaceae, Compositae, Chenopodiaceae, Poaceae, Polygalaceae and Podocarpaceae (Anzótegui, 1974; Caccavari and Anzótegui, 1987; Anzótegui and Acevedo, 1995). The cuticles and leaf impressions confirmed the presence of the Myrtaceae and Sapotaceae, and provided the first record of the Meliaceae and Lauraceae (Anzótegui, 1980). Basidiomycete (Polyporaceae) fungi were also recorded (Lutz, 1993).

The Puerto Alvear Formation (Lower Pleistocene) overlies the Ituzaingó Formation disconformably. This calcareous deposit is formed by nodules and irregular whitish horizontal and vertical plates composed of calcium carbonate (Fig. 2). It is situated beneath the Hernandarias Formation (Lower Pleistocene), which underlies the brownish fine clayey silts of the Tezanos Pinto Formation (Upper Pleistocene–Holocene). (Fig. 2)

MATERIALS AND METHODS

The specimen was collected by Dr Scalabrini from the fossiliferous level of large petrified woods located between 'El Brete' stream and 'Toma Vieja' (Báez, 1922) (Fig. 1). The fossil locality (31°42'10''S and 60°28' 45''W) is situated among the eastern riverside cliffs near the city of Paraná (Fig. 1). This material is deposited at the Museo de Ciencias Naturales y Atropológicas 'Prof. Antonio Serrano' (under the acronym 170a–c).

The fossil level (FL) is located 4 m up the '*conglomerado osífero*' (*sensu* Frenguelli, 1920: 80–89) in the typical ochre-yellowish sands at the Ituzaingó Formation (Fig. 2).

The material was preserved by siliceous cellular permineralization, and it was prepared for microscopic examination by surface polishing and thin sections. The specimen was studied with a light Nikon Eclipse E200 microscope (using $40\times$, $100\times$, $400\times$ and $1000\times$ magnification levels) and the microphotographs were taken with a Nikon Coolpix 990 digital camera. A drawn cross-section was made with a translucent camera of an Olympus SZH10 microscope.

The standardized terminology of Metcalfe (1960), McClure (1966, 1973), Judziewicz *et al.* (1999), Liese (1980, 1998), Sekar and Balasubramanian (1994), Liese and Grosser (2000), Londoño *et al.* (2002) and Rúgolo de Agrasar and Rodríguez (2003) was used to describe the fossil culm morphologically and anatomically.

Predictive models, applied to extant conifers and angiosperms, enabled the establishment of the relationship between stem diameter and height (Niklas, 1994). The correlation of these features can be used to reconstruct the height of fossil plants whose basal stem diameters are known or inferred (Niklas, 1994). Estimated height was calculated on the basis of ratio diameters observed in living plants using known stump diameters (Niklas, 1993, 1994). This approach was followed to estimate structural features of the fossil bamboo. The estimated height ($H_{est.}$) of the fossil bamboo was calculated using Niklas' formula (Niklas, 1993):

$$H_{est.} = 20.7 \, D^{0.538}$$

where D is the diameter of the culm.

The critical buckling height ($H_{crit.}$) was calculated using the following Niklas' formula (Niklas, 1992, 1994):

$$H_{crit.} = C \, (E/r)^{1/3} D^{2/3}$$

where C is the constant of proportionality (0·792), E is Young's modulus, r is the bulk density of the material (tissues) used to construct the columnar stem and D is the stem diameter. E/r is the quotient of the 'stiffness' of a material to the 'self-loading' the material engenders (Niklas, 1994). In this case, the critical height was calculated on the basis of E/r = 75·9, which corresponds to sclerenchyma tissue (Niklas, 1994). Thus, $H_{crit.} = 60·11 \, D^{2/3}$. The safety factor (SF) was obtained by dividing the $H_{crit.}$ by the estimated height (H_{est}) (Table 1). The SF, which can be taken as the ratio of the maximum loading likely to be experienced to the operational (normal) loadings on a structure, is typically based on the statistical probability that certain types of loadings will occur (Niklas, 1992).

TABLE 1. *Morphological characteristics of* Guadua zuloagae *culm and estimated values of height* (H$_{est\ 1}$), (H$_{est\ 2}$), *critical height* (H$_{crit}$) *and safety factor* (H$_{crit}$/H$_{est}$) *for the fossil bamboo*

Culm in cross-section	Circular Hollow internode Solid node Woody
Internode diameter (cm)	
External diameter	3·0–3·5
Internal diameter	1·6–1·7
Node diameter (cm)	3·5–4·5
Total length (cm)	21·1
Wall thickness (cm)	0·7–0·5
Estimated height ($H_{est.}$) (m)	3·4
Critical height ($H_{crit.}$) (m)	6·6
SF	1·9
Lower internode length (cm)	10·5
Upper internode length (cm)	9·5
Node with probable prophyll	
Probable prophyll	
Width (cm)	0·9
Height (cm)	1·2
Nodal region height (cm)	0·75
Node with bud and subsidiarybuds	
Central bud	
Width (cm)	0·9
Height (cm)	0·5
Subsidiary buds	
Width (cm)	0·2–0·5
Height (cm)	0·4
Nodal region height (cm)	0·92

RESULTS

Systematic paleobotany

Family. Poaceae (R. Brown) Barnhart 1895.

Sub-family. Bambusoideae Luerssen 1893.

Genus. Guadua *Kunth 1822.*

Type. Guadua angustifolia *Kunth 1822.*

Species. Guadua zuloagae *sp. nov.*

Holotype.
MAS Paleobot No. 170a and microscopic slides MAS Paleobot. No. 170b–c.

Repository. Museo de Ciencias Naturales y Antropológicas 'Prof. Antonio Serrano'. Stratigraphical and geological origin: Ituzaingó Formation (Pliocene), Paraná basin, Toma Vieja locality, Paraná, Entre Ríos province (31°42′10″S and 60°28′45″W)

Etymology. The specific epithet, *zuloagae*, is dedicated to Dr Fernando O. Zuloaga, an outstanding botanist who has studied different Argentinean grass groups.

Specific diagnosis. Petrified culm with conspicuous inter nodes and nodes. Circular in cross-section, woody and hollow at the internode; node solid. Nodal region delimited by the nodal line and the supranodal ridge; both more or less horizontal. Node with central bud and two subsidiary buds. Cross-sectional anatomy of the internode characterized from the outside in: epidermis consists of epidermal cells and including cells with silica bodies, probably so-called silica short cells. Hypodermis formed of 2–3 layers of sclerenchy matous cells. Cortical parenchyma homogeneous, showing 7–9 layers of thin- and thick-walled cells. The xylem of each vascular bundle shows two large metaxylem vessels. Protoxylem usually broken down to form an intercellular canal at the inner pole of each vascular bundle. Phloem con sists of sieve tubes and, in cross-section, cylindrical in form towards the outer pole of the bundle. Each vascular bundle surrounded by four sclerenchyma sheets, two located at each side of the metaxylem vessels, one around the protoxy lem and another one around the phloem. The vascular bundles associated with sclerenchyma tissue. Surrounding the hollow central cavity, a few layers with parenchyma and sclerenchyma cells were observed.

Morphological description

The culm or aerial vegetative axis has evident nodes and internodes. These are circular in cross-section, and woody and hollow, except in the node area, where they are solid (Figs 3A, and 4B and C, and Table 1). The specimen has two internodes, three nodes and one incomplete internode. Its length is 21·10 cm, with an internodal external diameter of 3·00–3·50 cm and an internodal internal diameter of 1·60–1·70 cm (Figs 3A and D, and 4D, and Table 1). The roots, rhizomes and leaves (except a possible prophyll, see below) were not preserved.

The central node has a diameter of 3·50–4·50 cm, with a probable prophyll that is 0·90 cm wide by 1·20 cm high (Figs 3C and 4A). Buds are not observed (Figs 3C and 4A, and Table 1). Externally, the lowermost boundary of the node is the nodal line (Figs 3D and 4D) and the uppermost boundary of the node is represented by the supranodal ridge (Figs 3D and 4D). The nodal line and supranodal ridge are more or less horizontal (Figs 3D and 4D). The nodal region is concave and 0·75 cm high (Figs 3D and 4D).

At the upper node, three buds are clearly observed (Figs 3B and 4B). The central bud is 0·90 cm wide by 0·50 cm high; the two subsidiary buds on both sides of the central bud measure 0·20 cm by 0·40 cm and 0·50 cm by 0·40 cm. respectively (Figs 3B and 4B). The nodal region is 0·92 cm high (Figs 3D and 4D, and Table 1).

The lower internode is 10·48 cm long and the upper internode is 9·50 cm long. The internodes are probably sulcate above the insertion of the bud. Each internode is cylindrical and hollow with an external diameter of 3·00–3·50 cm and an internal diameter of 1·60–1·70 cm (Figs 3A and 4C, and Table 1).

The fossil bamboo has a stem diameter of 3·00–3·50 cm with an $H_{est.}$ of 3·41 m. The H_{crit} is 6·58 m and the SF is 1·93 (Table 1).

Anatomical description

The cross-sectional anatomy of the aerial axis internode is described from the outside in (Fig. 5). The outer, 1 mm thick tissue zone has scarce cellular differentiation due to
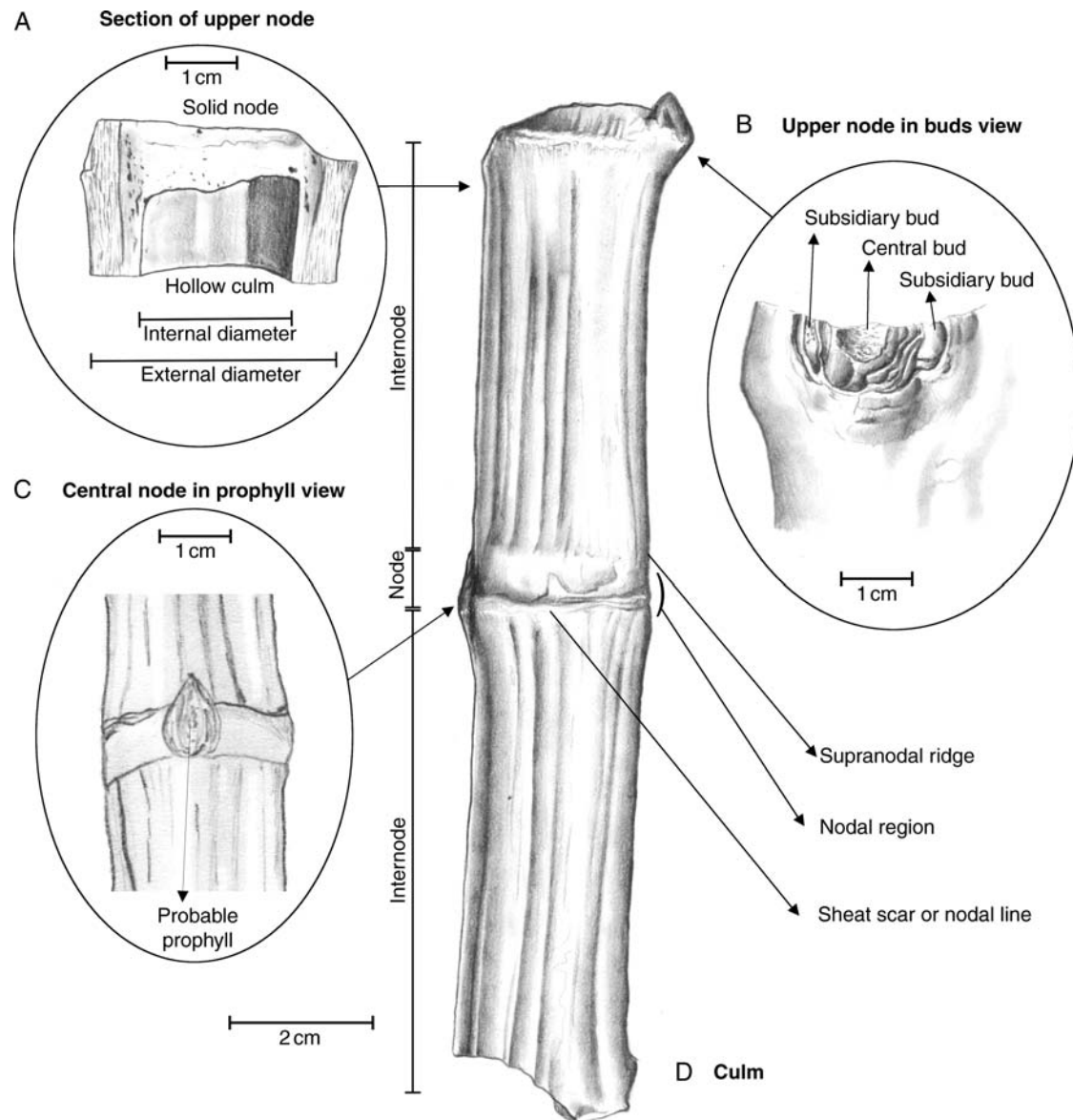
FIG. 3. *Guadua zuloagae*. (A) Section of culm where solid node and hollow culm are observed. (B) Node showing one central bud and two subsidiary buds. (C) Node with probable prophyll. (D) Culm showing internodes and nodes; in the zone of the node, showing supranodal ridge, nodal region and sheath scar or nodal line.

the poor preservation of the fossil, but presumably corresponds to epidermis and cortex. However, some anatomical structure was preserved (Fig. 6B and C).

The epidermis is formed by a layer of epidermal cells and cells with silica bodies (Fig. 6B and C). The phytolith morphotype found in this fossil, recognizable as rondels or Bam. 5 (*sensu* Piperno, 2006: 29–31), derive mainly from culms and inflorescence bracts (Piperno, 2006). Stomata were not observed. The hypodermis consists of 2–3 layers of sclerenchymatous cells. The cortical parenchyma is homogenous and formed by 7–9 layers of thin- and thick-walled cells.

There are scattered vascular bundles (Fig. 6A) associated with the sclerenchyma separated from one another by ground tissue or interfascicular parenchyma (Fig. 6F and G). This zone is 5 mm wide and shows the typical change in the size and form of the vascular bundles from the periphery to the central cavity (Figs 5 and 7G).

In longitudinal section the parenchyma cells are not clearly observed, but in cross-section it can be observed that the interfascicular parenchyma tissue is formed by isodiametric cells (Fig. 6F and G).

The radial diameter and tangential diameter of the metaxylem vessels vary within the different zones. Table 2 shows the values obtained for the density of vascular bundles (DVB), the metaxylem radial diameter, the metaxylem tangential diameter, the metaxylem radial/tangential diameter (R/T) and the percentage of fibre per vascular bundle in
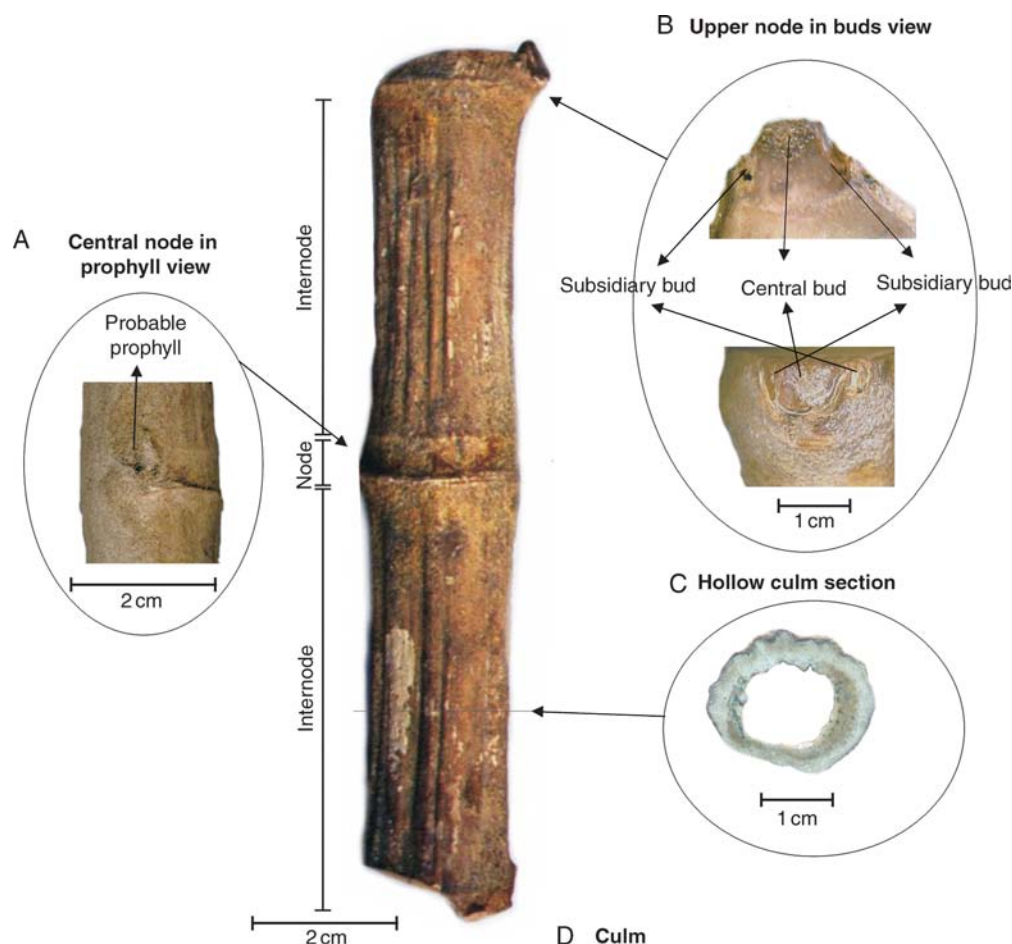
F<small>IG</small>. 4. *Guadua zuloagae*. (A) Central node showing probable prophyll. (B) Longitudinal section showing only one central bud and two subsidiary buds. (C) Section of hollow culm. (D) Culm showing internodes and nodes.

the different zones through a cross-section. The periphery vessels of the metaxylem are smaller and increase in size in the middle and inner zones (Fig. 5).

The xylem of each vascular bundle has two large metaxylem vessels and a protoxylem, which usually breaks down to form an intercellular canal at the inner pole of each vascular bundle. The phloem is made up of $12-26$ sieve tubes, and in cross-section it shows cylindrical form towards the outer pole of the bundle (Fig. 7F). The phloem fibres and phloem parenchyma associated with sieve tubes were not observed because the phloem was poorly preserved and difficult to identify.

Each vascular bundle is surrounded by four sclerenchyma sheaths, two of them located at each side of the metaxylem vessels, one around the protoxylem and another one around the phloem (Fig. 7F). The vascular bundles are associated with sclerenchyma tissue (Fig. 6D). This sclerenchyma tissue is more abundant in the middle and internal zones (Table 2, Fig. 6D).

The cross-section of the petrified culm shows a clear zonation. Four zones have been determined: periphery, transitional, middle and internal zone. The periphery zone measures 2·96 mm and consists of vascular bundles adjacent to the cortex (Fig. 7C).

The vascular bundles are circular, small and numerous compared with the other zones (DVB $= 340$ vb cm^{-2}). The metaxylem radial diameter ranges from 40·0 to 80·0 μm with a mean of 52·5 μm, and the metaxylem tangential diameter ranges from 20·0 to 45·0 μm with a mean of 37·0 μm. The R/T ratio was of 1·41. The percentage of fibre in the vascular bundle is 77·41 %.

The transitional zone measures 8·87 mm. In this zone, the vascular bundles are ovoid in shape and atypical for the genus *Guadua*. However, these vascular bundles should not be used for characterization of the species (Londoño *et al.*, 2002).

The middle zone measures 8·63 mm. The vascular bundles are ovoid and circular in shape, large and less abundant than in the other zones (Fig. 7D). In this zone, the DVB is 86 vb cm^{-2}. The average radial diameter of the metaxylem is 66·5 μm (45·0–100·0 μm) and its average tangential diameter is 69·5 μm (45·0–90·0 μm). The R/T ratio is 0·96. The percentage of fibre is 36·48 %.

The internal zone measures 7·39 mm. The vascular bundles in this zone are circular, larger and fewer (64 vb cm^{-2}) compared with the other zones (Fig. 7E). These vascular bundles have an R/T ratio of 0·76. The radial diameter of the metaxylem ranges from 80·0 to
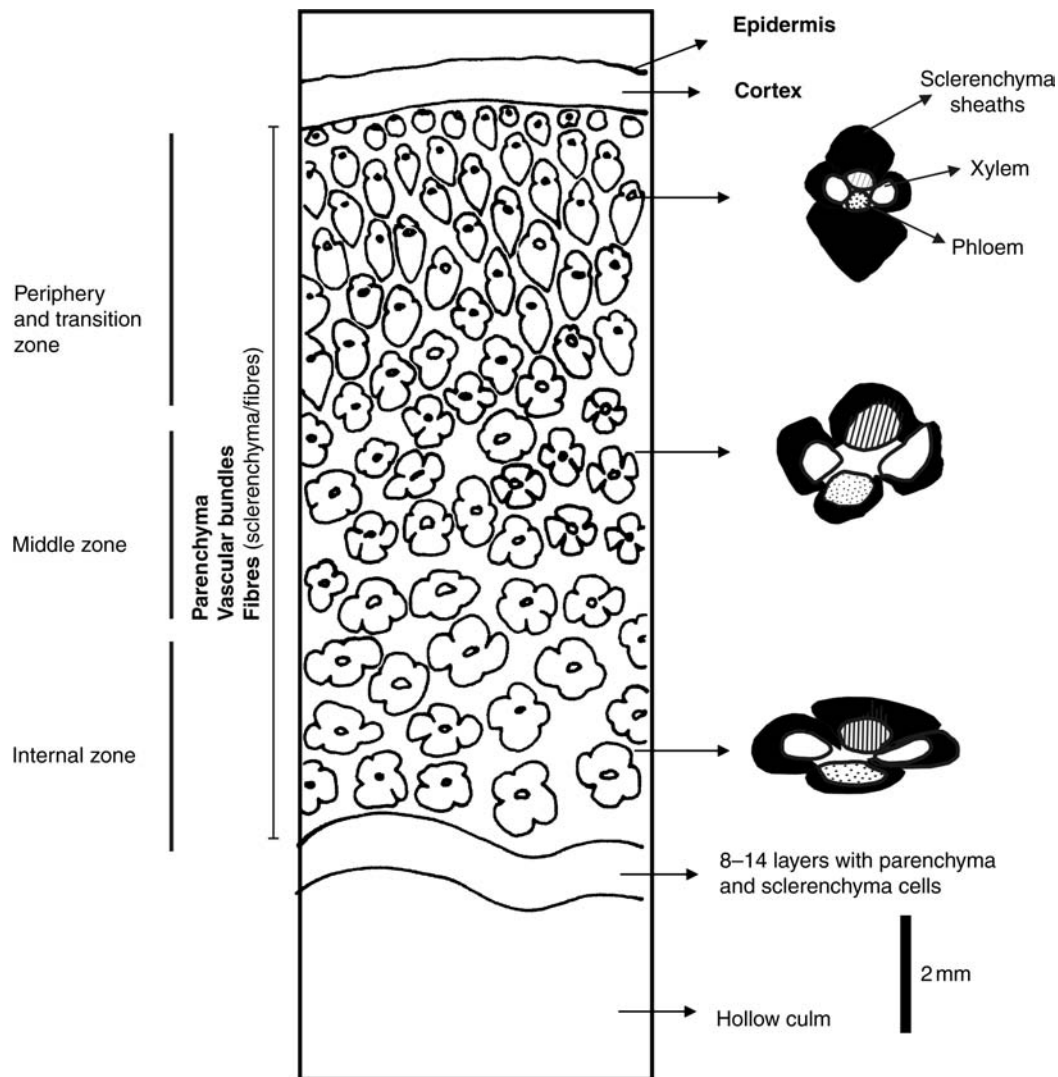
FIG. 5. Schematic cross-sectional anatomy of *Guadua zuloagae* culm showing different tissue zones and vascular bundles in the different zones through a cross-section.

140·0 μm with an average of 110·0 μm, and its tangential diameter ranges from 100·0 to 170·0 μm with an average of 145 μm. The percentage of fibre in this zone is 34·16 %.

Finally, about 8–14 layers with parenchyma and sclerenchyma cells (approx. 1–2 mm thick) surrounding the hollow central cavity are observed (Figs 6E, and 7A and B).

DISCUSSION

Comparison with extant species

The GPWG (Grass Phylogeny Working Group) has recently presented a taxonomic and phylogenetic study of the Poaceae based on six molecular sequence data sets, chloroplast restriction site data and morphological characters. The 12 subfamilies of grasses have been recognized by the GPWG on the basis of 53 characters. In this study, the presence of woody culms is an unambiguous and

unreversed synapomorphy of the Bambusoideae, and an autapomorphy of *Arundo*, *Thysanolaena* and *Gynerium* (GPWG, 2001).

The studied specimen was compared with taxa of the Bambusoideae sub-family, especially with the American woody bamboos (McClure, 1973; Watson and Dallwitz, 1992 onwards; Judziewicz *et al.*, 1999; Stevens, 2001 onwards; Clayton *et al.*, 2002 onwards; Londoño *et al.*, 2002; Rúgolo de Agrasar and Rodríguez, 2003) and other woody culms such as *Arundo*, *Thysanolaena* and *Gynerium*. The following features were taken into account when making the comparison: the presence of woody and hollow culms; the diameter and height of the culms; the type of the bud or buds; the appearance of the nodal region; the silica bodies; and the anatomical characteristics of the culms in cross-section.

According to these premises, besides the selected non-bambusoid genera (*Arundo*, *Thysanolaena* and *Gynerium*), the comparisons of the fossil culms were made with
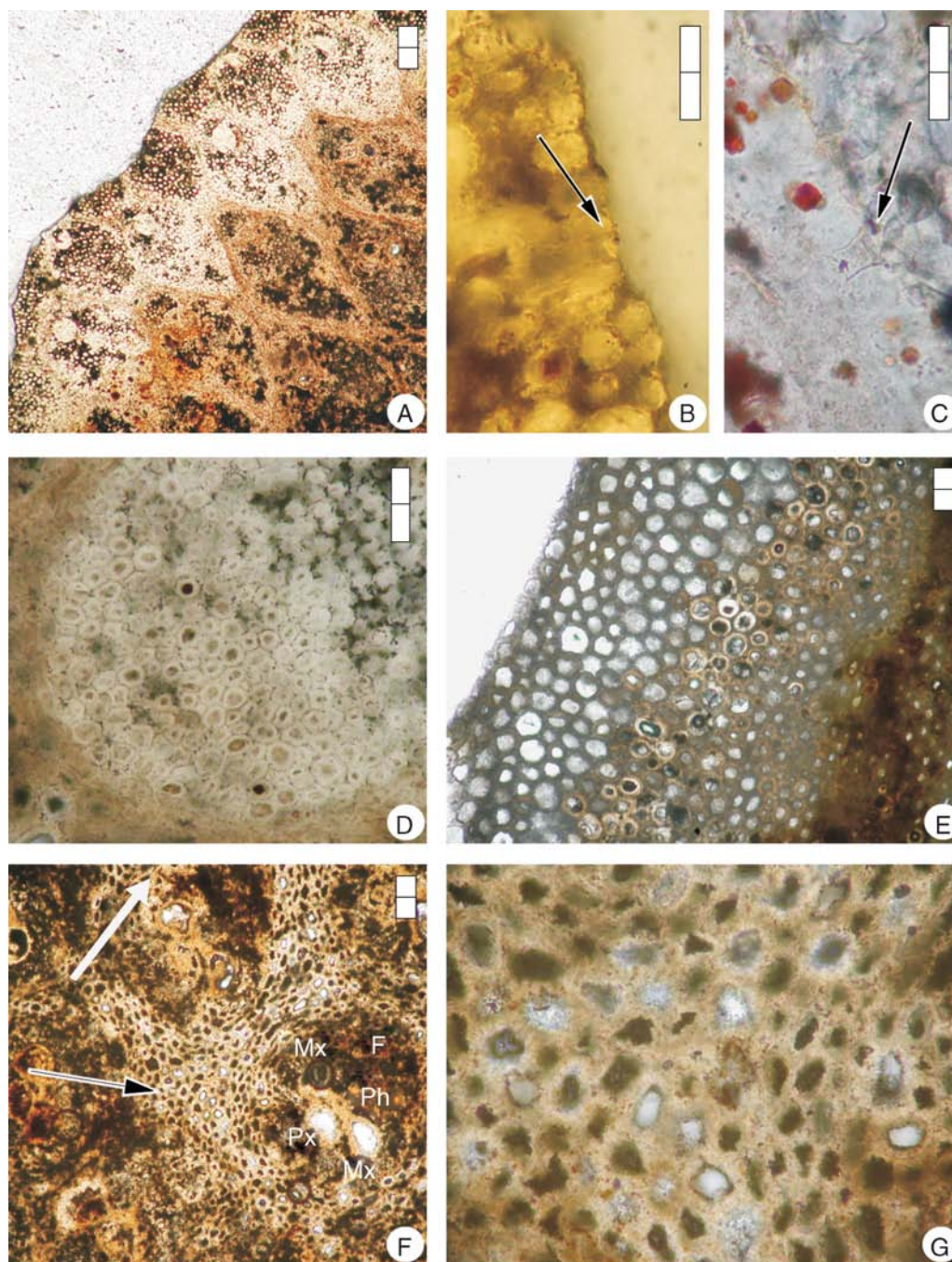
FIG. 6. (A) General view in cross-section of the *Guadua zuloagae* culm. (B and C) Detail of epidermis in cross-section; the black arrows show silica cells. (D) Detail of a vascular bundle showing a fibre sclerenchyma sheath. (E) Detail of the internal layer in contact with the hollow central cavity showing the characteristic cells. (F) General view in cross-section of vascular bundles and interfascicular parenchyma indicated by a black arrow; the white arrow indicates the centrifugal direction. F, fibre sclerenchyma sheath; Ph, phloem; Px, protoxylem; Mx, metaxylem. (G) Detail of interfascicular parenchyma. Scale bars: A, E, F, G = 100 μm; B, C = 20 μm; D = 40 μm.

the following bambusoids: *Glaziophyton*, *Chusquea*, *Alvimia*, *Neurolepis*, *Myriocladus*, *Actinocladum*, *Atractantha*, *Merostachys*, *Apoclada*, *Rhipidocladum*, *Aulonemia*, *Arthrostylidium*, *Colanthelia*, *Elytrostachys*, *Athroostachys*, *Swallenochloa* and *Guadua*.

Two of the selected non-bambusoid genera have solid internode culms (*Thysalonaena* and *Gynerium*), whereas *Arundo* differs from the fossil specimen in its internode bundle distribution. Unlike the fossil, *Arundo* possesses an arrangement of the culm internode bundles in three or more rings (Watson and Dallwitz, 1992 onwards). Apart from these differences, the fossil culm possesses some morphological and anatomical characteristics that link it to the bambusoid taxa. The presence of rondel (Bam. 5)
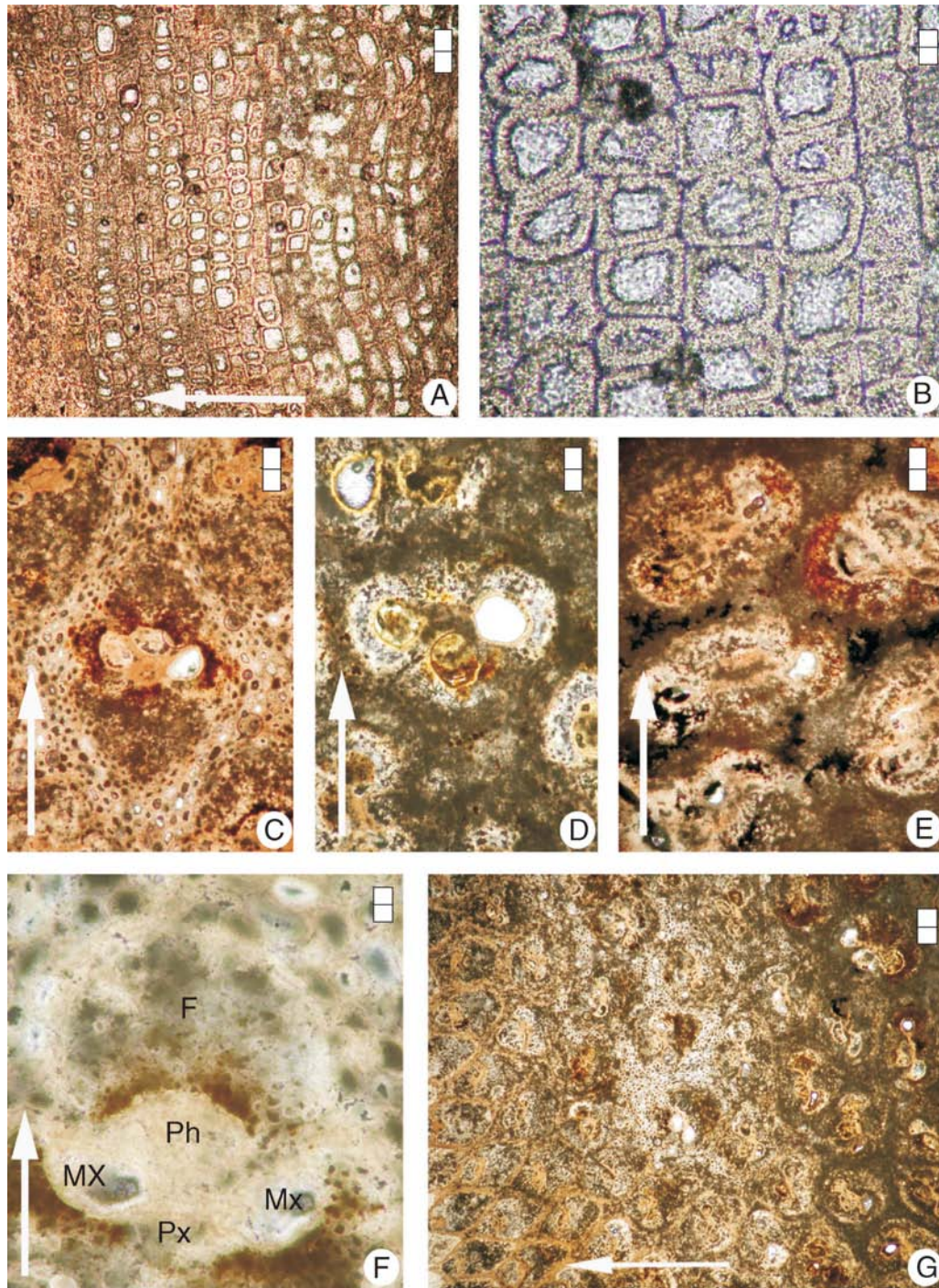
FIG. 7. (A) A general aspect of the cortical parenchyma in longitudinal section; the arrow indicates the centrifugal direction. (B) Detail of cortical parenchyma. (C–E) Composition of vascular bundles in the different zones through a cross-section of the *Guadua zuloagae* culm; arrows indicate the centrifugal direction. (C) PZ, periphery vascular bundle zone; the arrow indicates the centrifugal direction. (D) MZ, middle vascular bundle zone. (E) IZ, internal vascular bundle zone. (F) Detail of the vascular bundles, F, fibre sclerenchyma sheath; Ph, phloem; Px, protoxylem; Mx, metaxylem; the arrow indicates the centrifugal direction. (G) General view in cross-section of the *G. zuloagae* culm, showing the variability in the shape of vascular bundles; the arrow indicates the centrifugal direction. Scale bar A, E, F, G = 100 μm; B, C = 20 μm; D = 200 μm.

phytoliths, a typical Bambusoideae morphotype (Piperno, 2006), also points to Bambusoideae.

Among the selected bambusoids with small culms, *Glaziophyton* presents small culms, densely clump-forming, and rushlike woody bamboos, while *Alvimia*, *Neurolepis* and *Myriocladus* are smaller woody bamboos with mean culm diameters never reached by the studied specimen. *Actinocladum* is a medium-sized woody

TABLE 2. *Anatomical characteristics of the vascular bundles according to the wall thickness zone*

Vascular bundle ($n = 30$)	Fossil internode of *Guadua zuloagae*		
	Periphery zone	Middle zone	Internal zone
DVB ($n \, \text{cm}^{-2}$)	340	86	64
Metaxylem radial diameter (μm)			
Mean ± s.e.	52·5 + 4·10	66·5 + 4·66	110·0 + 6·95
Minimum diameter	40·0	45·0	80·0
Maximum diameter	80·0	100·0	140·0
Metaxylem tangential diameter (μm)			
Mean ± s.e.	37·0 + 2·71	69·5 + 4·18	145·0 + 7·71
Minimum diameter	20·0	45·0	100·0
Maximum diameter	45·0	90·0	170·0
R/T	1·4	0·96	0·76
Fibres (%)	77·4	36·5	34·1

DVB, density of vascular bundles; R/T, radial/tangential diameter of metaxylem vessel.

bamboo with hollow culms that often possesses a pithy centre.

In contrast, *Aulonemia* consistently has internodes or long internodes alternating with sets of 2–4 very short internodes and midculm nodes, each one bearing a single bud (Judziewicz *et al.*, 1999). It also differs in culm anatomy, particularly in the type of its vascular bundles (Rúgolo de Agrasar and Rodríguez, 2003). *Chusquea* does not resemble the new taxon studied in this paper because the culms are solid and differ in the size and form of the vascular bundles (Judziewicz *et al.*, 1999, Rúgolo de Agrasar and Rodríguez, 2003). It resembles *Atractantha* because it presents midculm nodes with three branches that often rebranch to form numerous smaller branchlets. *Merostachys* has hollow culms or, rarely, pithy to solid ones with solitary primary buds at the midculm nodes, producing numerous smaller branchlets from a truncate to shallowly fan-shaped meristem with no evident supranodal ridge (Judziewicz *et al.*, 1999).

In comparison with the other selected genera, *Apoclada* is different from the fossil specimen in its bud type. In this case, the hollow to sometimes solid culms have branch complements at the midculm nodes that range from one to 15 separate and equal branch buds in a single line above the nodal line, often rebranching near their bases (Judziewicz *et al.*, 1999). The fossil specimen also differs from *Rhipidocladum* because it possesses a single bud per midculm node and a small to medium sized culm in cross-section.

The fossil specimen is dissimilar to *Arthrostylidium* because the extant genus presents hollow culms with a small to large lumen or, rarely, solid and midculm nodes with a single branch bud at the summit of a promontory. *Colanthelia* differs in the anatomy of the culm, where the vascular bundles are depressed and alternate in five cycles with abundant fundamental parenchyma around them (Rúgolo de Agrasar and Rodríguez, 2003). Also, the midculm nodes present are prominently narrow crested

and the buds are borne on a weakly developed promontory that in some cases is absent (Judziewicz *et al.*, 1999). *Elytrostachys* presents hollow thin-walled culms with a branch complement arising from a single bud on a weakly developed promontory consisting of a single large branch with two to numerous smaller sub-equal branches on each side (McClure, 1973; Judziewicz *et al.*, 1999). In addition, *Athroostachys* and *Swallenochloa* are not related to the new species because of the bud type (McClure, 1973). In *Athroostachys*, the internodes are terete and fistular, and the primary branch buds at the culm nodes are apparently solitary (McClure, 1973). *Swallenochloa* has self-supporting culms; the internodes are typically fistular, either terete or more or less sulcate above the locus of insertion of a complement of buds or branches (McClure, 1973).

The described fossil specimen shares both morphological (Judziewicz *et al.* 1999) and anatomical (Londoño *et al.*, 2002) features with *Guadua* and, within that genus, it is particularly similar to *G. angustifolia* (see Table 3 for comparative characters).

Guadua is a medium to large bambusoid grass, with clump-forming, erect to scandent woody bamboos. The culms are hollow or solid and often very large; a height of up to 30 m corresponds to a culm diameter of 22 cm. The internodes are usually sulcate above the insertion of the complementary branch bud, and midculm nodes have a single branch bud, which branches intervaginally with a dominant branch and few or no smaller branchlets (Judziewicz *et al.*, 1999).

Cross-sections of the extant woody bamboo culms show that there are some characteristics which are common to all of them (Metcalfe, 1960). The outer part of the culm is bounded by an epidermis with cells that are generally very thin walled. The hypodermis consists of 1–3 layers of thick-walled hypodermal cells. Inside this, there is a narrow zone with eight layers of parenchymatous cells that often contain chloroplasts. Inside this photosynthetic layer, there is a vascular bundle zone. This zone of vascular bundles is associated with fibres, sclerenchyma and parenchymatic tissue. The centre of the culm is hollow or solid, and the nodes are completely solid. In some bamboos, there are a few cell layers next to and surrounding the central cavity. This zone is composed of parenchymatic cells and sclereids, and has been observed in *G. angustifolia* (Metcalfe, 1960).

Comparison with fossil species

Studies on monocotyledonous fossils are known, but none of them has reported bambusoid culms preserved as siliceous permineralizations (Becker, 1973; Thomasson, 1980; Daghlian, 1981; Herendeen and Crane, 1995). Thomasson (1980) made a compilation of the paleoagrostological studies between 1928 and 1979. During this period, fossil grasses were described on the basis of fossilized anthoecia, leaves and cuticle fragments. Bamboo fossil leaves and pollen grains have been reported in the Cenozoic deposits of Europe and Japan (Worobiec and Worobiec, 2005). Fossil bamboo macroremains are very rare in European deposits, in contrast to the occurrence of

TABLE 3. *Anatomical comparison of the vascular bundles* Guadua angustifolia *Kunth and* Guadua zuloagae *sp. nov.*

Vascular bundle	*Guadua angustifolia* segment									*Guadua zuloagae*		
	Basal zone			Middle zone			Apical zone			Middle zone		
	PZ	MZ	IZ	PZ	MZ	IZ	PZ	MZ	IZ	PZ	MZ	IZ
DVB (n cm^{-2})	377	68	61	392	82	77	612	224	215	340	86	64
R/T	1·4	0·91	0·82	1·4	0·92	0·52	1·3	0·85	0·56	1·4	0·96	0·76
Diameter max (μm)	30	190	220	30	200	260	30	130	160	45	90	170
Fibres (%)	64·5	23·1	22·7	59·4	19·3	19·7	63·3	71·7	21·9	77·4	36·5	34·1

PZ, periphery zone; MZ, middle zone; IZ, internal zone.

pollen grains assigned to the 'Bambusa' type (=*Graminidites bambusoides*) (Worobiec and Worobiec, 2005). Bamboo fossil leaves and pollen grains have been reported from the Middle Miocene in Poland. The bamboo leaves were determined as '*Bambusa*' *lugdunensis* Saporta and the fossil pollen grains were assigned to *Graminidities bambusoides* Stuchlik (Worobiec and Worobiec, 2005).

In South America, two fossils with bambusoid affinities have been cited. One of them corresponds to a large grass with relatively slender stems, large linear-lanceolate leaves and expanded rhizomal internodes from Tertiary sediments of Colombia, assigned to *Chusquea rolloti* Berry (Bambusoideae) by Berry (1929). The other one, found at 'Laguna del Hunco', Chubut province (Patagonia, Argentina), is a fossil leaf impression with bambusoid affinities for the Eocene, assigned to *Chusquea oxyphylla* by Frenguelli and Parodi (1941). This specimen corresponds to a 7 cm long leaf impression with a culm containing ten nodes covered by imbricated sheaths, where four leaves can be observed. The assignment of this specimen to the extant genus *Chusquea* is dubious according to today's standards (Lynn Clark, pers. comm.), although its affinity for the Bambusoideae sub-family is not questioned. In South America, specifically in Argentina, the material studied herein represents the first fossil record of petrified bamboo culms. Records of this fossil type have not been described in other parts of the world.

In summary, *G. zuloagae* is consistent with the diagnostic characters of the Bambusoideae subfamily. This fossil, *G. zuloagae*, and extant Bambusoideae, especially *Guadua*, are morphologically similar regarding the internode and the culm node, the form and characteristics of the buds and the internal anatomy of the culm (epidermis, hypodermis, cortical parenchyma, fibres, sclerenchyma tissue and the form of the vascular bundles). These characters place the *G. zuloagae* within the Bambusoideae sub-family, with close affinity for the tribe Bambuseae.

Paleoclimatic implications and distribution

Although there is currently not enough information about vegetal paleocommunities that developed in this region during the Upper Cenozoic period, it is possible to outline some paleoclimatic inferences based in the distribution patterns of the NRLs. Today, the distribution patterns of *Guadua* extend from Mexico (23°N), to Central and South America (35°S), except for Chile (Londoño, 1990). The majority of the species are present in lowland South America, including in Amazonian and Atlantic forests, gallery forests, savannas and Cerrado (Clark, 1995). *Guadua angustifolia* is native to northeastern South America and lives especially in humid regions. It is a typical species found on the banks of large tropical South American rivers, from Colombia to Argentina (McClure, 1966; Judziewicz *et al.*, 1999).

The presence of a bamboo culm with affinity for the genus *Guadua* from the Pliocene in the south-west of the Paraná basin (31°S) extends the area of paleofloristic distribution, suggesting a warmer climate than at present for this region. This assumption is supported by the palynological record, fossil woods, cuticles, leaf impressions, freshwater molluscs and vertebrates (Anzótegui and Lutz, 1987; Cione *et al.*, 2000; Morton, 2004). The paleobotanical record (Zucol *et al.*, 2004) indicates the presence of Sapotaceae, Winteraceae, Myrtaceae, Meliaceae, Aquifoliaceae, Fabaceae, Lauraceae and Euphorbiaceae, elements conforming to a humid mixed forest developing under temperate to warm climate.

The finding of *G. zuloagae* allows the inference of the presence of a bambusoideae understorey in the mixed forests already described for the Ituzaingó Formation (Anzótegui and Lutz, 1987). A comparison with the modern analogues of the paleofloral elements present during the Pliocene in the area strongly suggests that the sediments of the Ituzaingó Formation were deposited in humid temperate-warm climatic conditions. A sub-tropical climate is also supported by the record of fossil molluscs found at several fossil sites in Argentina and Paraguay (see Morton, 2004). The presence of elasmobranchs, teleosteans, crocodilians, chelonians, birds and mammals led Cione *et al.* (2000) to similar conclusions. In particular, the occurrence of iniid cetaceans, trichechid sirenians and a very high diversity of crocodiles is suggestive of varied paleoenvironments and a warmer climate than the one at present (Cione *et al.*, 2000). The predominance of aquatic birds supports the presence of woody lowlands and swamps along the river banks. This type of environments is also a requirement for the trichechids and iniids, which need lakes associated with the main river to live, feed and reproduce (Noriega, 1995).

Conclusions

Guadua zuloagae, a new species of Bambusoideae from the Pliocene at the Ituzaingó Formation, is described. In contrast to other grasses, for example pooid and panicoid grasses (GPWG, 2001), which are often the dominant element in open vegetation such as prairies, savannas and fields, the bamboos are exclusively associated with woody vegetation and are most diverse in tropical and subtropical regions (Clark, 1995, 1997).

The fossil bamboo culm described herein constitutes the first permineralized record of the Bambusoideae sub-family in the world and provide new evidence for its distribution in the past. The presence of this fossil record in the Pliocene sediments from the Ituzaingó Formation at the Toma Vieja fossil locality (Paraná basin, Argentina) supports the idea that the genus *Guadua* was more widespread in the past.

The fossil indicates a warmer and more humid climate in the region during the Pliocene, supporting previous paleo-climatic inferences for the region (Anzótegui and Lutz, 1987; Cione *et al.*, 2000; Morton, 2004; Zucol *et al.*, 2004).

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