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Research paper

A new Bambusoideae (Poaceae: Bambusoideae: Bambuseae: Guaduinae) from the Ituzaingó Formation (Pliocene–Pleistocene), Entre Ríos, Argentina

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ABSTRACT

This paper describes the anatomy and morphology of a new bamboo fossil, *Guadua morronei* sp. nov., from the Ituzaingó Formation in the Entre Ríos province, Argentina. The fossil culm is the second record of Bambusoideae in Pliocene–Pleistocene sediments from the Paraná Basin (Argentina) and the fifth record for South America. The culm or aerial vegetative axis fossil is woody with one solid node and one incomplete solid internode. The anatomy of the internode is characterized by an epidermal layer, subepidermal parenchyma and continuous sclerenchyma surrounding the first cycle of peripheral vascular bundles and cortical parenchyma. The vascular bundles consist of two large metaxylem vessels, protoxylem and phloem, and each vascular bundle is surrounded by sclerenchyma. The interfascicular parenchyma is composed of isodiametric cells. The anatomy of the node is characterized by xylem with only one metaxylem vessel. The results of the morphological and anatomical analyses of the fossil bamboo revealed a great affinity with the extant species of *Guadua paraguayana*. *Guadua morronei* sp. nov. is the first *Guadua* fossil species with a solid internode. The presence of this fossil bamboo culm in Pliocene–Pleistocene sediments may contribute to a better understanding of the evolutionary history and present diversity of these groups in the South American flora.

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1. Introduction

The Bambusoideae (Poaceae) subfamily, in which three tribes Arundinarieae (temperate wood bamboos), Bambuseae (tropical woody bamboos) and Olyreae (herbaceous bamboos) are recognized (Sungkaew et al., 2009), differs from the other grasses in leaf anatomy, i.e., non radiated mesophyll, fusoid cells and arm cells (Clark, 1997; Liese, 1998; Judziewicz et al., 1999; Londoño et al., 2002). The structural synapomorphy of the Bambusoideae is the presence of strongly asymmetrically invaginated arm cells in the chlorenchyma (Zhang and Clark, 2000; GPWG, 2001; BPG, 2012). Moreover, the tropical woody bamboos (tribe Bambuseae) have thickened culms that are lignified or woodlike with hollow or solid internodes (Judziewicz et al., 1999). Bamboos produce new shoots only by primary growth, without any secondary growth. Certain differences exist within the culm, and between species and genera that are considered of taxonomic value (Liese, 1998).

At present, the Bamboo Phylogeny Group (BPG) is preparing a manuscript about the reviewed global phylogeny of the Bambusoideae and an updated tribal, subtribal, and generic classification based on the phylogeny results (BPG, 2006, 2012).

Worldwide, only two fossil species of anatomically preserved bamboo culms have been described: *Guadua zuloagae* (Brea and Zucol, 2007) from the Pliocene–Pleistocene Ituzaingó Formation in central–eastern Argentina and cf. *Guadua* sp. (Olivier et al., 2009) from the pre-Holocene Madre de Dios Formation in the south-western Peruvian Amazon.

The fossil culm studied here was recovered from the Ituzaingó Formation in a new fossil locality, El Espinillo stream (Fig. 1), near Paraná city in the Entre Ríos province, Argentina. Its description is based on morphological and anatomical features of a petrified culm of 12 cm in length and 3.3 × 2.3 cm in diameter.

The palaeobotanical record of the Ituzaingó Formation is based on studies of palynomorphs, fossil leaves, cuticles, fossil culms, palm trunks and fossil woods (Brea and Zucol, 2007; Franco, 2010a, 2010b, 2010c, 2011and references therein; Brea and Zucol, 2011 and references therein).

The description and systematic assignment of the extant woody bamboos is based mainly on vegetative characters since most of them have long vegetative periods with a short reproductive stage (Judziewicz et al., 1999). The anatomy of extant bamboo culms has been described by several authors in the past (Metcalfe, 1960; Liese, 1980, 1998; Sekar and Balasubramanian, 1994; Liese and Grosser, 2000; Londoño et al., 2002; Rúgolo de Agrasar and Rodríguez, 2003).

The reliable fossil record of the Bambusoideae subfamily is based on phytoliths and petrified or carbonized culms (Strömberg, 2005; Brea and Zucol, 2007; Olivier et al., 2009).

A new petrified Bambusoideae is described in this contribution and is compared with the other two known fossil bamboo culms in order

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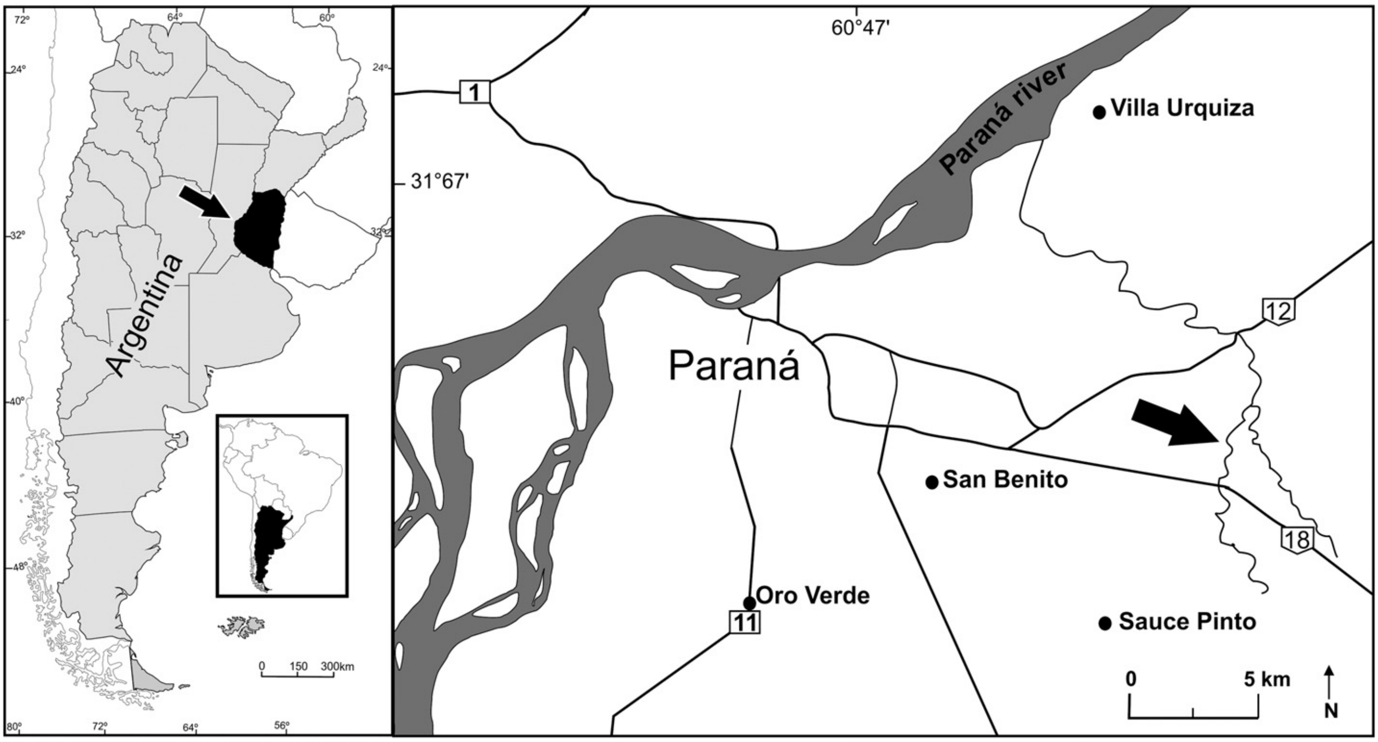

Fig. 1. Location map showing the El Espinillo fossiliferous locality, Entre Ríos province, Argentina.

to better understand the fossil anatomy of Bambusoideae in South America during the Cenozoic. The fossil culm described herein presents a combination of diagnostic morphological and anatomical features that allow the recognition of a new species of *Guadua*, *Guadua morronei*, from the Pliocene–Pleistocene. This fossil culm shares a great number of characters with the extant species of *Guadua paraguayana* Döll.

2. Geological setting

The Ituzaingó Formation is widely distributed in the western riverside cliffs of the Paraná River, from the north of Corrientes province (from Ituzaingó to Goya), and to the south up to near Paraná city in Entre Ríos province (De Alba, 1953; Herbst, 2000; Anis et al., 2005; Brea and Zucol, 2011). In the Argentine subsurface, it extends to the west of Corrientes and Entre Ríos up to the latitude of Paraná city, to the east of Chaco and most of Santa Fe, to the east of Córdoba, and to the north of Buenos Aires province (Herbst, 2000).

The Ituzaingó Formation is composed of fine to coarse sands and sandstones, almost exclusively of quartz. The sands are occasionally whitish, yellowish and brown-reddish. Also, dark brownish conglomerates and dark grey and greenish clay lens intercalations are frequent among the sands (Aceñolaza and Sayago, 1980; Herbst and Santa Cruz, 1985; Iriondo et al., 1998; Herbst, 2000; Franco, 2011). Troughs and planar bedding are also found, and low-angle rippled cross-laminations of fluvial origin are recognized towards the top of each stratum (Anis et al., 2005). This fluvial unit was deposited by the Palaeoparaná River under warm and humid climatic conditions (Iriondo et al., 1998). This interval was characterized by forest development under humid, subarid to arid climate conditions, palm forests and fresh water palaeocommunities. All these data suggest that during the Pliocene–Pleistocene, subtropical to tropical vegetation was well represented in the study area (Franco, 2011 and references therein).

3. Material and methods

The fossil specimen was collected by Raúl Kemer and César Travieso from the El Espinillo stream located near Paraná locality, Entre Ríos province, Argentina. The outcrop is situated at 31° 46′ 24.14″ S; 60° 18′ 57.56″ W (Fig. 1) and stratigraphically the outcropping sediments belong to the Ituzaingó Formation, which is assigned to Pliocene–Pleistocene in age (De Alba, 1953; Herbst, 1971, 2000; Herbst et al., 1976; Herbst and Santa Cruz, 1985). The specimen was preserved by siliceous permineralization and thin-sections were prepared using petrographic techniques for two transverse sections (one at internode level and the other one at node level) and one longitudinal section.

The standardized terminology by Metcalfe (1960), McClure (1966, 1973), Liese (1980, 1998), Londoño and Kobayashi (1991), Sekar and Balasubramanian (1994), Dransfield and Widjaja (1995), Judziewicz et al. (1999), Liese and Grosser (2000), Londoño et al. (2002) and Rúgolo de Agrasar and Rodríguez (2003) was used to describe the morphology and the anatomy of the fossil culm.

Each quantitative value provided in the anatomical description is an average of 30 measurements. The relationship between stem diameter and height can be used to reconstruct the height of fossil plants whose basal stem diameters are known or inferred (Niklas, 1994). The estimated height and the critical height were calculated on the basis

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Plate I. *Guadua morronei* sp. nov. Brea, Zucol and Franco. Holotype CIDPALBO 104.

1. Longitudinal section of bamboo culm showing internode and node.
2. Longitudinal section of bamboo culm showing internode and node with probable bud.
3. Cross section of bamboo culm where solid internode is observed.

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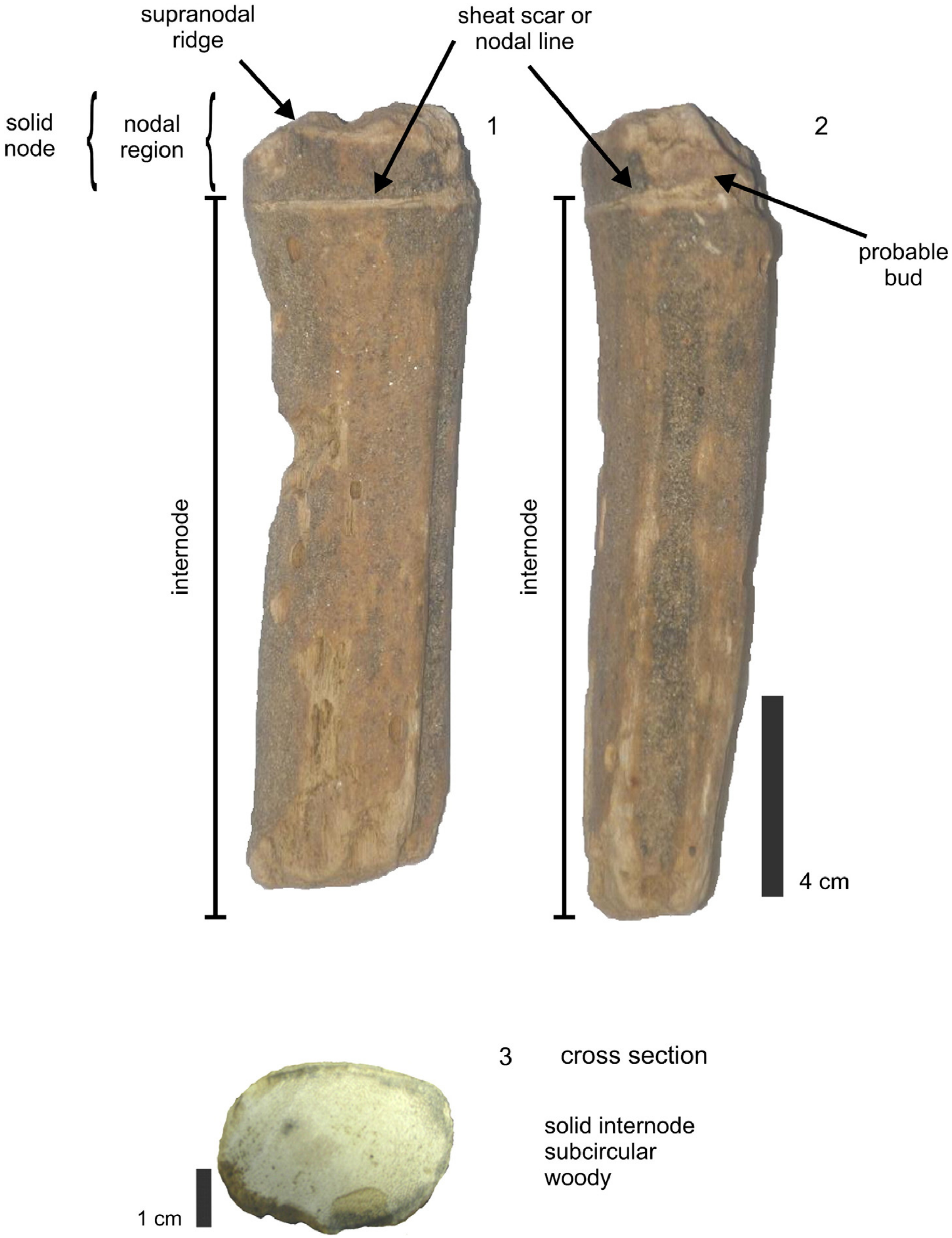

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of ratio diameters observed in living plants using known stump diameters (Niklas, 1993, 1994). The estimated height ($H_{est.}$) and the critical height ($H_{crit.}$) of the fossil bamboo were calculated using the formula of Niklas (1992, 1993, 1994); for more details about fossil bamboo height see Brea and Zucol, 2007).

The fossil culm sections were studied using a Nikon Eclipse E200 light microscope and photomicrographs were taken with a Nikon Coolpix S4 digital camera. The fossil specimen and slides were deposited at the Laboratorio de Paleobotánica, CICYYTP-CONICET, Entre Ríos province, Argentina, labelled as CIDPALBO 104 and CIDPALBOmic 1155 (a–c).

4. Results

4.1. Systematic palaeontology

Family POACEAE
Subfamily Bambusoideae
Tribe Bambuseae
Subtribe Guaduinae
Genus **Guadua** Kunth 1822

Type species: *Guadua angustifolia* Kunth 1822
Guadua morronei sp. nov. (Plates I, II, III)
Derivation of name: The specific name, *morronei*, is dedicated to the memory of Dr. Osvaldo Morrone, recently deceased, in recognition of his significant and extensive work on native grasses in South America.
Holotype: CIDPALBO 104, CIDPALBOmic 1155 (a–c).
Repository: Laboratorio de Paleobotánica, CICYTTP-CONICET, Diamante, Argentina.
Type locality and horizon: El Espinillo stream locality, Entre Ríos, Argentina (31° 46′ 24.14″ S; 60° 18′ 57.56″ W), Ituzaingó Formation (Pliocene–Pleistocene).
Diagnosis: Petrified culm with an internode and a node. Subcylindrical in cross-section, woody, solid at the internode and at the node, nodal region delimited by the nodal line and the supranodal ridge; both horizontal. Node with a probable single bud. Cross-sectional anatomy of the internode characterized by: epidermis consisting of a layer of sclerified epidermal cells with thick external wall. Subepidermal parenchyma formed by 3–4 layers of sclerified cells. Sclerenchyma continuous, surrounding the first cycle of peripheral vascular bundles. Cortical parenchyma composed of ≤10 layers of thin-walled cells. Vascular bundles in seven or more alternating cycles. Xylem of each vascular bundle with two large metaxylem vessels. Protoxylem consisting of ≤18 vessels. Phloem formed by ≤11 sieve tubes. Each vascular bundle surrounded by sclerenchyma. Interfascicular parenchyma composed of isodiametric cells. Cross-sectional anatomy of the node characterized by: xylem with only one metaxylem vessel. The position of the xylem and phloem may change by distortion and the development of vascular bundle anastomosis within the nodal region.
Morphological description: The culm or aerial vegetative axis has one node and one incomplete internode. It is subcylindrical in cross-section, woody, with the node and internode both solid (Plate I, 1–3). The culm is 12 cm long (Table 1). The roots, rhizomes and leaves were not preserved.

The node has a diameter of 3.3×2.3 cm, with a probable bud that is 0.7 cm wide by 0.5 cm high (Plate I, 1 and Table 1). The lowermost boundary of the node is the nodal line (Plate I, 1–2 and Table 1) and the uppermost boundary of the node is represented by the supranodal ridge (Plate I, 1–2 and Table 1). The nodal line and the supranodal ridge are horizontal (Plate I, 1–2 and Table 1). The nodal region is 1 cm high (Plate I, 1 and Table 1).

The incomplete internode is subcylindrical and solid with a diameter of 2.9×2.0 cm. The internode is sulcate above the insertion of the probable bud (Plate I, 2 and Table 1).

The fossil specimen has a culm diameter of 3.3–2.0 cm with a $H_{est.}$ of 3.08–3.30 m and a $H_{crit.}$ of 9.25–10.08 m (Plate I, 3 and Table 1).

Anatomical description: The cross-sectional anatomy of the aerial axis internode and node is described from the outside in. *Internode*: the outer, 1 mm thick tissue zone corresponds to the epidermis and cortex. Despite poor preservation and resulting scarce cellular differentiation in this zone, some anatomical characteristics were observed. The epidermis is composed of a layer of sclerified epidermal cells with thick external wall (Plate II, 10). The subepidermal parenchyma is formed by 3–4 layers of sclerified cells (Plate II, 10). The first cycle of peripheral vascular bundles is surrounded by continuous sclerenchyma. The cortical parenchyma is homogeneous and composed of 6–10 layers of thin-walled cells and intercellular spaces are observed (Plate II, 9).

The vascular bundles are in 7 or more alternating cycles. The vascular bundles always have the phloem oriented towards the external face in the peripheral cycles but their position varied in the inner ones (Plate II, 1–3).

The vascular bundles are associated with sclerenchyma separated from one another by ground tissue or interfascicular parenchyma (Plate II, 1–5, 8). The interfascicular parenchyma is composed of isodiametric cells of 13–28 (20±4.70) μm in diameter with a wall thickness of 1–5 (3) μm (Plate II, 9).

The cross-section of the petrified culm shows a clear zonation. Three zones have been recognized: peripheral, middle and internal. The peripheral zone measures 2.94–3.25 mm and is composed of vascular bundles adjacent to the cortex (Plate II, 1, 4). The vascular bundles are ovoid, smaller and more numerous compared with the middle and internal zones (Table 2). The radial diameter of the metaxylem ranges from 25 to 36 μm with a mean of 30 μm, and the metaxylem tangential diameter ranges from 22 to 35 μm with a mean of 30 μm. The R/T ratio was of 1 and the DVB is 195 vb cm^{-2}. The percentage of fibre in the vascular bundle is 82.38% (Table 2).

The middle zone measures 2.3–2.9 mm. The vascular bundles are subcircular, large and less abundant than in the peripheral zone (Plate II, 2, 5). The radial diameter of the metaxylem ranges from 28 to 81 μm with a mean of 42 μm, and the metaxylem tangential diameter ranges from 33 to 54 μm with a mean of 45 μm. The R/T ratio was of 0.94 and the DVB is 77 vb cm^{-2}. The percentage of fibre in the vascular bundle is 57.33% (Table 2).

The internal zone measures 3.99 mm. The vascular bundles in this zone are subcircular (Plate II, 3, 8), large and few (DVB = 48 vb cm^{-2}). The R/T ratio was of 1.23 and the percentage of fibre in the vascular bundles is 49.54% (Table 2). The radial diameter of the metaxylem ranges from 58 to 74 μm with a mean of 64 μm, and the metaxylem tangential diameter ranges from 35 to 71 μm with a mean of 52 μm (Table 2).

The xylem of each vascular bundle has two large metaxylem vessels and a protoxylem with 10–18 vessels, although it usually breaks down to form an intercellular canal at the inner pole of each vascular bundle. The phloem is formed of 7–11 sieve tubes and in cross-section it shows cylindrical form towards the outer pole of the bundle and, occasionally, a probable sieve-tube companion cell complex and fibres were observed (Plate II, 6).

The zone of the vascular bundles is 2.7 cm wide and shows the typical change in the size and form of the vascular bundles from the peripheral to the inner zone (Plate II, 1–3). The radial diameter and tangential diameter of the metaxylem vessels, density of vascular bundles (DVB), the metaxylem radial/tangential diameter (R/T) and the percentage of fibre per vascular bundles vary within the different zones through cross-section (Table 2). The periphery vessels of the metaxylem are smaller and increase in size in the middle and internal zones (Table 2). The peripheral vascular bundles are surrounded by sclerenchyma, and are more developed in connection with the protoxylem and phloem (Plate II, 1). The middle and internal vascular bundles are surrounded by sclerenchymatic sheaths with 4 caps to the level of the phloem, protoxylem and metaxylem, and are occasionally more developed in connection with the protoxylem and the phloem in the middle vascular zone. The sheaths are discontinuous in the middle and internal zones (Plate II, 2–3). The fibre sclerenchyma sheaths, which are associated at

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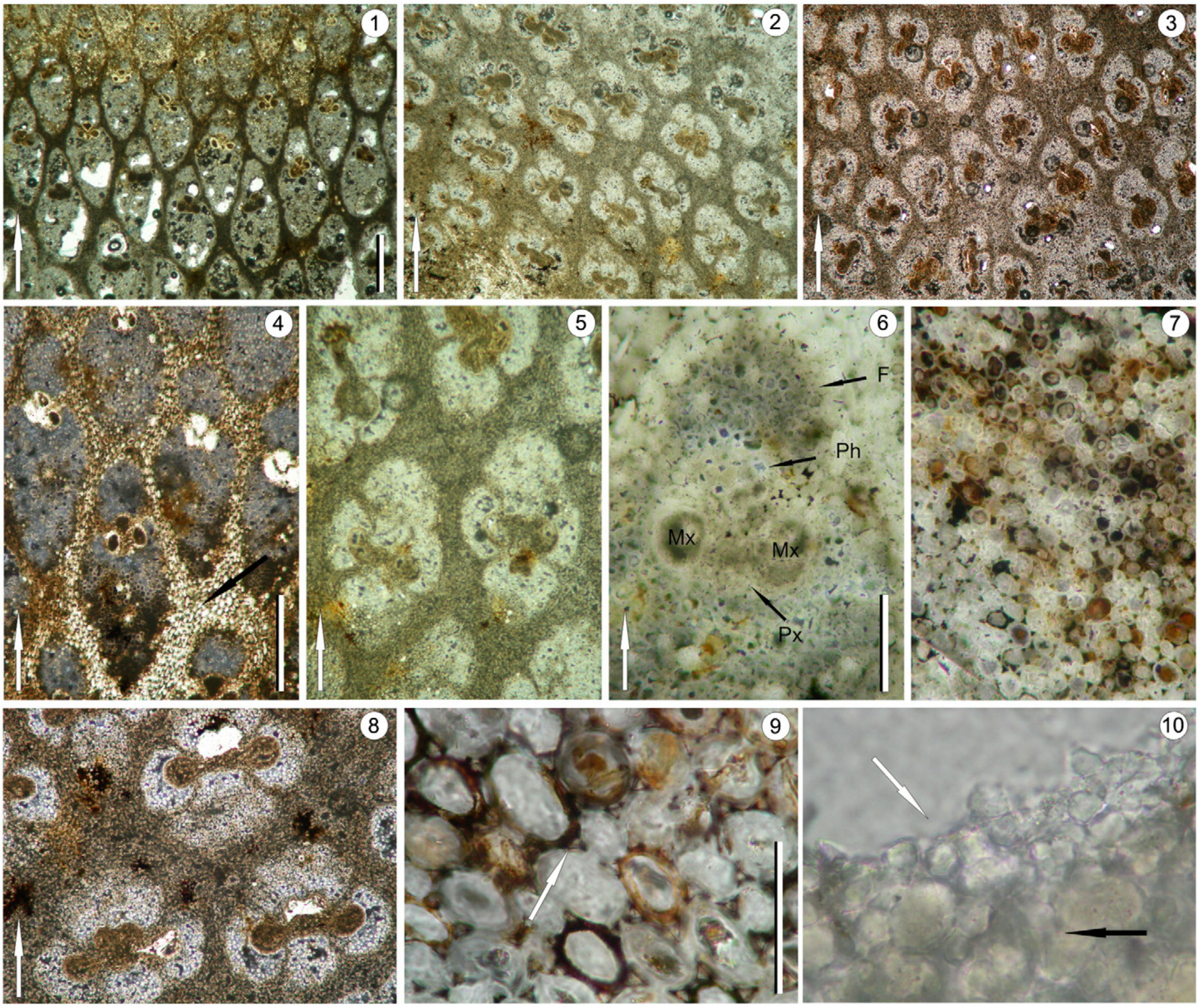

Plate II. *Guadua morronei* sp. nov. Brea, Zucol and Franco at internode region. Holotype CIDPALBO 104.

1. General view in cross section of periphery vascular bundles.
2. General view in cross section of middle vascular bundles.
3. General view in cross section of internal vascular bundles.
4. Detail of the periphery vascular bundle showing metaxylem vessels, fibre sclerenchyma sheath and interfascicular parenchyma (black arrow).
5. Detail of the middle vascular bundle showing metaxylem vessels and sclerenchymatic sheaths with 4 caps to level of phloem, protoxylem and metaxylem.
6. Detail of the vascular bundle showing fibre sclerenchyma sheath (F), phloem (Ph) where occasionally probable sieve tube-companion cell complex and fibres were observed, protoxylem (Px), metaxylem (Mx).
7. Detail of a fibre sclerenchyma sheath.
8. Detail of the internal vascular bundle showing metaxylem vessels and sclerenchymatic sheaths with 4 caps to level of phloem, protoxylem and metaxylem.
9. Detail of interfascicular parenchyma showing thin-walled cells and intercellular space (white arrow).
10. Detail of epidermis in cross section composed of a layer of sclerified epidermal cells with thick external wall (white arrow). The white arrow indicates the centrifugal direction in 1–6 and 8 (scale bar in 1, 2 and 3 = 300 μm; in 4, 5 and 8 = 200 μm; in 6 and 7 = 50 μm; in 9 and 10 = 30 μm).

the vascular bundles, are composed of isodiametric cells of 9–15 (12 ± 2.09) μm in diameter with a wall thickness of 2–6 (3 ± 1.16) μm (Plate II, 7). The fibres have simple pits.

Node: The anatomical structure of the internode has been extensively examined (Liese, 1998 and reference therein; Londoño et al., 2002; Rúgolo de Agrasar and Rodríguez, 2003), but the anatomy of the node has not been described in detail and this aspect has only been developed in a few papers (Liese, 1998 and reference therein). The epidermis is formed by sclerified epidermal cells with thick external wall (Plate III, 4). The subepidermal parenchyma is formed by 2–3 layers of sclerified cells (Plate III, 4). The cortical parenchyma is composed of ≤10 layers of thin-walled cells (Plate III, 4). The parenchyma cells are mostly rounded, but irregular shapes also have been observed (Plate III, 5). In the node of the *Guadua morronei* sp. nov. the typical vascular bundles structure observed in the internode disappears (Plate III, 1–3). The xylem consists of only one metaxylem vessel (Plate III, 3) and the position of xylem and phloem may change by distortion and the development of vascular bundles anastomosis within the nodal region (see fig. 75–76, p. 93–94 in Liese, 1998). The radial diameter of the metaxylem ranges from 38 to 53 μm with a mean of 49 ± 2.90 μm, and the

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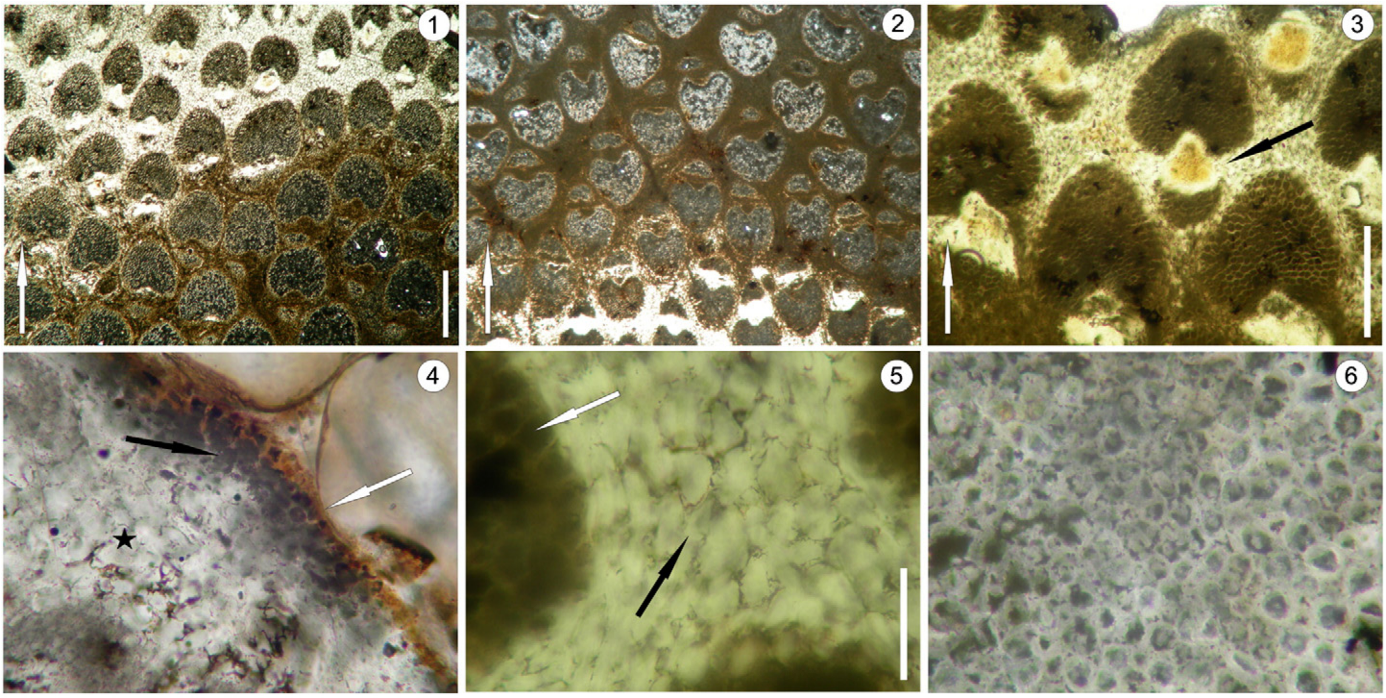

Plate III. *Guadua morronei* sp. nov. Brea, Zucol and Franco at node region. Holotype CIDPALBO 104.

1. Cross section showing vascular bundles at the node region.
2. Cross section showing vascular bundles at the node region.
3. Detail of vascular bundles where only one metaxylem vessel is observed (black arrow).
4. Detail of epidermis in cross section composed of a layer of sclerified epidermal cells with thick external wall (white arrow), subepidermal parenchyma formed by 2–3 layers of sclerified cells (black arrow) and parenchyma cells mostly rounded (black star).
5. Detail of interfascicular parenchyma (black arrow) and fibre sclerenchyma sheath (white arrow).
6. Detail of a fibre sclerenchyma sheath. The white arrow indicates the centrifugal direction in 1–3 (scale bar in 1 and 2 = 300 μm; in 4 = 200 μm; in 5, 6 and 7 = 50 μm).

metaxylem tangential diameter ranges from 30 to 50 μm with a mean of 40 ± 7.30 μm. The R/T ratio was of 1.24 and the DVB is 179 vb cm^{-2}. The percentage of fibre in the vascular bundle is 79% (Plate III, 5–6).

5. Discussion

5.1. Comparison with fossil species

In South America four fossils with bambusoid affinities have been recorded. Berry (1929) cited the first fossil leaf impression record of *Chusquea rolloti* from the Miocene in Colombia. This fossil specimen could correspond to any leaf grasses and does not probably represent a bamboo. Another leaf impression assigned to *Chusquea oxyphylla* by Frenguelli and Parodi (1941) was found in Laguna del Hunco (Patagonia, Argentina). At present, the assignment of this specimen to the extant genus of *Chusquea* is dubious, although its affinity to the Bambusoideae subfamily is not questioned (see Brea and Zucol, 2007).

Table 1
Morphological characteristics of *Guadua morronei* sp. nov. culm and estimated values of height ($H_{est.}$) and critical height ($H_{crit.}$) sensu Niklas (1993, 1994).

Culm in cross-section	Subcylindrical Solid internode Solid node Woody
Internode diameter (cm)	2.9 × 2.0
Node diameter (cm)	3.3 × 2.3
Total length (cm)	12
Estimated height ($H_{est.}$) (m)	3.08–3.30
Critical height ($H_{crit.}$) (m)	9.25–10.08
Probable bud	
Width (cm)	0.7
Height (cm)	0.5
Nodal region (cm)	1.0

The first reliable mention of petrified bamboo culm was made known by Brea and Zucol (2007), who referred to the presence of *Guadua zuloagae* in the Ituzaingó Formation. *Guadua zuloagae* showed a great affinity with the extant species of *Guadua angustifolia* (Table 3) (Brea and Zucol, 2007). Recently, the fourth macrofossil bamboo record assigned to cf. *Guadua* was found in the Madre de Dios Formation, in the southwestern Peruvian Amazon (Olivier et al., 2009). These bamboo macrofossils, assigned to cf. *Guadua* by Olivier et al. (2009) are not well preserved anatomically, which limits comparisons with *Guadua morronei* sp. nov. The Peruvian fossil specimens correspond to a nodal region and show circular sheath scars, monopodial ramifications, thorny or spiny buds or complex branches and a hollow stem structure. *Guadua morronei* sp. nov. differs from the cf. *Guadua* described by Olivier et al. (2009) by the presence of a solid stem structure, vascular bundle shapes and the arrangement of both vascular bundles and sclerenchyma sheaths. The evidence of thorns in the Peruvian fossils and the lack thereof in *G. morronei* sp. nov. are another difference. The thorns are characteristic of almost all modern *Guadua* species (Judziewicz et al., 1999). The lack of thorn-like structures in the *G. morronei* sp. nov. could suggest that this node and internode segment correspond to a basal portion, to different stages of development or that is related to poor preservation of these delicate structures in the fossil material. It must also be taken into account that this fossil specimen was preserved in fluvial sediments where fragile structures usually break and are abraded during transport.

Guadua zuloagae differs from the *Guadua morronei* sp. nov. by the presence of hollow internodes, a culm circular in cross-section, the type of vascular bundles and the occurrence of layers with parenchyma and sclerenchyma cells surrounding the hollow central cavity (Table 3).

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Table 2
Anatomical characteristics of the vascular bundles according to the wall thickness zone. DVB, density of vascular bundles; R/T, radial/tangential diameter of metaxylem vessels.

Vascular bundle (n = 30)	Fossil internode of *Guadua morronei* sp. nov.		
	Periphery zone	Middle zone	Internal zone
DVB ($n\ cm^{-2}$)	195	77	48
Metaxylem radial diameter (μm)			
Mean ± s.e.	30 ± 3.41	42 ± 10.44	64 ± 4.64
Minimum diameter	25	28	58
Maximum diameter	36	81	74
Metaxylem tangential diameter (μm)			
Mean ± s.e.	30 ± 4.73	45 ± 6.42	52 ± 12.40
Minimum diameter	22	33	35
Maximum diameter	35	54	71
R/T	1	0.94	1.23
Fibres (%)	82.38	57.33	49.54

Others leaves and pollen grains in bamboo fossils have been reported in Europe and Japan from the Miocene through the Pliocene (Worobiec and Worobiec, 2005). In European deposits pollen grains assigned to the *Graminidites bambusoides* Stuchlik and leaves of *Bambusa lugdunensis* Saporta have been reported from the middle Miocene in Poland (Worobiec and Worobiec, 2005). There is no convincing evidence to support this assignment because there is no way to confidently assign grass pollen to the subfamily level. Moreover, the Polish fossil leaves are more likely to represent an aquatic monocot than a bamboo.

5.2. Comparison with extant species

The presence of highly lignified culms is an unambiguous and unreversed synapomorphy of the Bambuseae (encompassing what would now be the Arundinarieae and Bambuseae tribes) (GPWG, 2001; BPG, 2012). The tribe Bambuseae is currently recognized as not monophyletic because the Olyreae, the herbaceous bamboos, is a sister to the tropical Bambuseae (Clark et al., 1995; GPWG, 2001; Bouchenak-Khelladi et al., 2008; Sungkaew et al., 2009; Hodkinson et al., 2010).

The woody bamboos were classified geographically according to Clark et al. (1995) into temperate, palaeotropical and neotropical groups (see more information in Clark et al., 1995 and Sungkaew et al., 2009). The Neotropical woody bamboos are a monophyletic lineage with three Bambusoideae subtribes: Arthrostylidiinae, Chusqueinae and Guaduainae (Ohrnberger, 1999 in Sungkaew et al., 2009; Sungkaew et al., 2009 see fig. 1 p. 102; Ruiz-Sanchez, 2011).

The fossil bamboo culm described herein was compared with taxa of Neotropical bamboos (McClure, 1973; Watson and Dallwitz, 1992 onwards; Judziewicz et al., 1999; Clayton et al., 2002 onwards; Londoño et al., 2002; Rúgolo de Agrasar and Rodríguez, 2003; Ruiz-Sanchez,

Table 3
Comparison of morphological and anatomical characteristics between *Guadua morronei* sp., nov. and *Guadua zuloagae* and most related extant species, *Guadua paraguayana* and *Guadua angustifolia*, respectively.
Data taken from Döell, 1880; Burkart, 1969; Judziewicz et al., 1999; Londoño et al., 2002; Rúgolo de Agrasar and Rodríguez, 2003; Brea and Zucol, 2007; Flora Argentina, http://www.floraargentina.edu.ar; Lizarazu et al., 2012.

	Guadua morronei sp. nov.	*Guadua paraguayana* Döll. 1880	*Guadua zuloagae* Brea and Zucol 2007	*Guadua angustifolia* Kunth, 1822
Morphological characteristics				
Culm in cross-section	Subcylindrical Solid internode Solid node Woody	Subcylindrical[d] Solid internode[a,d,e] Solid node Woody	Cylindrical Hollow internode Solid node Woody	Cylindrical Hollow internode[b,c,d] Solid node Woody
Height and height estimated for fossils (m)	3.08–3.30	3–5[a,c]	3.4	10–12[b] ≤30[c]
Internode external diameter (cm)	2.9 × 2.0	2–4[b,d,e]	3.0 × 3.5	10–14[b] 15–20[c]
Internode internal diameter (cm)	–	–	1.6 × 1.7	–
Node diameter (cm)	3.3 × 2.3		3.5 × 4.5	
Nodal region height (cm)	1.0		0.75	
Supranodal ridge	Horizontal	Horizontal	More or less horizontal	More or less horizontal
Sheat scar or nodal line	Horizontal	Horizontal	More or less horizontal	More or less horizontal
Anatomical characteristics				
Vascular bundle in periphery zone				
Shape	Ovoid, small, numerous	Subcircular[f]	Circular, small, numerous	Circular, small, numerous[g]
DVB ($n\ cm^{-2}$)	195	?	340	392[g]
R/T	1	?	1.4	1.4[g]
MTD max (μm)	36	?	45	30[g]
Fibres (%)	82.38	?	77.4	59.4
Vascular bundle in middle zone				
Shape	Subcircular	Subcircular[f]	Ovoid and circular	Ovoid and circular[g]
DVB ($n\ cm^{-2}$)	77	?	86	82[g]
R/T	0.94	?	0.96	0.92[g]
MTD max (μm)	54	?	90	200[g]
Fibres (%)	57.33	?	36.5	19.3[g]
Vascular bundle in internal zone				
Shape	Subcircular	Subcircular[f]	Circular	Circular[g]
DVB ($n\ cm^{-2}$)	48	?	64	77[g]
R/T	1.23	?	0.76	0.52[g]
MTD max (μm)	71	?	170	260[g]
Fibres (%)	49.54	?	34.1	19.7[g]

Key to abbreviations used:

- [a]Döell (1880), [b]Burkart (1969), [c]Judziewicz et al. (1999), [d]Flora Argentina, http://www.floraargentina.edu.ar, [e]Lizarazu et al. (2012), [f]Rúgolo de Agrasar and Rodríguez (2003), [g]Londoño et al. (2002).
- DVB: density of vascular bundles.
- R/T: radial/tangential diameter of metaxylem vessels.
- MTD max (μm): metaxylem tangential maximum diameter.

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2009; Lizarazu et al., 2012). The comparison was based on the following characteristics: the presence of woody and solid culms; the diameter and height of the culms; the type of the bud or buds; the appearance of the nodal region; and the anatomical characteristics of the culms in cross-section.

Therefore, the comparisons of *Guadua morronei* sp. nov. were made with the genera included within the subtribe Guaduinae and *Chusquea* Kunth. The subtribe Guaduinae comprises the following genera: *Apoclada* McClure, *Eremocaulon* Soderstr. and Londoño, *Guadua*, *Olmeca* Soderstr., and *Otatea* (McClure and E. W. Sm.) C.E. Calderón and Soderstr. (Judziewicz et al., 1999; BPG, 2012). Recently, plastid DNA sequence data (Clark et al., 2007; Ruiz-Sanchez et al., 2008) unequivocally support the status of *Guadua* as an endemic neotropical genus (Olivier et al., 2009). In addition, this molecular analysis supports the recognition of the monophyletic subtribe Guaduinae, including its five genera.

The solid internodes are characteristics of the majority of the *Chusquea* species but this genus differs from the new fossil described herein in the size and form of the vascular bundles (Rúgolo de Agrasar and Rodríguez, 2003) and in its bud types (Judziewicz et al., 1999).

Guadua morronei sp. nov. differs from *Apoclada* because the extant genus presents hollow to sometimes solid culms with branch complements at the midculm nodes that range from 1 to 15 and a separate equal branch with buds in a single line above the nodal line, often rebranching near their bases (Judziewicz et al., 1999; BPG, 2012). *Eremocaulon* and *Olmeca* are not related to the new species because they have hollow culms (Judziewicz et al., 1999). It resembles *Otatea* because it presents a single bud, but differs from it because the extant genus is pith-filled throughout when young and tends to become hollow throughout at maturity, whereas some species are thick-walled to almost solid culms (Judziewicz et al., 1999; Ruiz-Sanchez, 2009, 2012). The anatomy of the vascular bundles of *Otatea* is unknown.

Based on the above, the fossil culm study herein shows more affinity to *Guadua* than to any other Neotropical genus. The most significant similarities are the unique combination of the well-marked nodal region with the horizontal nodal line, the type of bud and the solid culm. Moreover, the anatomical characteristics are very similar to *Guadua*, especially the epidermis with a layer of sclerified cells with thick external wall, subepidermal parenchyma formed by 3–4 layers of sclerified cells, vascular bundles in 7 or more alternating cycles, and the type and shape of the peripheral, middle and internal vascular bundles. All these characteristics establish a close relationship with the extant *Guadua paraguayana* (Table 3) (Döell, 1880; Judziewicz et al., 1999; Rúgolo de Agrasar and Rodríguez, 2003; Flora Argentina, 2012; Lizarazu et al., 2012). The culm of *G. paraguayana* has a length of 3–10 m and a diameter of 2–4 cm and is subcylindrical in cross-section, woody, with node and internode solid. The nodal line and the supranodal ridge are horizontal (Flora Argentina, 2012; see specimens SI 21636 and SI 26828).

6. Conclusions

The number of recorded fossil taxa assigned to the Bambusoideae subfamily in the Ituzaingó Formation is increased with the description of the new petrified bamboo culm. The morphological and anatomical characteristics observed in this specimen support the proposal of a new species, *Guadua morronei* sp. nov. This bamboo culm is the first *Guadua* fossil species with a solid internode.

Guadua morronei sp. nov. indicates a warmer and more humid climate during the Pliocene–Pleistocene for this region and is probably associated with tropical and subtropical forests that developed during the deposition of the Ituzaingó Formation.

Moreover, the presence of this fossil supports the hypothesis of a South American origin for the Neotropical woody bamboos and adds new information for future research regarding the phylogeny of the subfamily Bambusoideae.

The fossil evidence suggests that *Guadua* has been present in northeastern Argentina at least since the Pliocene–Pleistocene and reconfirms the idea of Brea and Zucol (2007) that the genus *Guadua* was more widespread in the past.

The record of *Guadua zuloagae* (Brea and Zucol, 2007) together with the new fossil described here, *Guadua morronei* sp. nov., coincides with the diversification of *Guadua* during the Pliocene according to the molecular dating proposed by Ruiz-Sanchez (2011).

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