The occurrence of Potamomyces palmarensis sp. nov. in the Late Holocene of El Palmar National Park (Colón, Entre Ríos, Argentina) and transfer of fossil species of Mediaverrunites to Potamomyces

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The occurrence of *Potamomyces palmarensis* sp. nov. in the Late Holocene of El Palmar National Park (Colón, Entre Ríos, Argentina) and transfer of fossil species of *Mediaverrunites* to *Potamomyces*

Noelia Nuñez Otaño[a], Mercedes di Pasquo[a] and M. Virginia Bianchinotti[b]

[a]Laboratorio de Palinoestratigrafía y Paleobotánica, CICYTTP—CONICET, Dr. Matteri y España S/N, Diamante (E3105BWA), Entre Ríos, Argentina; [b]CERZOS-UNS, CONICET-CCT Bahía Blanca, Camino La Carrindanga km 7, Bahía Blanca (B8000FWB), Buenos Aires, Argentina

ABSTRACT

We present the first record of *Potamomyces* Hyde (Ascomycota, Dothideomycetidae) from soil sediments of the El Palmar National Park, Entre Ríos, Argentina. Nineteen samples were taken (each 2–4 cm from the surface) of a 80 cm thick core composed of a homogeneous lithology of argillaceous fine-grained sands. This taxon was only identified in the basal sample of the core (371 ± 30 years BP), located in a palm area (*Butia yatay*) with a semi-dense herbaceous-shrub layer. We propose an amendment of the generic diagnosis based on the revision of the species described up to now, and of a new one here defined (*P. palmarensis*). Additionally, we confirm that the morphotaxon *Mediaverrunites* Jarzen & Elsik ex Nandi & A. Sinha is its junior synonym, so we propose new combinations for seven species. We recommend the use of this natural taxon instead of the morphotaxon in future contributions. In terms of the geographical and stratigraphical distribution of *Potamomyces*, our record is the first mentioned for Argentina and the southernmost for South America. Based on its ecological requirements, a humid sub-tropical environment and abundant organic matter in the soil are suggested for the Latest Holocene of the study region. This hypothesis is supported by current knowledge of regional climatic and environmental conditions for the study area during the short humid interval of the Little Ice Age.

1. Introduction

Palaeopalynological studies can provide, among other things, evidence for past changes in climate (e.g. Overpeck et al. 1990; Davis & Shaw 2001), biomes (e.g. Jolly et al. 1998; Tarasov et al. 1998; Williams et al. 2004) and biodiversity (e.g. Rull 1987; Brown 1999; Odgaard 1999) across the geological record. The accurate identification of fossil pollen, spores and other biological remains underpins our ability to reconstruct the vegetation of the past and subsequently infer variations in the Earth's systems. Among the non-pollen palynomorphs, fungi are recognised as valuable palaeoindicators (Cugny et al. 2010; Gelorini et al. 2011, 2012; van Geel et al. 2011). Fossil fungi are generally fragmentary; their spores are by far the best preserved and more commonly found fungal remains. Naming fossil fungal spores is a matter of debate; the morphological approach (van der Hammen 1956) is still in use and several artificial taxonomic systems that rely only on spore attributes have been developed (Misra & Deshmukh 2009; Taylor et al. 2015). However, when relationships can be established among fossil spores and extant taxa from which the ecology, life cycle or other biological features are known, the value of a fungal spore as a palaeoecological proxy undoubtedly increases (van Geel & Aptroot 2006; Haas

2010; Kramer et al. 2010; Cook et al. 2011; Wieckowska et al. 2012). This is not an easy task, and it can be achieved only when spores have some distinctive features. The distinctive combination of biconic shape, absence of septa and presence of verruca-like, hollow projections led Schlütz & Shumilovskikh (2013) to establish the link among the fossil genus *Mediaverrunites* Jarzen & Elsik ex Nandi & A. Sinha with the extant *Potamomyces* Hyde (Ascomycota, Dothideomycetidae). *Potamomyces* was originally described from wood submerged in fresh water, recovered from a tropical river (Hyde 1995). Our aim is to present the first record of *Potamomyces* in the Late Holocene of Argentina. The revision of the generic status and its species allows us to propose an amendment of its diagnosis and a new species. *Mediaverrunites* is confirmed herein as the junior synonym of *Potamomyces*, and new taxonomic combinations are proposed. These taxonomic revisions are necessary because the use of fossil form-genera, where the fungi can clearly be assigned to a modern genus, is in violation of the Melbourne Code (McNeill et al. 2012; Zhang et al. 2013). A palaeoenvironmental interpretation of the horizon in which it occurs is discussed on the basis of its ecological requirements, and palaeoclimatic and biogeographical inferences are addressed.

2. Material and methods

2.1. Location

The El Palmar National Park is part of the El Palmar river basin located in the Entre Ríos province, Argentina (Figure 1A), and is where the southernmost ecotome defined by the palm *Butia yatay* associated with grasslands has been preserved since 1965. In 1970, intentional fires were suppressed and domestic cattle were removed and excluded from the park. Since then, several shrub and tree species, both native and exotic, have
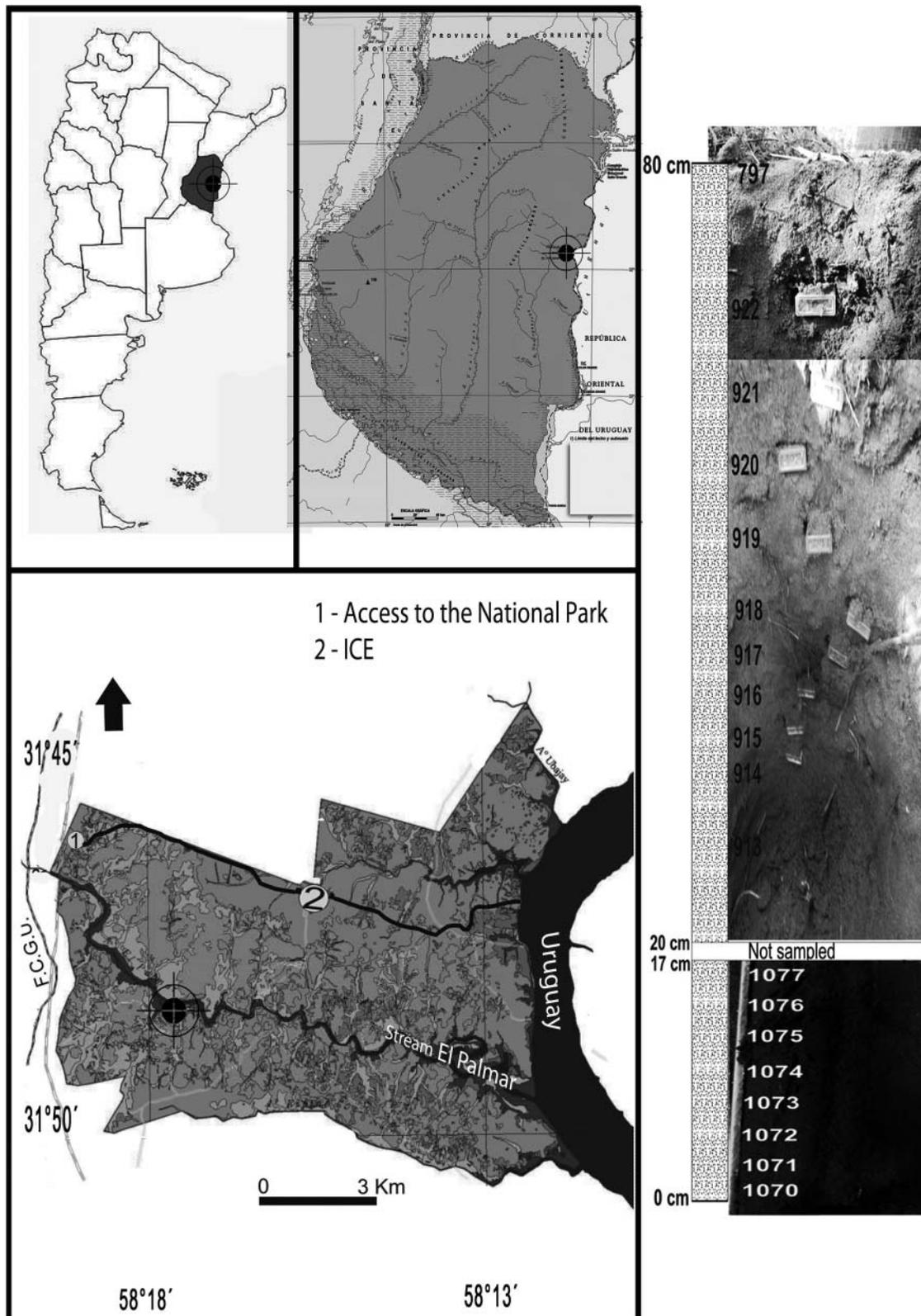

Figure 1. Geographical location of the El Palmar National Park, Entre Ríos Province, Argentina, and of the borehole in the protected area of the park. On the right is presented the distribution of the samples in the borehole (the numbers correspond to the CICYTTP-Pl acronym of the Palynological Collection at the CICYTTP). The isotope data of the samples are: CICYTTP-Pl 1070 (371 ± 30 ^{14}C yr BP) and CICYTTP-Pl 1077 (277 ± 30 ^{14}C yr BP). ICE = División de Incendios, Comunicaciones y Emergencias [English: ICE (Fire, Communications and Emergency Division)].

started a rapid process of colonisation (Ruiz Selmo et al. 2007; Rolhauser et al. 2011). This region is characterised by a humid temperate levee ecosystem within a mosaic of habitats with different vegetation structures distributed according to soil conditions, classified as: grasslands and palm zones; xerophytic or semi-xerophytic forests; riparian forests; scrublands; flooding zones; and quarries (Ciccero & Balabusic 1994; Bilenca & Minarro 2004; Batista et al. 2014).

The general climate of this open unrestricted plain is temperate humid. It is characterised by the influence of humid northeast winds; cool and dry southwest winds (causing sudden changes in the weather); and southeasterly winds (cold air saturated with moisture), which lead to weeks of overcast, rainy and stable temperatures. The average annual temperature is 19°C and frost may occur from May to September, with variations from 51 to 134 days between the first and last frosts. The annual average rainfall is 1346 mm (Rolhauser et al. 2011), concentrated in the summer months. However, high temperatures induce frequent water deficits, increasing the chances of fire events during this period (Goveto 2006).

The present subsurface palynological analysis is the first carried out in the park. The core (Figure 1B) was obtained in a palm zone (Palm savanna, 31°53′53.07″S; 58°16′38.66″W), which is the most important ecosystem in the park and covers 60% of the total protected area. It is composed of a high diversity of plant species, but it is mostly dominated by *Butia yatay*, the indigenous palm species. Shrub (e.g. Mimosoidea) and epiphytic species (mostly pteridophytes, bromeliads, bryophytes and lichens) are also present. The herbaceous layer (similar to the grassland areas) is characterised by several types of grasses, and the fern *Adiantopsis chlorophylla* is widely represented in a dense and high herbaceous tapestry. It keeps its green colour through most of the year, except in times of drought when it takes a greyish-yellow cast, and is prone to fires. Soils are well drained and composed of a mixture of brown sand and clay. The aeropalynological analysis of this region reveals a diverse array of fungal spore morphotypes mostly correlative to its local vegetation (Nuñez Otaño et al. 2015a).

2.2. Sample collecting and processing

Nineteen samples were obtained (March 2014) from the surface down to a depth of 80 cm in a borehole and a short core extracted from a homogeneous lithology consisting of brown argillaceous fine-grained sands (Figure 1B). A surface sample (2 cm) was collected and, beginning 8 cm below the surface sample, samples were taken from the wall of a 50-cm bore using small boxes inserted into it and spaced between 3 and 5 cm apart. The exposed sediments were then covered with a film to prevent caving while a short core was taken of the underlying interval. The remaining 20 cm of the section to the base of the interval was sampled with a tube/pipe 25 cm in diameter; the uppermost part (3 cm) of the core was discarded due to contamination concerns. The core was sliced in half in the laboratory immediately upon return from the field, and 2-cm-thick slabs were taken through an entire half of the core. The samples were processed following a combination of

techniques for Quaternary and pre-Quaternary palynomorphs (e.g. Traverse 2007; Salgado−Labouriau 2007). Hydrochloric acid (HCl) was not used initially, as samples are not calcareous. Two *Lycopodium* tablets (batch #177745) and hydrofluoric acid (HF, 45%) were added to the tube and allowed to digest for 3 days, during which time the samples were periodically agitated. Samples were neutralised through several cycles of rinsing with distilled water, centrifugation and decanting. The resulting residue was sieved with 25-μm and 10-μm mesh, and returned to a tube. One slide of each residue was made by mixing a drop of the residue with glycerine and sealing it beneath a coverslip with paraffin. All the samples yielded palynomorphs along with other organic particles, and they were treated as appropriate to reduce non-palynomorph debris (i.e. HF for a second time, boiling with HCl, potassium hydroxide (KOH), zinc chloride ($ZnCl_2$)) before acetolysis (Erdtman 1960). Finally, several slides were mounted in glycerin and sealed with paraffin whilst others were mounted in glycerin jelly (as permanent mounts) to be stored in the Centro de Investigaciones Científicas y Transferencia de Tecnologías a la Producción (CICYTTP) palynological repository catalogued under the acronym CICYTTP-Pl, housed in the Laboratory of Palynostratigraphy and Paleobotany (CICYTTP-CONICET), Diamante, Entre Ríos (di Pasquo & Silvestri 2014). Palynomorphs were studied and illustrated with a trinocular transmitted light microscope equipped with a digital camera (Leica DM500 and Leica EC3, 3.0 Mp).

2.3. Chronology

Two samples, one from the bottom (CICYTTP-Pl 1070) and another from the top (CICYTTP-Pl 1077) of the short core, were selected for carbon isotope analysis and prepared for that purpose as follows: samples were dried at 60°C and carefully cleaned of roots, small stems and other possible contaminants, following the instructions given by the Accelerator Mass Spectrometry (AMS) Arizona Laboratory (University of Arizona, USA), where they were analysed. The two results, obtained in February 2015, were 371 ± 30 ^{14}C yr BP and 277 ± 30 ^{14}C yr BP respectively. They were calibrated with SHCal13 (Hogg et al. 2013) and have a 95.4% probability (Figures 1B, 2).

3. Taxonomy

While molecular genetics are used for modern fungal taxonomy, many palynologists and geologists still depend on artificial taxonomic systems based on spore features. These systems do not necessarily result in names with any bearing on the biology or actual taxonomy of the organism, but provide a useful identifier for use in biogeography, biostratigraphy, palaeoenvironmental reconstructions and interpretations of palaeoclimatic changes. Due to the distinctive morphology of its spores, the monotypic *Potamomyces* (Hyde 1995) can be easily recognised in both modern and ancient settings. It was not considered by Nandi & Sinha (2007), Elsik & Jarzen (2009) and Sancay (2014), probably due to the lack of collaboration between modern mycologists and palynologists. This genus, while an uncommon component of individual floras, seems to be widely distributed

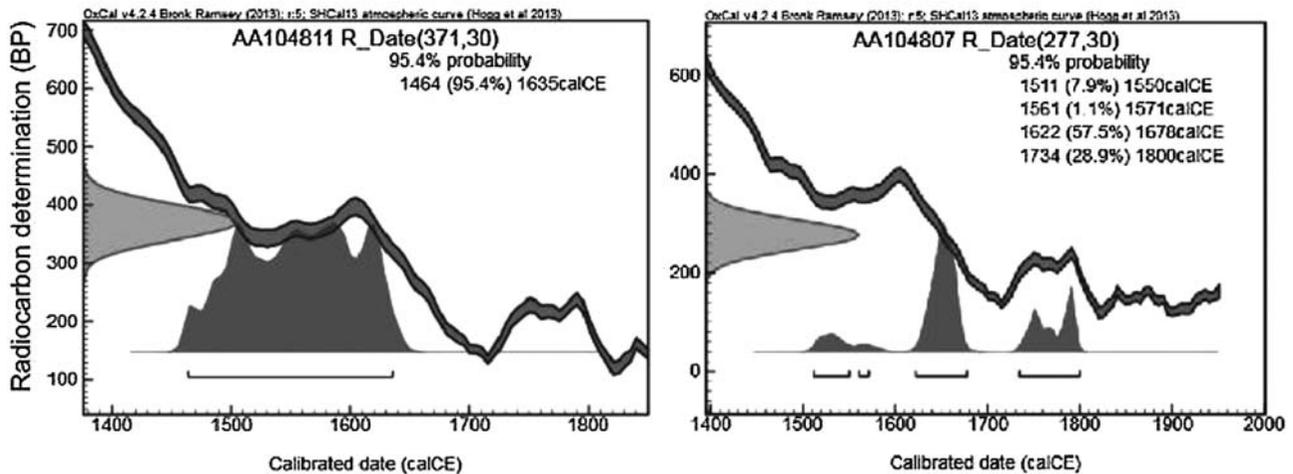| Lab No. (CICYTTP-PI)	Field Sample Number	Lab ¹⁴C Arizona AMS	Age 14C yr BP	Calibrated age (calCE) (SHCal13 Hogg et al. 2013, CALIB 7.0.0)
1077	Tauber 3 (M8)	AA104807R AMS	277 ±30 BP	1622-1678 (57,5%), 1734-1800 (28,9%), 1511-1550 (7,9%)
1070	Tauber 3 (M1-Base)	AA104811 AMS	371 ±30 BP	1464-1635 (95,4%)

Figure 2. Data from carbon isotope analysis provided by the Accelerator Mass Spectrometry (AMS) Arizona Laboratory (University of Arizona, USA) calibrated with SHCal13 (Hogg et al. 2013).

in pantropical and subtropical regions (Schlütz & Shumilovskikh 2013). As Schlütz & Shumilovskikh (2013) predicted, the study of subsurface samples in a previously unexplored subtropical habitat allowed us to identify a previously undescribed species of *Potamomyces*, a genus recorded for the first time in Argentina. Schlütz & Shumilovskikh (2013) originally reported the link between *Mediaverrunites* and *Potamomyces* based on material from Nepal, and summarised significant contributions concerning the ecology of *Potamomyces* and its past and present distribution. These authors described a new species (*P. nepalensis*) and compared it with the type species of the genus and other species of *Mediaverrunites*. However, their publication is considered invalid as they published the name without an identifier from a recognised repository (Zhang et al. 2013) and without submitting it to Mycobank. As stated in Art. 42.1 of the last International Code of Nomenclature for algae, fungi and plants (McNeill et al. 2012), this is a requirement for the valid publication of names of organisms treated as fungi (including fossils). Therefore, the name is here validated and ascribed to Schlütz & Shumilovskikh (2013) based on their original descriptions and illustrations. The same consideration applies for *Mediaverrunites batii* and *M. pontidiensis*. Both species are here validated and ascribed to Sancay (2014) based on original descriptions and illustrations, although Sancay did not himself deposit the types or register them with Mycobank. Also, as we effected the taxonomic revision of this genus, we confirm that *Mediaverrunites* is a junior synonym of *Potamomyces*. Hence, we propose new combinations of its species in *Potamomyces*, and recommend the usage of this name even when studying fossil assemblages. We make this recommendation because the natural taxon is

ecologically useful for reconstructing palaeoenvironmental and palaeoclimatic changes over time, more so than morphotypes even through their known biological affinities (van Geel & Aptroot 2006; Cook et al. 2011; Wieckowska et al. 2012; Schlütz & Shumilovskikh 2013; Sancay 2014).

3.1 Systematics

Kingdom Fungi
Phylum ASCOMYCOTA
Subphylum PEZIZOMYCOTINA
Class DOTHIDEOMYCETES
Subclass DOTHIDEOMYCETIDAE
Genus *Potamomyces* Hyde 1995, emend. nov. Mycobank
MB 27626

Type species. *Potamomyces armatisporus* Hyde 1995. Mycobank MB 413894

Original description. Ascomata ovoid, nonostiolate, immersed, semi-immersed or some superficial, splitting by rupture of the wall. Peridium comprising an outer stratum of black tissue and an inner layer of brown angular cells. Asci eight-spored, cylindrical, thin-walled. Ascospores biconical, dark-brown when mature, one-celled, thick-walled, armour-like, and with four black tubercles around the equator and a germ pore at one end.

Holotype. *Queenslandia septentrionali*, Atherton Tablelands, Clohesy River, Australia, ad ligmun submersum, June 1991, K.D. Hyde 822, BRIP 21490.
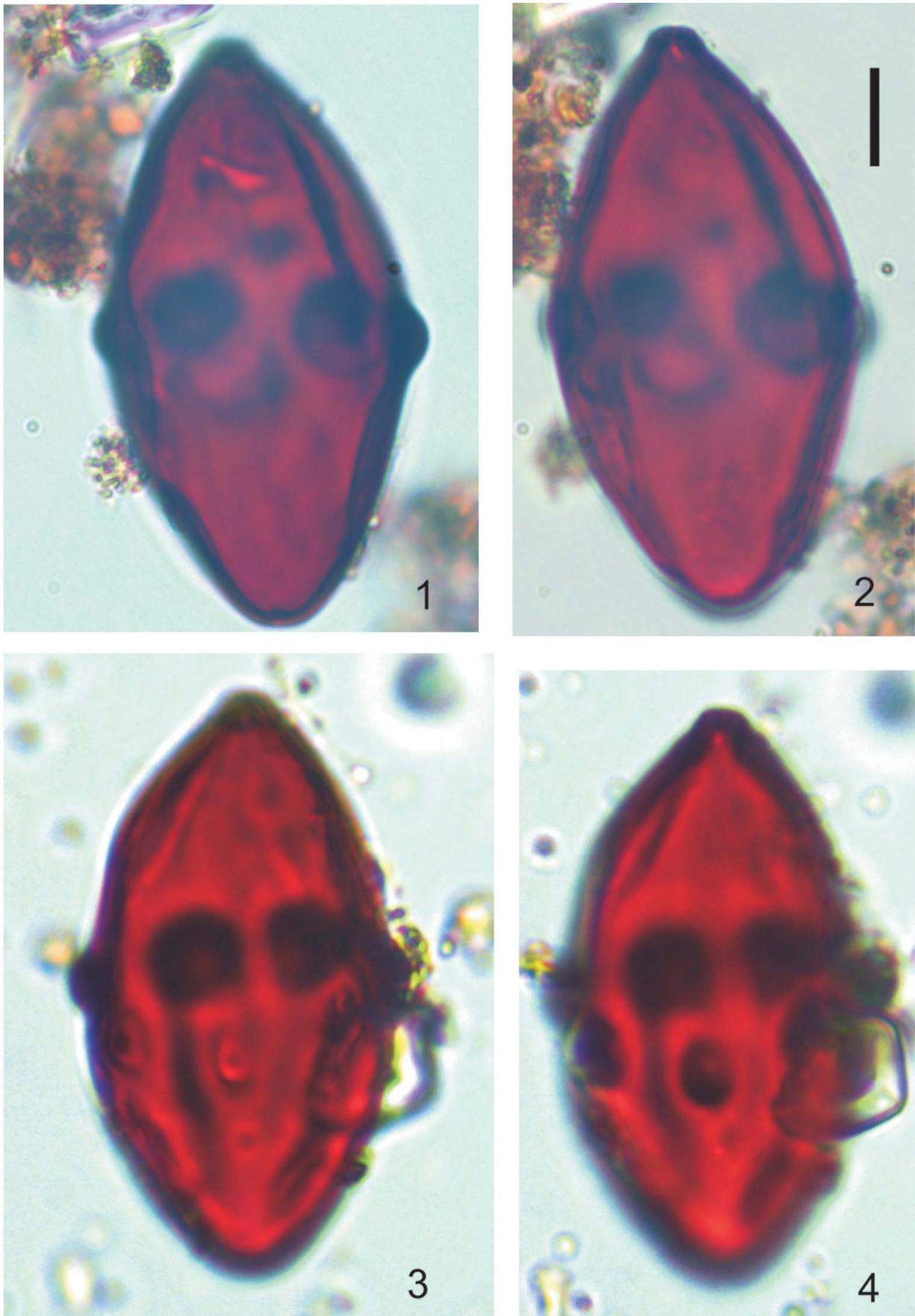
Plate 1. *Potamomyces palmarensis* holotype (MB 814693). Figure 1. Focus on the equatorial knobs. Figure 2. Focus on the pore structure. Figure 3. Focus on the equatorial knobs. Figure 4. Focus on three knobs below the equator. Scale bar = 10 μm. All the material in this paper is curated at the Laboratorio de Palinoestratigrafía y Paleobotánica, CICYTTP-CONICET, Dr. Matteri y España S/N, Diamante (E3105BWA), Entre Ríos, Argentina.

Emended diagnosis. Ascomata ovoid, nonostiolate, immersed, semi-immersed or some superficial, splitting by rupture of the wall. Peridium comprising an outer stratum of black tissue and an inner layer of brown angular cells. Asci eight-spored, cylindrical, thin-walled. Ascospores one-celled, biconical, fusiform, oval to elliptical, dark-brown, thin or thick-walled, armour-like, with four or more distinct tubercles or verrucae, and a single pore, simple or complex, at one end of the polar axes. Tubercles mostly arranged around the equator within a thin to wide, dark to light and low to high equatorial shadow-like rim. Verrucae rarely distributed irregularly on the spore.

Remarks. The emendment is proposed to include specimens with four or more verrucae or tubercles mainly around the equator.

Potamomyces palmarensis sp. nov.
MycoBank MB 814693. Plate 1, figures 1−4

Description. Ascospore unicellular, biconic, overall outline oval to oval-elliptical, gradually narrowing at both ends, wall thick, dark brown, smooth and two-layered, 60 × 35 µm. Monoporate, pore situated at one end of the spore, slightly protruding, 3−4 µm in diameter. Four distinctive knobs/verrucae are arranged unevenly around the equator, and another three slightly below the equator; knobs/verrucae 2.5−4.5 µm height and 6−9.5 µm in diameter. The subfossil ascoma has not been recorded.

Holotype. CICYTTP-Pl 1070-1(+10). England Finder coordinates Z25/0.

Etymology. It refers to the place where it was found.

Location. Concordia Formation (Late Holocene; Iriondo 2010), El Palmar National Park, Entre Ríos, Argentina (Figure 1A).

Remarks and comparisons. This species differs from others of the genus by the particular combination of spore size and shape, and number and position of verrucae (Plate 1; Tables 1 and 2).

Extant species here accepted (Plate 2; Table 1).

Potamomyces armatisporus Hyde, Nova Hedwigia. 61
(1−2): 132. 1995.
MycoBank MB 413894
Potamomyces nepalensis Schlütz & Shumilovskikh
MycoBank MB 814694

Holotype. Permanent slide Nepal OP1027.1, LSh-78 a, b (surface sample from Nepal); 2013, p. 311

Validating description and illustrations. Schlütz F, Shumilovskikh LS. 2013. On the relation of *Potamomyces armatisporus* to the fossil form-type *Mediaverrunites* and its taxonomical and ecological implications. Fungal Ecology 6: 309−315.

Fossil species here transferred to *Potamomyces* (Plate 2; Table 2).

Potamomyces batii (Sancay) comb. nov.
MycoBank MB 814793

Basionym. *Mediaverrunites batii* Sancay, Palynology 38 (1): 35. 2014.

Holotype. Well B, Archive Number 17644, England finder coordinates M-16, 64.8 mm.

Validating description and illustration. Sancay RH. 2014. The occurrence of *Mediaverrunites* in the Upper Miocene of the Black Sea, Turkey. Palynology 38(1): 28−37.

Potamomyces elsikii (Nandi & A. Sinha) comb. nov.
MycoBank MB 814695

Basionym. *Mediaverrunites elsikii* Nandi & A. Sinha, Palynology 31: 99. 2007. MycoBank MB 568744.

Potamomyces fournierii (Elsik & Jarzen) comb. nov.
MycoBank MB 814696

Basionym. *Mediaverrunites fournierii* Elsik & Jarzen, Palynology 33(2): 102. 2009. MycoBank MB 568003.

Potamomyces invaginatus (Elsik & Jarzen) comb. nov.
MycoBank MB 814698

Basionym. *Mediaverrunites invaginatus* Elsik & Jarzen, Palynology 33(2): 102. 2009. MycoBank MB 568011.

Potamomyces magnus (Elsik & Jarzen) comb. nov.
MycoBank MB 814697

Basionym. *Mediaverrunites magnus* Elsik & Jarzen, Palynology 33(2): 102. 2009. MycoBank MB 568012.

Potamomyces mulleri (Nandi & A. Sinha) comb. nov.
MycoBank MB 814692

Basionym. *Mediaverrunites mulleri* Nandi & A. Sinha, Palynology 31: 98. 2007. MycoBank MB 568745.

Potamomyces pontidiensis (Sancay) comb. nov.
MycoBank MB 814794

Basionym. *Mediaverrunites pontidiensis* Sancay, Palynology 38 (1): 35. 2014.

Table 1. Comparison of the ascospores of the extant species of *Potamomyces*.

	Potamomyces armatisporus		P. nepalensis	P. palmarensis
Dimensions	42−51 × 18−25 µm	41−45 × 20.5−22 µm	(44−) 50−54 × 21.5−27 µm	60 × 35 µm
Verrucae number and position	4	4	6 (8)	4 equatorial − 3 subequatorial
Height		2.5 µm	2−2.5 µm	3−4 µm
Diameter		12 µm	5−14 µm	6−6.3 × 9−9.4 µm
Cavities observed	n.d.*	(+)	(+)	(-)
Folds				
Wall				Smooth and two-layered
Apical pore				3−4 µm
Reference	Hyde (1995)	Schlütz & Shumilovskikh (2013)	Schlütz & Shumilovskikh (2013)	This paper

*n.d. = not defined.

Table 2. Comparison of ascospore features in fossil species of *Potamomyces*.

	Potamomyces elsikii	P. mulleri	P. fournierii	P. invaginatus	P. magnus	P. batii	P. pontidiensis
Dimensions	25−45 × 40−55 μm	70−85 × 35−45 μm	42−52 × 27−37 μm	46 × 28 μm	78 × 46 μm	32.2−41.3 × 53.1−64.4 μm	25.2−37.2 × 40.9−59.6 μm
Equatorial verrucae	6−8 (> 8)	4 o > 8	5 a 6	(3−) 4 (−5)	7 a 8	3 a 4	3 a 4
Verruca height	1−2 μm	2−6 μm	1.5−3 μm		1.5−2 μm	0.7−1 μm	2.3−3 μm
Verruca diameter	4−6 μm	8−10 μm	5−7 μm	10−12 μm	8−10 μm	7.3−10.1 μm	7.1−11.8 μm
Cavities observed	Not defined	Not defined	(+)	(+)	(+)		
Folds		Equatorial shadow-like rim	Unique with elongate costae (folds?)			Equatorial shadow-like rim	Equatorial shadow-like rim, mostly distinct
	Nandi & Sinha (2007)	Nandi & Sinha (2007)	Elsik & Jarzen (2009)	Elsik & Jarzen (2009)	Elsik & Jarzen (2009)	Sancay (2014)	Sancay (2014)

Holotype. Well A, Archive Number 19285, England finder coordinates H-9/2, 53.4 mm.

Validating description and illustration. Sancay RH. 2014. The occurrence of *Mediaverrunites* in the Upper Miocene of the Black Sea, Turkey. Palynology 38(1): 28−37.

4. Discussion

4.1. Age and regional climatic inferences

We present the finding of *Potamomyces* in the basal sample of the stratigraphical section that was dated at 371 ± 30 ^{14}C yr BP, likely equivalent to 1635 years cal CE (seventeenth century). Hence, the horizon corresponds to the Upper Holocene upper member of the Concordia Formation after Iriondo & Kröhling (2008), which was considered the lower terrace of the Uruguay River, as old as 1000 years BP. In agreement with previous authors, the lithology of this unit is characterised by homogeneous silt-fine grained sands with variable proportions of clay, which is unconsolidated and free of calcareous matter. Based on the carbon-14 (^{14}C) information here provided, the uppermost 10 cm of the upper part of the borehole would represent ca. 30 years, and in its lower part the sedimentation rate suggests 1 cm for 5 years. The accumulation of sands in these soils occurs protected from the erosion of wind and rain by the vegetation (palms and shrubs). Hence, the differences in time average registered along the borehole are likely the consequence of slight compaction.

Two palaeoclimatic phases were documented during the Latest Holocene, the Medieval Warm Period (1050−700 yr. BP, Cohen et al. 2001) and the Little Ice Age (LIA, 550−200 yr. BP, Haug et al. 2001), as characterised on the basis of several proxy data, mostly from Europe. In the Pampa region of Argentina, the first interval (1400−800 yr. BP) was described by Iriondo (2010) as being more humid and warmer than today, and associated with the development of soils and alluvial systems, while the LIA was colder and drier, and aeolian processes dominated during the American colonisation (1492 yr. cal CE). Hence, our single record of *Potamomyces* dated ca. 1635 years cal CE (seventeenth century), would have been part of a short interval of more humid conditions (similar to current climatic conditions) documented from the end of the sixteenth century up to the beginning of the eighteenth century during the LIA (Cioccale 1999, in Iriondo 2010). This amelioration of the climatic conditions is in agreement with the ecological requirements of *Potamomyces*, as it is found growing on wood in tropical rivers and in moist terrestrial environments of tropical and subtropical regions. Moreover, under subtropical conditions, it proliferates during rainy seasons (Hyde 1995; Schlütz & Shumilovskikh 2013). As an example of the latter, from subsurface sediments of the Vereda Laçador in Chapadão dos Gerais (Mina Gerais, Brazil), Cassino & Meyer (2013) recorded *Mediaverrunites* sp. in variable proportions from ca. 13,000 years BP up to 1300 years BP (Figure 3). They found a positive relationship between the abundance of this taxon and the palm *Mauritia flexuosa* during more humid intervals interpreted as the forest expansion into the savanna. In our study area at the El Palmar National Park, a high availability of organic matter in the soil under humid conditions can be supported on the basis of the preliminary palynological analysis of the basal level bearing *Potamomyces*. Several fungal morphotypes (more than 13), pollen grains of angiosperms and gymnosperms (*Butia yatay*, *Pinus* sp., Asteraceae Asteroidea, Amaranthaceae, Malpighiaceae, Bromeliaceae, Poaceae, Polygonaceae), fern spores (*Adiantopsis chlorophylla*, *Microgramma mortoniana*), and unidentified spores of bryophytes and *Chlamydomonas* were encountered. However, this hypothesis will be fully tested using ecological data provided by the complete palynological analysis of our sample suite.

4.2. Biogeography

Concerning the stratigraphical and geographical distribution of the species of *Potamomyces* and those formerly named *Mediaverrunites*, they are known since the Miocene (Figure 3) in Africa (Jarzen & Elsik 1986), Australia (Hyde 1995; Macphail et al. 2001), India (Banerjee & Nandi 1992; Nandi & Sinha 2007; Schlütz & Shumilovskikh 2013), Jamaica (Germeraad 1979), the Mediterranean (Sancay 2014), North America (Elsik 1996; Saxena 2006), Pacific Islands (McPhail & Hope 2006; Jarzen & Dilcher 2009), Venezuela (Rull & Vegas-Vilarrubia 1999), Colombia (Muller 1959; Elsik & Jarzen 2009; Montoya et al. 2010; Navarrete et al. 2015) and Brazil
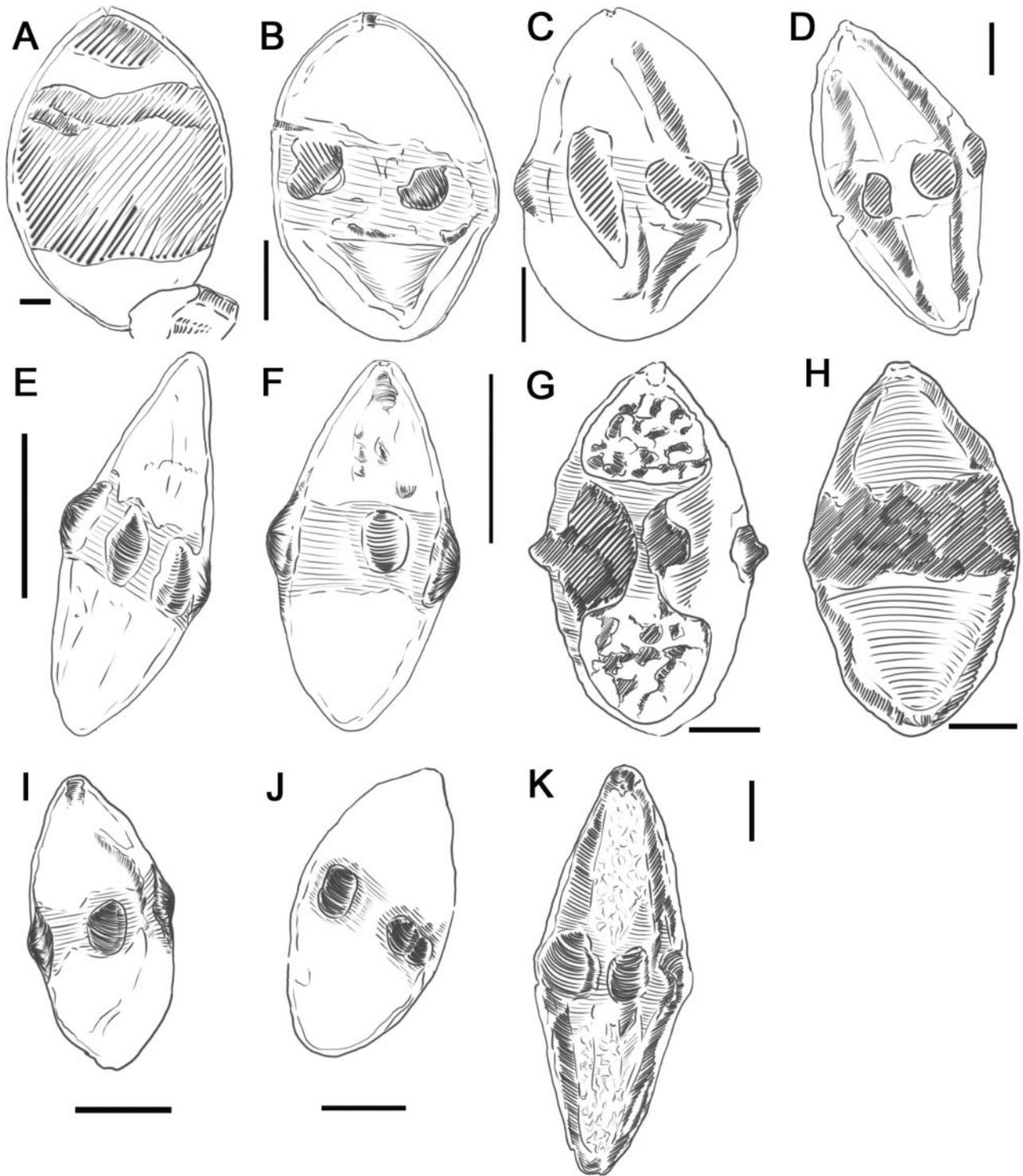
Plate 2. A. *Potamomyces magnus*. B. *P. invaginatus*. C. *P. fournieri*. D. *P. elsikii*. E. *P. nepalensis*. F. *P armatisporus*. G, H. *Potamomyces armatisporus*. I. *P. batti*. J. *P. pontidiensis*. K. *P. mulleri*. Scale bars A, B, C, D, G, H, K = 10 μm; E, F, I, J = 20 μm. Illustrations by N. Nuñez Otaño.

(Dupont et al. 2009; Guimarães et al. 2013; Cassino & Meyer 2013). Therefore, our record is the southernmost one for South America although it is not present today in the region studied (Nuñez Otaño et al. 2015a, 2015b). This implies that under similar ecological conditions, either the climatic tolerance of this taxon may be broader than previously thought, or the extension of its geographical limits is favoured by warmer and more humid conditions.
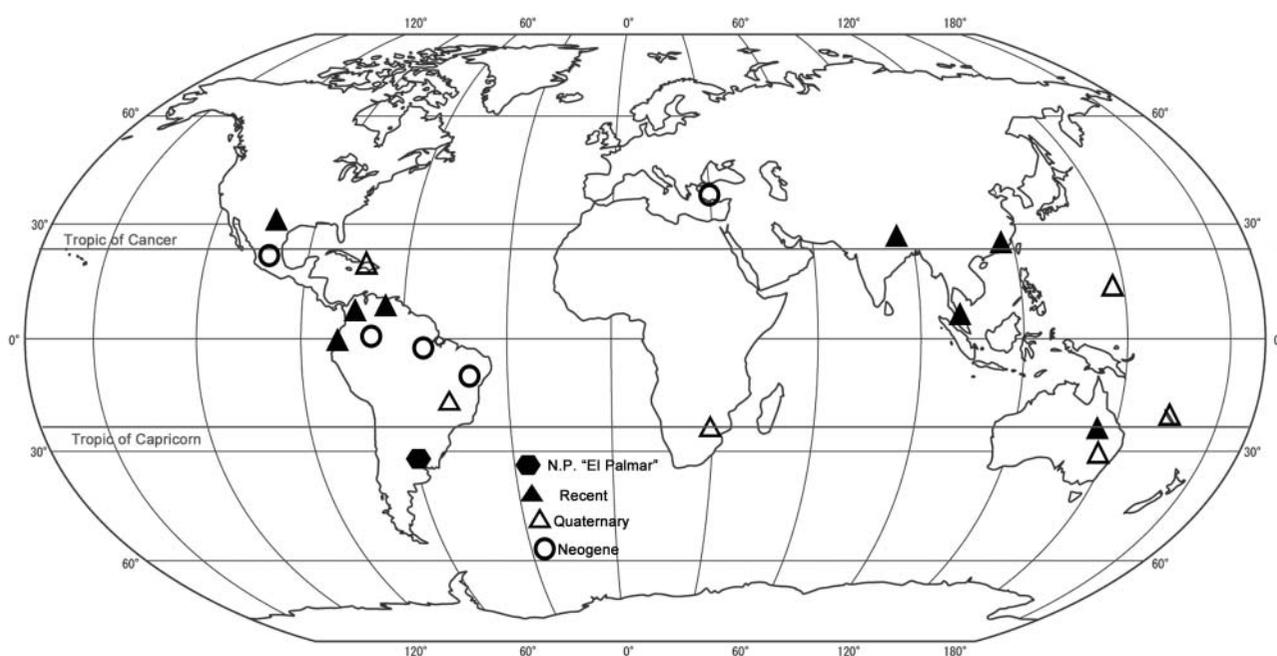
Figure 3. Geographical and stratigraphical distribution of *Potamomyces* (modified from Schlütz & Shumilovskikh 2013). N.P = National Park.

5. Conclusions

Potamomyces (Ascomycota, Dothideomycetidae) is recorded for the first time in the subsurface sediments of the El Palmar National Park, Entre Ríos, Argentina, and from the geographical and stratigraphical revision of its species it is the southernmost record of the genus in South America. The single record came from the basal sample of a borehole down to a depth of 80 cm in a homogeneous lithology of argillaceous fine-grained sands located in an ecotome dominated by the palm *Butia yatay* with a semi-dense herbaceous-shrub layer.

The taxonomic revision of the two extant species of *Potamomyces* and the seven species of its junior synonym *Mediaverrunites* (a palynological morphotaxon) allowed us to propose the emendment of the diagnosis of the former, the definition of a new species from our locality (*P. palmarensis*) and the recombination of the species of the latter genus. The ecological information provided by the extant taxa is preferred in palaeoenvironmental reconstructions and in this way it complies with the Melbourne Code (McNeill et al. 2012) for valid publication of names of organisms treated as fungi (including fossils).

Based on the ecological requirements of *Potamomyces*, a humid sub-tropical environment and a high availability of organic matter in the soil are suggested for the Latest Holocene in the study region, which is dated at 371 $\pm$ 30 ^{14}C years BP, ca. 1635 years cal CE. For this region, we infer that a short interval of more humid conditions (similar to the current climatic conditions) occurred from the end of the sixteenth century up to the beginning of the eighteenth century during the Little Ice Age. This hypothesis will be tested with the complete palynological analysis of the borehole samples.

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Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributors

Noelia Nuñez Otaño studied at the Universidad Nacional de La Plata, Argentina, where she received a doctorate degree in natural sciences in 2013. She is currently a postdoctoral fellow of the National Research Council of Argentina (CONICET) at the Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción (CICYTTP). Her expertise is in the study of fungal diversity from recent and past natural habitats.

Mercedes di Pasquo received her PhD in 1999 from the University of Buenos Aires (UBA) in Argentina and in 2002, she became a permanent researcher of CONICET. She was a teacher at UBA between 1988 and 2008, of the semestral courses of Paleontology and Palynostratigraphy, courses of Geology and Biology (up to 2008), and Micropaleontology and Paleontology (2005−2008). In 2009, she was a Fulbright Research Fellow at the University of Idaho. Since 2010 she has been an affiliate associate professor

in the Department of Geological Sciences, University of Idaho (Moscow, Idaho, USA), collaborating on the study of Upper Palaeozoic palynofloral changes in Bolivia and Argentina during the Gondwanaland glaciation. During 2010, she became a senior researcher and was transferred to the CICYTTP in Diamante, Entre Ríos, Argentina. There she founded the Palynostratigraphy and Palaeobotany Laboratory. Her expertise is in the palynology of the Silurian to Permian, Cretaceous and Cenozoic of South America, the Devonian and Carboniferous boundary of Montana (USA), the Holocene of the Entre Ríos Province and the Devonian plant fossils of Bolivia-Argentina. Mercedes is currently President of the *Asociación Latinoamericana de Paleobotánica y Palinología* (2009−2016, www.ufrgs.br/alpp), and was a special researcher with the Brazilian Program 'Science without borders' CNPq 2013−2014. She worked at the UFRGS (Porto Alegre) and UNISINOS (São Leopoldo, Brazil) on the Carboniferous and Permian palynofloras of the Paraná Basin and its comparison to South American basins. Since 2000, she has been a consultant to the oil industry and worked on palynostratigraphical and palaeoenvironment issues from different intervals of the Phanerozoic in South America.

M. Virginia Bianchinotti studied at the Universidad Nacional del Sur, Argentina, where she received a doctoral degree in biology in 1994. She is currently a researcher at CONICET. Her research is focused on the biodiversity and taxonomy of ascomycetes.

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