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Bovista pezica (Basidiomycota, Agaricales) – A new species with unusually ornamented capillitium, from Patagonia, Argentina

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With 3 figures and 1 table

Abstract: Collections of the genus *Bovista* in southern South America have been traditionally identified under northern-hemisphere names. Although many puffball species show a wide distribution, the identity and distribution of Patagonian species still need to be revisited. Recent materials collected in Patagonia and displaying a unique capillitium ornamented with oblique membranes are shown here to correspond to a new species, *Bovista pezica,* from the Nothofagaceae forests. An unusually thick and coriaceous endoperidium also supports the separation of these specimens verified by our molecular analyses. We present here a full description of *B. pezica* sp. nov. along with a key for the species recorded in Patagonia, and we discuss the possible distributional range.

Keywords: Agaricaceae; Argentina; gasteroid fungi; Patagonia

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Introduction

Gasteroid fungi constitute a polyphyletic group in which the ballistic basidiospore discharge has been lost many times (Hibbett et al. 1997). Within puffballs, this modification is associated with wind-related dispersal of the spores, which are released by a loose filamentous mass known as gleba, enclosed within the peridium (Reijinders 2000, Gube & Dörfelt 2011). Since this feature seems to be highly adaptive (e.g., to dry conditions) the study of the diversity and distribution of this interesting group of saprotrophic fungi along the steep humidity gradient in Patagonia will help us understand the complex adaptations of fungi to these conditions.

The Andean Patagonia consists of large extensions of temperate and cool-temperate forests dominated by tree species in the Nothofagaceae family. The mean annual temperature ranges from 12 °C in the north to 3 °C in the south. Towards the eastern slope of the Andes mountains, total annual precipitation decreases exponentially, which turns the forest into a cold and dry bushy steppe. These climatic peculiarities make up a continuum of conditions that strongly constrains the transitions between biological communities (Paruelo et al. 1998).

This type of environmental variation, associated with altitude in the Andean Mountains, has a strong influence on fungal communities. As an example, the spore ornamentation of puffballs in a similar gradient in northern Argentina, has been shown to be correlated with moisture (Kuhar et al. 2012). However, the state of our knowledge on Patagonian puffballs needs to be assessed against molecular evidence in order to bring to the modern times the information provided by mycologists that studied the area in the past.

Species of *Bovista* Pers. occur all around the world (Kreisel 1967). According to Kirk et al. (2008) the genus *Bovista* was represented by approximately 55 species. More recent taxonomic novelties increased this number (e.g., Yousaf et al. 2013, Jeppson et al. 2016, Rebriev 2016, Rebriev et al. 2017). In Argentina, *Bovista* is represented by sixteen species, six of which were collected in Patagonia (Spegazzini 1881a, 1881b, 1887a, 1887b, 1898, 1902, 1912, 1927, Kreisel 1967, Domínguez de Toledo 1989, Suárez & Wright 1994, Kuhar et al. 2012, Hernández Caffot et al. 2013). Despite the continuous efforts dedicated to the regional gasteroid fungi, the presence and true identity of *Bovista* species need to be revised in many provinces and environments of this region.

Capillitial configurations have been extensively used as an important feature to separate gasteroid fungi at the genus and species levels (e.g., Kreisel 1967). Materials collected in the Argentinean Patagonia exhibit a novel capillitial style, characterized by membranaceous projections that form an irregularly oblique reticulum on the main axes and branches of a classic Bovista-type arrangement. To our knowledge, this configuration has not been reported so far. After revising *Bovista* BAFC collections (Herbario de la Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires) we found that many similar specimens, also collected in Patagonia, but identified as *B. pila* Berk. & M.A. Curtis (Berkeley 1873) have this type of capillitium. Careful analyses of these supposedly *B. pila* type materials confirmed striking diagnostic differences with the *B. pila* species, which was originally described from materials collected in Wisconsin, USA. We describe herein *B. pezica* as new to science and provide a full description and images, as well as an identification key of the species known to occur in Patagonia.

Materials and Methods

Specimens: Materials are deposited at the Museo Botánico de Córdoba (CORD), Universidad Nacional de Córdoba (UNC). Basidiomes were studied macroscopically with stereoscopic binocular (Nikon® C-PS). The colors were typified following Ridgway (1912). Microscopic features were observed under an optical microscope (Nikon® SMZ745T). SEM micrographs were obtained using a scanning electron microscope (Zeiss LEO 1450VP) at the Laboratory of Electron Microscopy and Microanalysis (LABMEM) of the National University of San Luis (UNSL). Chemical composition data were obtained using an energy-dispersive X-ray spectrometry (EDAX Genesis 2000) device in combination with the SEM (SEM-EDX). Samples were mounted on double-sided carbon adhesive tape on aluminum stubs and metalized with gold prior to examination, and observed at 15 KeV.

DNA extraction and amplification

DNA was extracted from glebal tissue with CTAB (hexadecyltrimethylammonium bromide) method as described by Doyle & Doyle (1990). For amplification of the ITS region, the primer combination of ITS5 and ITS4 (White et al. 1990) was used. PCR reactions were performed in 2.5 ml reaction tubes with 1.13 ReddyMix™ PCR Master Mix (ABgene, Thermo Fisher Scientific Inc., UK) according to manufacturer instructions. Cycling parameters for the ITS were 1 cycle of 95 °C for 5 min, 30 cycles of 95 °C for 1 min, 55 °C for 30 s, and 72 °C for 1 min, with a final extension at 72 °C for 10 min. Amplified products were sent to Macrogen Inc. (Seoul, South Korea) for purification and sequencing.

Phylogenetic analyses

ITS sequences of two specimens of *B. pezica*, LSD 3230 (type; GenBank accession number: MT444002) and LSD 3232 (GenBank accession number: MT444003), and one specimen of *B. pila* OSC40127 (GenBank accession number: MT444004), were generated for this study and combined into a dataset with 33 additional sequences of the genus available from GenBanK also including the outgroup taxa (Fig. 3) to evaluate the monophyly of our proposed new species within a broader phylogenetic scheme. This dataset was aligned using L-INS-i strategy as implemented in MAFFT v 7.0 (Katoh & Standley 2013). Maximum likelihood analyses were performed in PHYML using the South of

France bioinformatics platform (http: //www.atgc-montpellier.fr/phyml/) following Guindon et al. (2010) with 300 bootstrap replicates with the option Smart Model Selection (SMS) in the same platform. Bayesian posterior probabilities were calculated with MrBayes (Huelsenbeck & Ronquist 2001). 7.000.000 generations were run in four simultaneous chains. The first 70.000 generations were discarded as burn-in. Stationarity was achieved after the first 100.000 generations and verified using Tracer1 (http://evolve.zoo.ox.ac.uk/software.html/tracer/).

Results

The final dataset of 846 bases has shown to be better explained by the substitution model HKY85 +G+I as estimated by SMS, with the proportion of invariable sites estimated at 0.172, 4 substitution rate categories and a Gamma shape parameter estimated at 0.718. The outgroups represented by sequences in the genera *Tulostoma*, *Disciseda* and *Lycoperdon* showed significant support, whereas deeper nodes within the *Bovista* ingroup were not supported. However, the monophyly of the species proposed herein is well supported both by 79% of ML bootstrap repetitions as well as by 1.0 of Bayesian posterior probabilities including a North American sequence.

Bovista pezica Kuhar, L.S. Domínguez & Hern. Caff. sp. nov. Figs. 1–3

MycoBanK MB 834718

Etymology: from the name "pezica" ascribed to the ancient Greeks by Pliny the Elder to name a fungus "without any stem or root".

Diagnosis: basidiomes mainly globose to irregular, semi-lobed at the base, 2.5–5 (–6.5) cm in diam. × 2–3.5(–5) cm high, without visible rhizomorph. Peridium smooth, rather thick, rigid, two-layered, splitting radially and irregularly at maturity. Endostratum of the exoperidium brown to reddish-brown, shiny, and orange to yellowish-golden, silvery. Endoperidium persistent, rigid, coriaceous, silvery. Capillitium of *Bovista*-type, main thread 15–20(–24) µm diam., walls 2 to 3 layered, pits absent, strands covered by membranes irregularly obliquely arranged. Spores apedicellate, globose, (5–)6–7 (–7.5) µm; chestnut yellow to amber, slightly roughened under light microscope, granulate, unigulated, apiculus conspicuous.

Type: ARGENTINA, *Prov. Santa Cruz:* Dpto. Lago Argentino, Chaltén, 49°19'39.0" S 72°53'33.5" W, 408 msnm, under *Nothofagus antarctica*, 30-XI-2013, LSD 3230 (CORD).

Description: basidiome mainly globose to irregular or semi-lobed and basally ridged, 2.5–5(–6.5) cm in diam. × 2–3.5(–5) cm high (Fig. 1A), without visible rhizomorph, detached from soil when mature, when fully mature with metallic-silver reflections. Peridium rather thick, rigid, smooth, two-layered. Exostratum of the exoperidium not seen. Endostratum of the exoperidium with two different shades when dried, a brown to reddish-brown, shiny (Warm Sepia, XXIX, 13-m) and orange to yellow-golden, shiny (Snuff

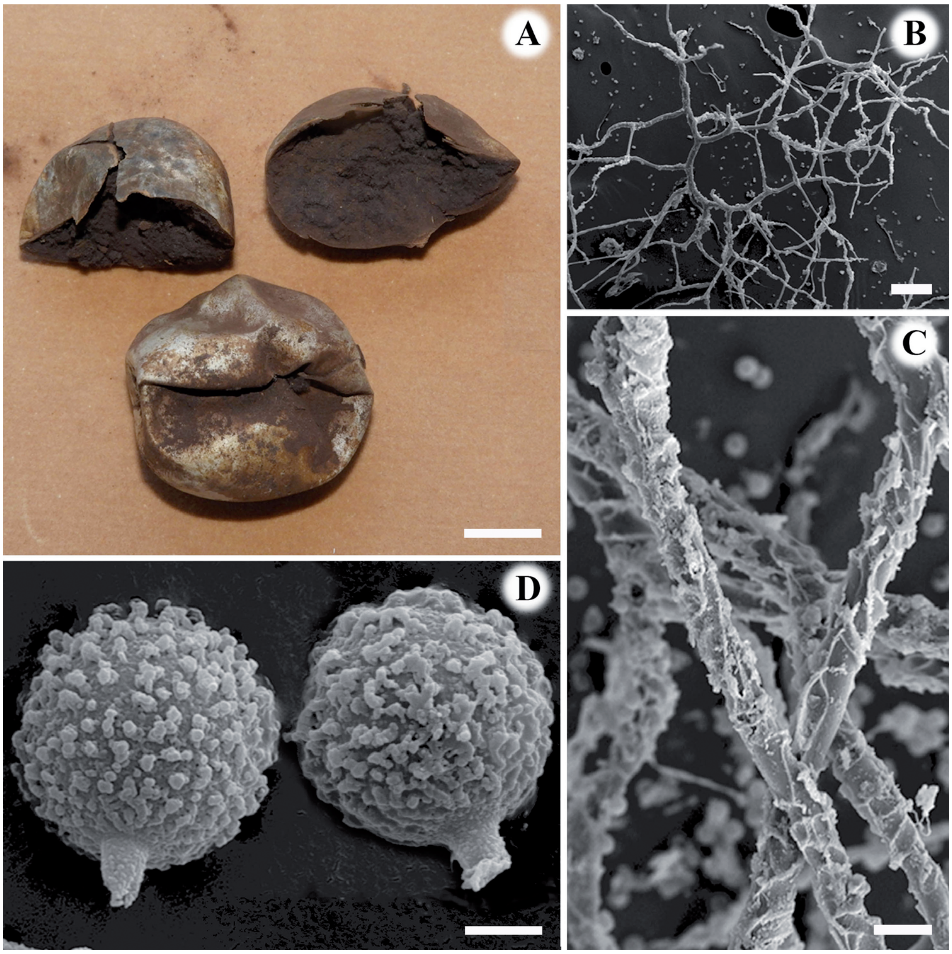

Fig. 1. *Bovista pezica.* A. basidiome. B. capillitium thread. C. detail of capillitium strand covered by membranes. D. spores. Bars: A: 1 cm. B: 100 µm. C: 10 µm. D: 2 µm.

Brown, XXIX, 15-k), 30–40 µm thick, cyanophilic, pseudoparenchymatous layer of thin walled isodiametric to polygonal cells, 10–15 µm in diam., when completely mature the cells collapse, with abundant small crystals on it. Endoperidium persistent, 200–500 µm thick, rigid, coriaceous, shiny gray (Drab, XLVI, 17-i) consisting of a plechtenchyma of non-septate and unbranched hyphae, with the outermost, detachable layer (15–30 µm thick) with a metallic luster being a semi-plectenchyma of parallel and tangentially arranged, cyanophilic, hyaline and thin-walled hyphae, compact when completely mature, hyphae 2–5 µm in diam., intermingled with brown colored, thick walled hyphae (0.5–1 µm diam.), more loosely arranged towards the gleba where they turn tomentose, with a regular lumen and a lax disposition (Fig. 2A). Dehiscence initially by a lacerate slit, then extending radially and irregularly.

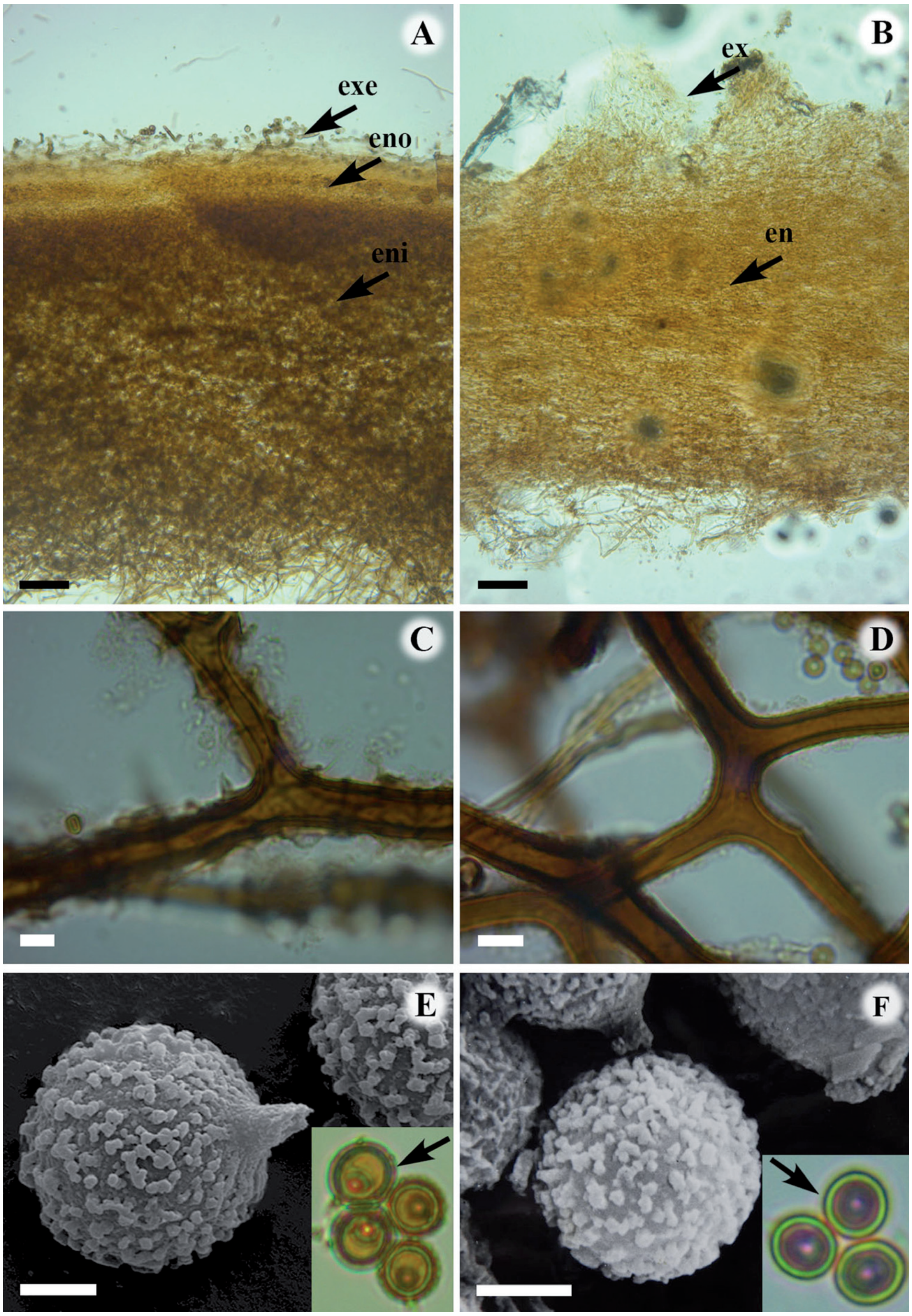
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Fig. 2. Microscopic features of type materials of *B. pezica* vs. *B. pila. B. pezica*: A. peridium. C. capillitial strand. SEM of the spores with detail of light microscopy. *B. pila*: B. peridium. D. capillitium strand. F. SEM of the spores with detail of light microscope view of the wall. Bars: A–B: 100 µm. C–D: 10 µm. E–F: 2 µm. Abbreviations: ex: exoperidium, exe: exoperidium endostratrum, en: endoperidium, eno: endoperidium outer layer, eni: endoperidium inner layer.

Gleba light brown to dark brown, sometimes with a dark lilac tinge (Hay's Brown, XXXIX, 9-m), initially homogeneous and then forming loose masses up to 1 mm in diam. Subgleba and sterile base absent. Capillitium of the Bovista-type, floccose, of discrete elements (up to 1 mm long), brittle, with short inflexible branches, forking more or less dichotomously, rapidly tapering, blunt to rounded tips, ochre to reddish-brown in KOH, main thread 15–20(–24) µm diam., regular lumen; wall 2–3 layered, up to 5 µm thick, regularly thickened, without septa, pits absent, strands covered by hyaline membranes irregularly and obliquely arranged, curling up over the wall or grouped covering the entire surface of the strand, resembling spines (Fig. 1B–C, 2C), some areas might be without membranes. Spores globose, apedicellate, chestnut yellow to amber, (5–)6–7(–7.5) µm; under light microscope slightly roughened, granulate, walls 1 µm thick including ornamentation; unigutulated, apiculus conspicuous, up to 2 µm long × 1–1.5 µm in diam., in SEM with low granules and bacules, some fused and forming a short reticule (Fig. 1D, 2E).

Habit, habitat, and seasonality: basidiomes solitary, scattered to gregarious, in open areas, grasslands or close to *Nothofagus* forests, Nov.–Feb.

Comments: All specimens examined were weathered with the exception of a single fruiting body that still shows the partially well preserved endostratum of the exoperidium. The exostratum of the exoperidium was not observed probably because no young specimens were collected. We believe that it might fall apart in early stages of the development, as it happens in many species of the genus (Kreisel 1967). Rhizomorphs were not visible in any of the specimens collected, including the BAFC collections. Dehiscence occurs by cracking of the endoperidium, as in *Mycenastrum* Desv., a genus characterized by a thick and coriaceous peridium. All capillitial threads are covered by irregular oblique cell wall thickenings or foldings resembling membranes or even spines under the light microscope. X-ray spectrometry of the gleba showed that the composition of the capillitial membranes is, across all values, intermediate between spores and the main axe of the capillitial threads. This result suggests that these unusual ornamentations might consist of materials originated in both structures (Table 1). *Bovista pila* type material exhibits several differences with *B. pezica* (Fig. 2): 1 – exoperidium hyphal, of the plumbea type, with walled hyphae (2–10 µm diam.) up to 300 µm thick (Fig. 2B); 2 – capillitial threads flexible, light brown, without membranes with some pseudosepta (Fig. 2D); 3 – spores are smaller 4–5(–5.5) µm, and look smooth under light microscope, under SEM they are granular (Fig. 2F).

Remarks: Distribution of *Bovista pezica* in Argentina is confined to the Southwest region: Patagonia Region and Tierra del Fuego. Specimens were collected at the roadside, steppe and urban areas, and inside and outside forests, a typical behavior of *Bovista* spe-

Table 1. Weight percent (%) of each element from glebal components (calculated taking only in account the analyzed elements).

Element	Spores	Capillitium	Capillitium Membranes
C	67.18	37.66	58.29
N	10.69	40.84	21.88
O	28.85	12.45	15.11
Ca	1.28	9.06	4.72

cies; they occur in natural and human-perturbed ecosystems (Kreisel 1967, Domínguez de Toledo 1989) and its local distribution pattern seems to be mainly regulated by climatic and edaphic factors (Kreisel 1967). Six *Bovista* species have been registered from different environments from Patagonia and Tierra del Fuego, Argentina. Spegazzini described four of them; *B. antarctica*, *B. arachnoides*, *B. elegans* and *B. pachydermica*. This author also described *B. magellanica* from Ushuaia (now *B. brunnea* Berk.) and recorded *B. aspera* Lév. as well as *B. cervina* Berk. later transferred to *Disciseda* (Spegazzini 1887a, b).

Bovista pezica presents macro and microscopic differences when compared with the aforementioned species. *Bovista arachnoides* differs from *B. pezica* in having basidiomes 6–12 mm in diam., a mycelial cord, a loose and hyaline capillitium and globose spores, about 2.5–3 µm in diam. (Spegazzini 1887a). *Bovista aspera* differs in the small size of the basidiomes (8–20 mm), the presence of a mycelial cord, capillitium of the Lycoperdon-type, and pedicellate spores (Kreisel 1967). *Bovista brunnea* (type material of *B. magellanica* Speg.) differs from our species mainly in its brownish and papyraceous endoperidium, and spores with sterigmata up to 10–20 × 1 µm. *Bovista elegans* type material exhibits a small basidiome (1.5 cm in diam.), a thin, dark brown and papyraceous endoperidium, capillitium of the Lycoperdon-type, spores asperulate 3.5–4 µm in diam. *Bovista pachydermica* type material presents a papyraceous brownish-red endoperidium, capillitium of the Lycoperdon-type and spores 4.5–5 µm with coarse ornamentation. Regarding the *B. antarctica* type material (LPS 16358) we observe some features such as the curled, fragmented capillitium, which do not fit the modern conception of *Bovista* and strongly support the position of this species in the genus *Disciseda*.

Material studied: ARGENTINA, **Santa Cruz**, Dpto. Lago Argentino, Chaltén, 49°19'39.0"S; 72°53'33.5"W, 408 msnm, bajo ñire, flotando, 30-XI-2013 TIPO, LSD 3230 (CORD); Ibid., suelo desnudo rodando por el viento, LSD 3232 (CORD), Ibid., en pasto, LSD 3231 (CORD). **Chubut**, Dpto. Languiñeo, Lago Vintter, 43º59'29.81"S; 71º37'31.47"W, 925 msnm, suelto en descampado, 21-II-2013, LSD 2535 (CORD). Dpto. Lago Argentino, Huemules, 42°48'40.3"S 71°28'35.7"W, 1281 msnm, bajo lenga, 13-X-2013, LSD 3229 (CORD).

Additional material studied: *Bovista pila:* ARGENTINA, **Tierra del Fuego**, Lago El Indio, Leg. Wright - Del Busto 29-I-73, 33328 (BAFC); Río Grande, Ea. La Esperanza, Leg. M. Rajchenberg, 28-II-88, sobre rama caída de *N. antarctica*, 31961 (BAFC); Kaiken, Leg. Suárez-Carmarán, 12-II-93, alrededores de la hostería, 33961 (BAFC); Ea. María Behety, Leg. Cabral, 23-I-92, Potrero 10 chico, 32680 (BAFC); Ibid. 32679 (BAFC); Ruta H camino a Yehuin, Ea. La Esperanza, a orillas del camino, Leg. Cabral, 2-II-93, Pradera comida por ovejas, color blanco sucio con rajaduras, gleba grisácea verdosa, 34022 (BAFC); Leg. G. Bovis, 50002 (BAFC); Dpto. Ushuaia, Ruta 3 a 17 Km de Tolhu, Leg. Carmarán, XII-1997, Complejo Aguas Termales, 34745 (BAFC); Kosobo, Leg. Clarice Leite, 27-X-89, 31959 (BAFC); **Río Negro**, Camping L. Roca, Leg. Capelli, II-81, 26 771 (BAFC); Ibid. 26760 (BAFC); **Santa Cruz**, Ruta Nacional, L. Roca, sobre gramíneas (suelto), lugar denominado Pampa del Cóndor, 30665 (BAFC); Ibid. 30664 (BAFC); Ibid. 30621 (BAFC). CHILE, Valdivia, Leg. González, XII-77, sobre tierra y raíces de *Populus* sp., 32236 (BAFC). UNITED STATES of AMERICA, **Oregon**, Linn Co., Albany, Leg. T. Gross, J. Trappe, 20-VI-80, completely hypogeous among roots of orchard grass, 40127 (OSC).

Type materials studied: UNITED STATES of AMERICA: *Bovista pila* Berk & M.A. Curt., Wisconsin, Lapham, 6213 (K), Dupl. 32238 (BAFC). ARGENTINA. *Bovista antarctica*, Ushuaia, Punta Arenas, VIII-1882, Leg. C. Spegazzini, 16358 (LPS). *Bovista elegans*, Río Negro, II-1898, Leg. C. Spegazzini, 45632 (LPS). *Bovista magellanica*, Ushuaia, Punta Arenas, IV-1882, Leg. Spegazzini, 29230 (LPS). *Bovista pachydermica*, Ushuaia, Punta Arenas, 1882, Leg. C. Spegazzini, 16360 (LPS).

Identification Key for *Bovista* species from Patagonia Argentina

1. Spores smooth, up to 3 µm in diam., basidiome not exceeding 12 mm in diam. . . ***B. arachnoides***

1'. Spores ornamented, exceeding 3 µm in diam., basidiome exceeding 12 mm in diam. **2**

2. Spores pedicellate **3**

2'. Spores apedicellate **4**

3. Capillitium of the Lycoperdon-type, spores 3–4.5 µm in diam., pedicels 5–15 µm. . . ***B. aspera***

3'. Capillitium of Bovista-type, spores about 5–5.5 µm, pedicels 10–20(–25) µm. . . . ***B. brunnea***

4. Capillitium of Bovista-type, surrounded by membranes, endoperidium coriaceous, rigid . . . . ***B. pezica***

4'. Capillitium of Lycoperdon- or Intermediate-type, smooth, endoperidium membranaceus, thin . . **5**

5. Capillitium of Intermediate-type, pitted. . . . . ***B. fuegiana***

5'. Capillitium of Lycoperdon-type, not pitted **6**

6. Spores asperulate, 3.5–4 µm, capillitium main axe up to 4 µm diam., with false septa, basidiomes up to 1.5 cm diam. . . . . ***B. elegans***

6'. Spores with coarse ornamentation, 4.5–5 µm, capillitium main axe up to 8 µm, with true septa, basidiomes about 2–4 cm. . . . . ***B. pachydermica***

Discussion

Our materials show a very high ITS similarity (over 99.5%) with one sequence corresponding to a North American collection (APBP100) deposited as *Bovista cretacea* T.C.E. Fr. in GenBank under MK966425 and also included in our analyses (Fig. 3). Our analyses also included sequences of *B. cretacea* documented in the family revision undertaken by Larsson & Jeppson (2008) and the significant support of this species as an independent entity separate from *B. pezica* is confirmed. Also striking morphological differ-

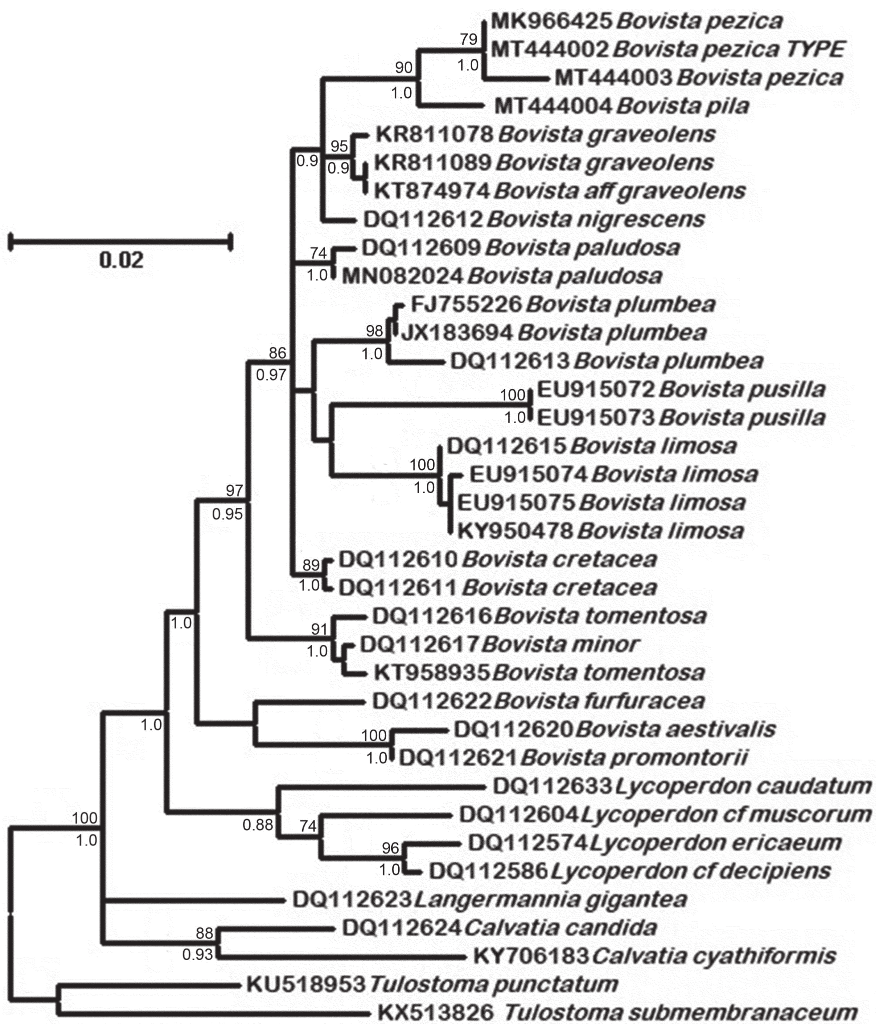

Fig. 3. Highest likelihood tree obtained from the ITS dataset. Statistically significant support values are indicated above (ML bootstrap) and below (Bayesian posterior probabilities) the branches.

ences as the long pedicel (up to 14 µm) of *B. cretacea* spores and the papery nature of its endoperidial layer preclude any possibility of conspecificity with our materials and we conclude that the name appended to the sequence must be a preliminary identification. However, this sequence evidences the presence of this species in North America, raising the question of the geographic origin of *B. pezica*. The long history of plant species introduction in Patagonia (Simberloff et al. 2003) may suggest that our findings might correspond to an alien species. However, the Albany Pine Bush, NY, collection site of the specimen APBP100, also has a large record of plant species introduction (Milne 1985) and for this reason, it would be inaccurate to define it as part of the original distribution range based only on a recent collection. Further findings are needed in order to better assess the current distribution and to establish the putative origin of this interesting species.

Most Argentinean species identifications have been performed based on European and North American descriptions (e.g., Cocker & Couch 1928, Smith 1951, Kreisel 1962, Calonge 1992, 1998, Pegler et al. 1995). It is possible that mycologists working in South America had difficulty accessing reference collections in the past, and this might have obscured some species concepts within this group, resulting in the inclusion of unrelated organisms under the somewhat same comprehensive diagnoses. On the other hand, our attempts to obtain amplifiable DNA from herbarium type materials did not succeed probably due to different preservation methods of the specimens dating from more than a century ago, resulting in a highly fragmented DNA limiting PCR function (Bruns et al. 1990, Cubero et al. 1999, Cota-Sánchez et al. 2006, Särkinen et al. 2012). This seems to be the case with the Argentinean *B. pezica* specimens in the BAFC collection, incorrectly identified as *B. pila*. Fortunately, we have access to *B. pila* type material and we corroborated macro- and microscopic features that allowed us to clarify the confusion surrounding *B. pezica*. Further research based on DNA amplification of reference materials will provide more accurate information that may help in the identification of more South American species that may lie hidden under Northern-Hemisphere names.

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