

The fungal spore *Annella capitata* Srivastava from the Jurassic (Late Toarcian-Late Bajocian) Cañadón Asfalto Formation of Patagonia, Argentina

Daniela E. Olivera^{a,b*}, Mirta E. Quattrocchio^b and Ana M. Zavattieri^c

^aDepartamento de Geología, Universidad Nacional del Sur, San Juan 670, 8000 Bahía Blanca, Argentina; ^bCONICET-INGEOSUR, San Juan 670, (8000) Bahía Blanca, Argentina; ^cIANIGLA, CCT-CONICET MENDOZA Centro Científico Tecnológico-Mendoza, A. Ruiz Leal sh, Parque General San Martín, CC 330, 5500 Mendoza, Argentina.

The fungal spore *Annella capitata* Srivastava is recorded for the first time in Argentina, within the continental Jurassic strata of the Cañadón Asfalto Formation, Cañadón Asfalto Basin, Patagonia. It is identified on pollen grains belonging to the Cheirolepidaceae, Araucariaceae and Podocarpaceae. This paper contrasts *A. capitata* with ubisch bodies (small sporopollenin spherules attached to the exine). *A. capitata* has the same characteristics in the different pollen taxa, while the ubisch bodies exhibit taxon-dependent differences in ultrastructure, size and morphology. The presence of hyphae and spore germlings reinforces a fungal origin of *A. capitata*. The degree and type of deterioration associated with these fungal microfossils are presented. Based upon the ecological requirements of the plant families recognized in the Cañadón Asfalto palynoflora, it is inferred that *A. capitata* Srivastava thrived in low-energy environments under warm-temperate and humid conditions.

Keywords: *Annella capitata*; Fungi; Cañadón Asfalto Formation; Jurassic; Argentina

1. Introduction

Studies of sporomorph spectra constitute a useful tool for the reconstruction of past vegetation and of the palaeoenvironments in which plant communities developed. Palynological studies from terrestrial sequences focus mainly on the occurrence of sporomorphs of bryophytes and tracheophytes, but these may be supplemented with other proxies, such as fungal remains and algae, in order to enhance our understanding of the ecological conditions. Unfortunately, the earliest (Precambrian) history of the fungi is complicated by a common failure to reliably differentiate them from the algae (Elsik 1996). Nevertheless, a remarkable variety of algal- and fungal-like filaments and spherules have been identified from the Precambrian of Siberia (e.g., Hermann 1990). Although the fungal kingdom certainly ranges from the Proterozoic to the Recent, it was evidently not until the Jurassic that these organisms commonly produced resistant (chitinous?) hyphae or spores that allowed their preservation as palynological maceration resistant microfossils. Although there are some Permo–Triassic exceptions, they are not common (Traverse 1988). Simple spore morphologies, frequently recorded as *Inapertisporites* (Hammen) emend. Sheffy & Dilcher (1971), from Triassic and Jurassic deposits (de Jersey 1959, 1962; Traverse & Ash 1994) are very similar to the spores produced by some extant ascomycetes,

suggesting that the fungal record may be underestimated. By contrast, fungal forms have been widely identified in organic petrographic studies of Upper Carboniferous and younger coals (D’Rozario et al. 2011; O’Keefe & Hower 2011; O’Keefe et al. 2011, 2013; Hower et al. 2013).

There can be little doubt that the fungi are important agents in the degradation of all plant materials, including palynomorphs. Many authors have published accounts of the biogenic origin and diverse forms of degradation in recent pollen (Skarvala & Anderegg 1972; Delcourt & Delcourt 1980; Limaye et al. 2007; Musotto et al. 2013), as well as in fossil spores and pollen grains from the Paleozoic, Mesozoic and Cenozoic (e.g., Moore 1963; Elsik 1966; Srivastava 1976; Marcinkiewicz 1979).

There are also common accounts of sporopollenin spherules (‘ubisch bodies’) attached to fossil gymnosperms (e.g., Gamarro 1968; Reyre 1970; Villar de Seoane 2005), as well as to recent spores related to the families Polypodiaceae and Grammitidaceae, and on pollen grains (e.g., Poaceae family) (Giudice et al. 2004; Ramos Giacosa et al. 2007; Lovisolo & Galati 2012).

The spherules found on palynomorphs in palynological samples, referred to in the bibliography as ‘ubisch bodies’, might be fungal in origin (Srivastava 1976; Kalgutkar & Jansonius 2000).

*Corresponding author. Email: daniela.olivera@uns.edu.ar

This paper reports the first record of *Annella capitata* Srivastava from the late Early–mid Middle Jurassic Cañadón Asfalto Formation, Cañadón Asfalto basin, Chubut Province. It is also the first record of this fungus in palynological assemblages from Argentina. Spores of *A. capitata* were originally recognized by Srivastava (1976) in Late Jurassic sequences of England. This paper compares *A. capitata* Srivastava with ubisch bodies and discusses the morphological differences between them. The aim of this work is to describe *A. capitata* spores and the taphonomic effects with which they are associated, and to highlight the potential importance of their recognition.

A full palynological study of the Cañadón Asfalto Formation from the Cerro Cóndor depocenter, Chubut province, forms part of the PhD thesis of Olivera (2012).

Pollen grains with fungal spores and hyphae of *A. capitata* were recorded in the Cañadón Lahuincó 'A' section (S43°30'59", W69°8'20"), located 15 km south of Cerro Cóndor village (Figures 1 and 2).

The stratigraphic position of the samples is given in Table 1.

2. Geologic setting and sedimentary environment of the Cañadón Asfalto Basin

There is no consensus concerning the tecto-sedimentary evolution of the Cañadón Asfalto Basin. According to Silva Nieto et al. (2007) and Volkheimer et al. (2008, 2009) it represents several depocenters associated with small pull-apart sub-basins that shared a similar geological history. Conversely, Figari & Courtade (1993), Cortiñas (1996), Figari et al. (1996) and Figari (2005) proposed that sedimentation was related to the development of a rift during the early break-up of Gondwana.

The studied interval crops out in the Cerro Cóndor depocenter situated in the middle valley of the Chubut river (Figure 1). Assigned palynologically to the Late Toarcian–Late Bajocian (Olivera 2012), the Cañadón Asfalto Formation rests unconformably on the Lonco

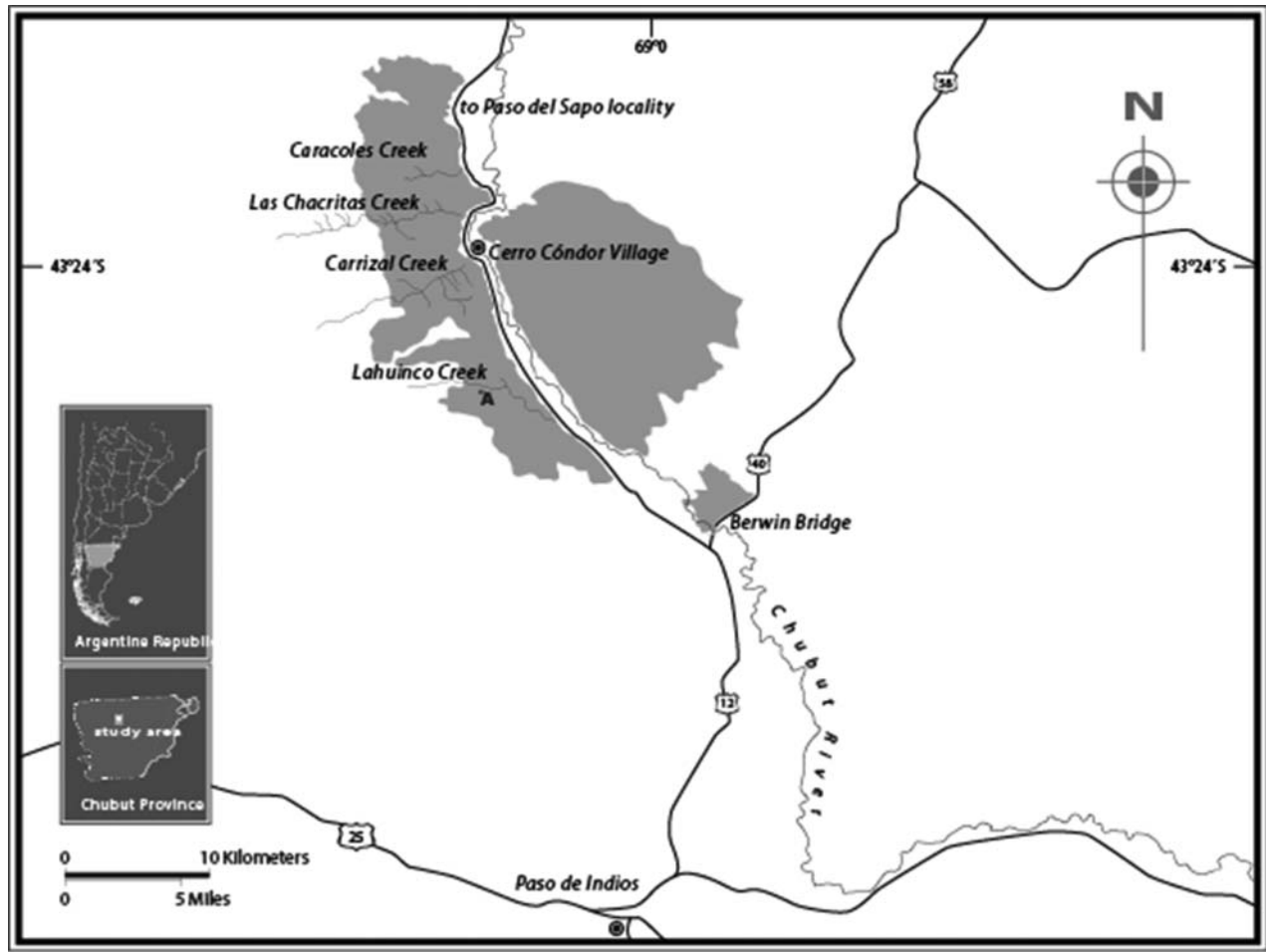


Figure 1. Distribution of outcrops of the Cañadón Asfalto Formation in the middle Chubut River valley, Patagonia, Argentina. A: Location of the Cañadón Lahuincó 'A' section.

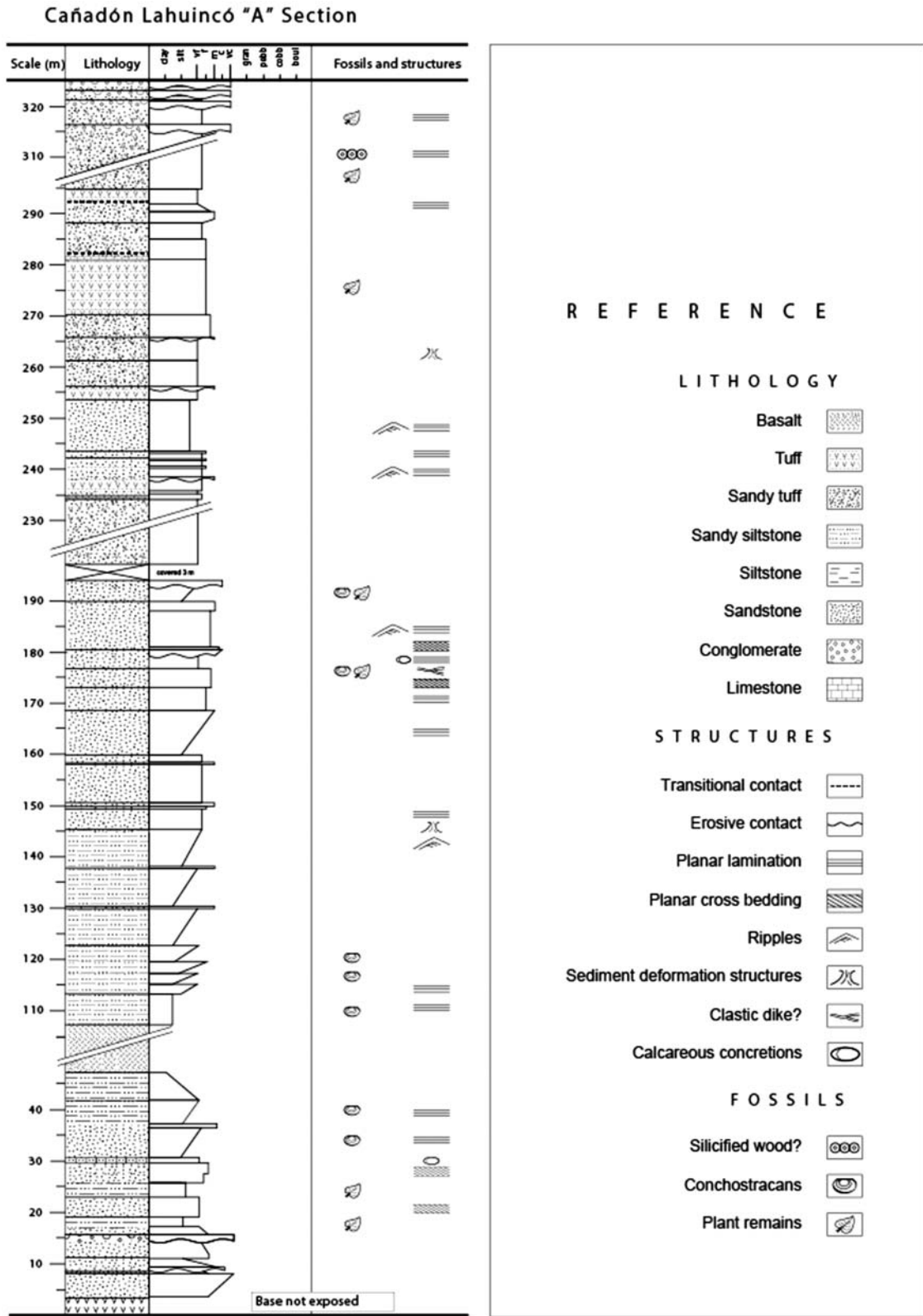


Figure 2. Columnar section of the Cañadón Asfalto Formation at the Cañadón Lahuincó locality.

Table 1. List of 20 palynologically productive samples from the Cerro Cóndor area used for the present study, and their stratigraphic position.

Stratigraphic section	Field number	Slide/lab code	Depth from base (m)
Cañadón Lahuincó 'A'	CL06	MPEF-PALIN104	29.0
	CL08	MPEF-PALIN106	30.8
	CL18	MPEF-PALIN116	45.3
	CL21	MPEF-PALIN119	111.0
	CL22	MPEF-PALIN120	114.4
	CL23	MPEF-PALIN121	116.2
	CL24	MPEF-PALIN122	116.7
	CL25	MPEF-PALIN123	117.2
	CL26	MPEF-PALIN124	117.8
	CL27	MPEF-PALIN125	121.0
	CL28	MPEF-PALIN126	122.3
	CL29	MPEF-PALIN127	124.1
	CL30	MPEF-PALIN128	125.1
	CL31	MPEF-PALIN129	126.1
	CL32	MPEF-PALIN130	127.1
	CL33	MPEF-PALIN131	128.6
	CL34	MPEF-PALIN132	133.1
	CL35	MPEF-PALIN133	134.8
	CL36	MPEF-PALIN134	136.5
	CL38	MPEF-PALIN136	140.9

Trapial Formation. The Cañadón Asfalto Formation is composed of three informal units. The basal unit comprises limestones, minor conglomerates and sandstones, plus tuffs and basaltic intercalations reflecting the interdigitation of a lacustrine environment with an active volcanic system. The middle unit consists predominantly of sandstones and siltstone, while the upper unit is not recognized in the studied area (Olivera 2012). The formation is unconformably overlain by the Cretaceous deposits of the Chubut Group (Cabaleri & Armella 2005).

3. Materials and methods

A total of 57 outcrop samples of very fine sandstone, siltstone and mudstone were collected from the Cañadón Lahuincó 'A' section (Figure 2). Twenty palynologically productive samples (those yielding at least 300 palynomorph counts per sample) were studied (Table 1). The physical and chemical extraction of palynomorphs was carried out at the Palynological Laboratory of the Instituto Geológico del Sur/Universidad Nacional del Sur-Bahía Blanca and at the Paleopalynological Laboratory of the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales/Centro Científico Tecnológico-Consejo Nacional de Investigaciones Científicas y

Técnicas-Mendoza, Argentina. Processing of samples involved hydrochloric acid (HCl)/hydrofluoric acid (HF) treatment and subsequent sieving (through a 10 μ m mesh), followed by 2 minutes of oxidation with concentrated nitric acid (HNO₃). This residue was briefly washed (45 seconds) in 5% ammonium hydroxide to remove the oxidation by-products. The slides were examined using transmitted light and differential interference contrast (DIC) microscopes (both an Olympus BX40 and a Nikon Eclipse 80i). Photomicrographs of selected palynomorphs were taken using either an Olympus or a Nikon digital camera. In addition, a Philips XL30 TMP New Look scanning electron microscope was used to study two samples (MPEF-PALIN122 and MPEF-PALIN123), which were selected because they contained high percentages of *A. capitata* Srivastava spores. The palynological slides are housed in the Paleontological Museum Edigio Feruglio Repository, Trelew city, Chubut province, Argentina. They are identified by the catalogue number preceded by the abbreviations MPEF (Museo Paleontológico Edigio Feruglio) and PALIN (Palynology). Specimen locations are referred to England Finder coordinates (EFco).

4. Systematic palynology

Table 2 shows that the studied samples contain a low-density and low-diversity assemblage of spores (four species) but abundant and diverse pollen grains (38 species), accompanied by organic walled microplankton comprising four species of the Zygnemataceae and Botryococcaceae families, and acritarchs (*Leiosphaeridia* spp.). The relative abundances of the major palynomorph groups are expressed in percentages in Figure 3. Nearly 90% of the sporomorphs identified in the Cañadón Lahuincó 'A' section (Figure 1) are gymnosperm pollen grains, and many of these were apparently infected by the fungus that formed *A. capitata* spores. It is notable that none of the scarce spores of lycophytes and ferns within the palynoflora exhibit this infection.

Kingdom Fungi

Genus *Annella* Srivastava 1976

Type species. *Annella capitata* Srivastava 1976, p. 97, pl. 2. fig. 10–11.

Annella capitata Srivastava 1976

Plate 1, figures 1–15

1983 *A. coccoidea* Taugourdau-Lantz, & Ram, 1983, page 77, pl. 1. fig. 15–19.

Table 2. Botanical affinities of spores, pollen and organic-walled microplankton from the Cañadón Asfalto Formation. Affinities of the dispersed palynomorphs are based on Dettmann (1963), Filatoff (1975), de Jersey & Raine (1990), Balme (1995), Sajjadi & Playford (2002a, 2002b), McKellar (1998) and Martínez et al. (2008).

Division	Class	Order	Family	Genera-palynoflora	
Tracheophyta	Lycopsida	Selaginellales/ Lycopodiales	Selaginellaceae/ Lycopodiaceae	<i>Retitriletes</i>	
	Filicopsida	Filicales	Cyatheaceae/Dicksoniaceae Dipteridaceae/Matoniaceae Osmundaceae	<i>Deltoidospora</i> <i>Osmundacidites</i>	
	Gymnospermopsida	Pteridospermales	Corystospermaceae		<i>Alisporites</i>
			Caytoniaceae		<i>Vitreisporites</i>
		Coniferales	Araucariaceae		<i>Inaperturopollenites</i> , <i>Araucariacites</i> , <i>Callialasporites</i>
			Cheirolepidiaceae		<i>Classopollis</i>
			Pinaceae		<i>Indusiisporites</i> , <i>Cerebropollenites</i>
			Podocarpaceae		<i>Podocarpidites</i> , <i>Microcachrydites</i> , <i>Podosporites</i> , <i>Trisaccites</i>
					<i>Ovoidites</i>
	Charophyta	Zygnematophyceae	Zygnematales	Zygnemataceae	
Chlorophyta	Trebouxiophyceae		Botryococcaceae	<i>Botryococcus</i> <i>Leiosphaeridia</i>	

Description. Aseptate and inaperturate spores. Ambicircular to subcircular with psilate exine. Small hyphae produce spores and then disintegrate when the spores are mature.

Dimensions. Equatorial diameter of the spores: 0.5–1.5 μm (70 specimens).

Main material studied. MPEF-PALIN121: B47/1, D50/3; MPEF-PALIN122: B46/3, B47/1, C26/2, M38/0, R27/1, P50/3, S37/0; MPEF-PALIN123: C44/0, O35/0, B20/0; MPEF-PALIN126: K25/0, Q50/3; S45/1.

Previous records. *A. capitata* has been previously recorded in palynofloras from the Oxfordian of England (Srivastava 1976), from the Middle Jurassic of Poland (Marcinkiewicz 1979), from the Early Jurassic of Iran (as *A. coccoidea* Taugourdau-Lantz & Ram, 1983) and the Early Jurassic (Pliensbachian) of England (Srivastava 2011).

Remarks and comparisons. The Argentinian spores can be differentiated from the English species in showing hollow forms attached to pollen grains (Plate 1, figures 1–2). These spores are similar to *Inapertisporites* (Hammen) emend. Sheffy & Dilcher (1971), a monocellate, aseptate and inaperturate fungal spore with circular to subcircular outline. *Inapertisporites*

differs from *A. capitata* Srivastava in having a larger size (5–11 μm), and being typically found as dispersed isolated spores. In the studied material, *A. capitata* is recognized clearly because it only occurs attached to the host palynomorphs, and also by its degradation effect on their surfaces.

A. pulchra Srivastava 1976, from the Oxfordian of England, differs from *A. capitata* in having angular spores. *A. coccoidea* Taugourdau-Lantz & Ram 1983 is here synonymized with *A. capitata* as the former does not exhibit significant differences.

5. Discussion

5.1. *A. capitata* and comparison with orbicules or ubisch bodies

The Cañadón Asfalto palynoflora is characterized by an abundance of gymnosperm pollen grains. Among these, the coniferous genera are particularly prominent, mainly those belonging to the Cheirolepidiaceae and Araucariaceae families. Cheirolepidiaceae (*Classopollis*) reach up to 93% of the total assemblage of palynomorphs. Specimens with different degrees of preservation have been found, ranging from very well preserved to lacking most of their original morphological features. A significant proportion of the studied palynomorphs that yield fungal spores assigned to *Annella capitata* Srivastava (Plate 1, figures 1–6) are

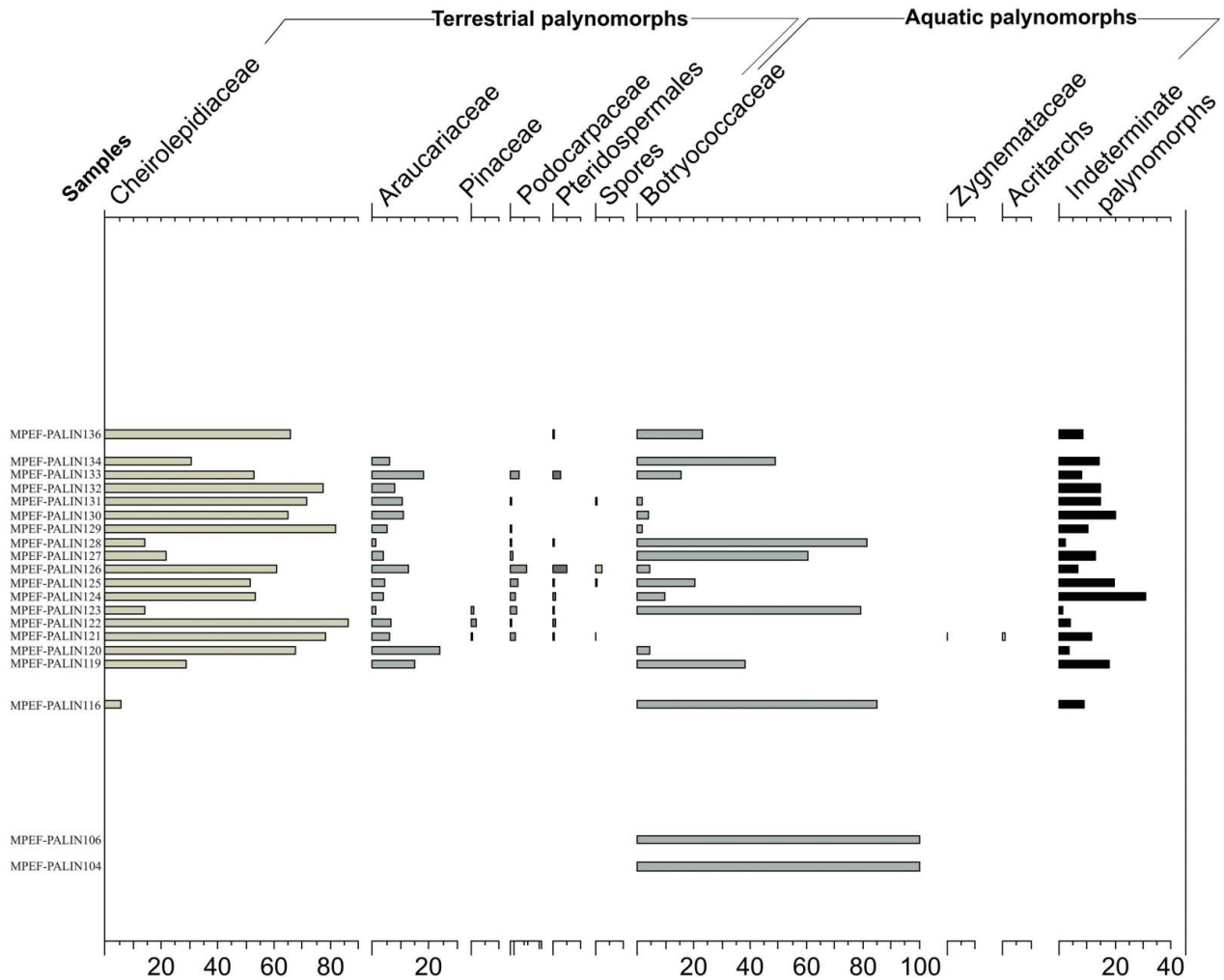
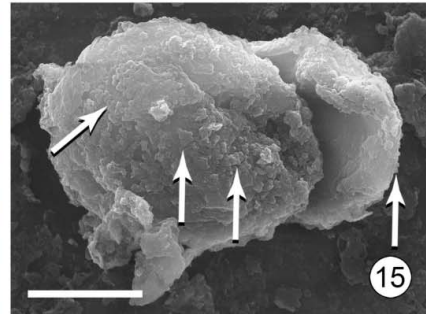
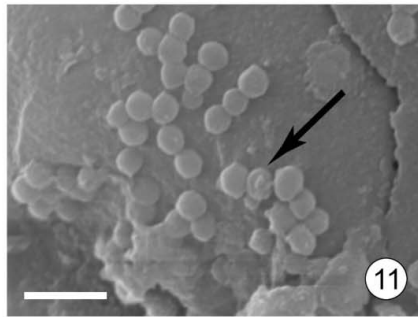
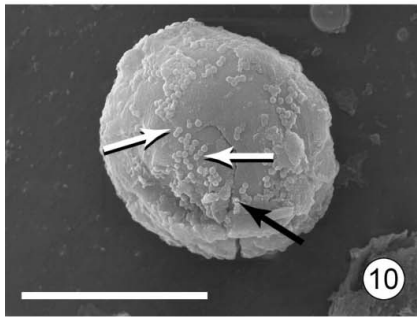
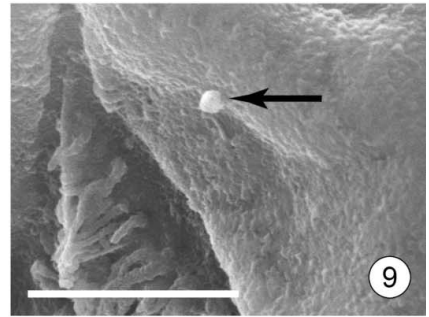
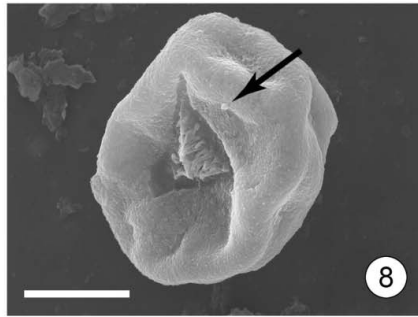
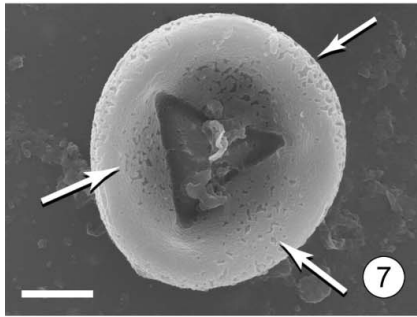
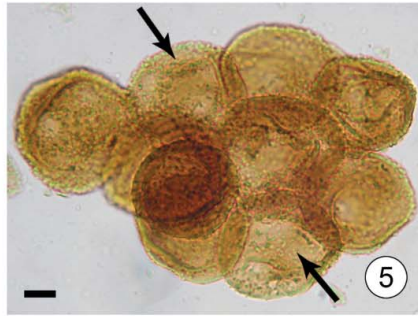
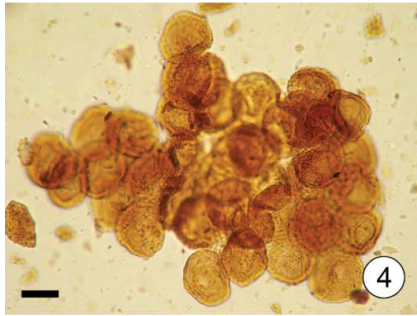
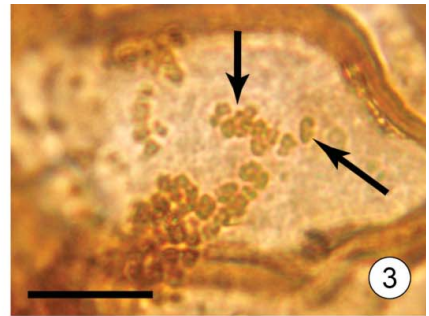


Figure 3. Quantitative distribution of major palynomorph groups in the Cañadón Lahuincó 'A' section.

identified as *Classopollis* sp., and the result of fungal activity on these grains is marked (Plate 1, figure 7). Different phases in the development of this fungus were recognized. The development of fungal spores from the hyphal bodies begins with the spores initially forming in isolation but eventually in rows, and finally producing dense agglomerations of spherules (Plate 1, figures 2, 8–10). It has also been possible to observe the fossil germination of some spores (Plate 1, figures 10–11). Hyphae, which are present only in the early stages of spore development, as described by Srivastava (1976), were recognized in a few pollen grain hosts (Plate 1, figures 5, 8–9). According to Srivastava (1976), when the spores reach a mature stage, the hyphae disintegrate. In a final phase of development, the spores detach from the palynomorphs, revealing their exines. The resulting pattern of exine degradation consists of a series of pits and perforations (Plate 1, figure 7). Because of the large number of *Classopollis*

sp. grains studied, the different stages of deterioration were discernable. *A. capitata* initially infects the outer layer of the exine (the sexine), modifying some morphological features of the grain surfaces until only relicts of the morphostructure remain to permit identification of the taxon (e.g., endostriae). In the advanced stage of bio-corrosion (microbiological activity *sensu* Delcourt & Delcourt 1980), the sexine becomes fully detached from the inner wall, and generally broken, making it possible to observe the internal wall or nexine (Plate 1, figures 12–13). These remnant nexines can often be identified without their outer wall, whether clearly colonised by the fungi or not (Plate 1, figure 14). The damage caused by *A. capitata* could lead to a misclassification of the host specimens, even at the family level. For example, *Inaperturopollenites* sp. A and *Spheripollenites* sp. in Volkheimer (1972) show general characteristics (e.g., dimensions, wall thickness, shapes) which agree with the morphological features of



the nexines of *Classopollis* grains found in this work. Therefore, they might have been mistakenly included in the Araucariaceae and/or Cupressaceae families.

Kalgutkar & Jansonius (2000, p. 26) mentioned 'that Jansonius & Hills (1977, card 3294) interpreted the spherules as glomerules or ubisch bodies'. Ubisch bodies are circular structures produced during the final stages of the formation of pollen grains through an excess sporopollenin in the tapetal structure. These are generally minute, variously ornamented bodies, usually with a central cavity. These 'orbicules' show the same chemical and optical characteristics as pollen exine (Traverse 1991). Gambero (1968) described tapetal membranes and ubisch bodies found in male cones of *Apterocladus lanceolatus* Archangelsky (pollen grain: *Callialasporites*), *Brachyphyllum irregular* Archangelsky (*Inaperturopollenites*), *Tomaxelia biforme* Archangelsky (*Classopollis*) and *Trisocladus tigrensis* Archangelsky (*Trisaccites*). Ubisch bodies identified in *Callialasporites* Sukh Dev emend. Maheshwari show a subcircular to round elongate shape (1 to 3 μm wide), and few of them present a central cavity. Orbicular spheres adhered to *Inaperturopollenites* Pflug & Thomson present diverse shapes and sizes (1.5 to 6 μm or more in diameter) and show an irregular distribution on the grain surface. Some of them present a central cavity. Similarly, ubisch orbicules adhered to *Classopollis* Pflug grains have a homogeneous shape and size (1.3 to 1.5 μm in diameter) and are regularly distributed on the surface of the grain. They are subhexagonal in outline and have a defined central cavity. Ubisch bodies identified in *Trisaccites* Cookson & Pike show a subhexagonal shape and a clear central cavity, their overall size being smaller than those of the previously mentioned species (up to 1.5 μm). More recently, Lovisolo & Galati (2012) described 10 species of Poaceae and recognized four different types and four subtypes

of orbicules or ubisch bodies. They concluded that the different ubisch body-types were representative of the studied tribes and suggested that orbicule morphology may be a useful character in systematic studies.

Srivastava (1976) compared the fungal spores with the ubisch bodies and claimed that the structure, fossilization and adherence type of the former differ significantly from those of the latter. Ubisch bodies are attached superficially to the pollen surface and readily fall off during pollen grain dispersal and/or by physical-chemical laboratory treatments; they are thus found only rarely in the fossil record (Srivastava 1976).

In the present material, we recognized the different stages in the development of the fungal spore *Annella capitata*, beginning as small hyphae (Plate 1, figures 3, 8–10), then spores (Plate 1, figures 1–6, 8–15), then remnant evidence, such as pits and holes on the host (Plate 1, figure 7), as well as the presence of a few spores as record of its biogenic activity. These characteristics are distinctive and are not present in grains having sporopollenin ubisch bodies. Identifying the different growing phases and the results of the fungal activity constitute potentially valuable tools in systematic palynomorph studies. Therefore, the accurate taxonomic assignment of deteriorated palynomorphs requires the evaluation of the overall association and the degree and type of deterioration, and identifying the activity of the different microorganisms that could hide or obliterate specific characters. This paper is a contribution to understanding the taphonomic effects of fungi on palynomorphs.

5.2. Palaeoenvironment and palaeoecology of *A. capitata*

The role of fungal activity in the decomposition process of organic matter in streams, lakes, wetlands and

Plate 1: Scale bar 10 μm , unless otherwise specified. Figures 4 and 6 were taken with differential interference contrast (DIC) illumination. 1. *Classopollis itunensis* Pocock 1962 infected by hollow spores of *Annella capitata* Srivastava 1976. The fungal spores are indicated by a black arrow and the cavities or perforations leaved after spores decay are indicated by a white arrow MPEF-PALIN122: R27/1. 2–3. *Annella capitata* Srivastava on *Inaperturopollenites giganteus* Góczán 1964, MPEF-PALIN122: P50/3. 2. Complete specimen with clusters of fungal spores and some hollow spores indicated by a black arrow. 3. Detail of rows of spores and small hyphae indicated by black arrows. 4. Scale bar 25 μm , polyad of *Classopollis* sp. infected by *Annella capitata* Srivastava 1976, MPEF-PALIN122: B46/3. 5–6. Polyad of *Classopollis* sp. completely infected by *Annella capitata* Srivastava 1976, MPEF-PALIN122: C26/2. 5. Polyad with small hyphae indicated by black arrow. 6. Detail of three grains showing isolate spores, rows and small clusters of *A. capitata* Srivastava. 7. Scale bar 5 μm , *Classopollis classoides* (Pflug) Pocock & Jansonius 1961, cavities (biodegradation) created by fungi are shown by the arrows, MPEF-PALIN123 (scanning electron microscopy, SEM). 8–9. *Classopollis classoides* (Pflug) Pocock & Jansonius 1961, hypha at the base of an isolate spore indicated by the black arrow. 8. Complete pollen grain. 9. Scale bar 5 μm , detail of the hypha and spore, MPEF-PALIN123 (SEM). Figures 10–11. *Classopollis* sp., MPEF-PALIN123 (SEM). 10. Scale bar 20 μm , complete specimen, pairs and rows of fungal spores indicated by white arrows, and a germinated spore indicated by a black arrow. 11. Scale bar 2 μm , detail of germinated spore (black arrow). 12–13. *Classopollis* sp. with broken sexine and exposed nexine, MPEF-PALIN121: D50/3. 12. Focus on the broken sexine. The sexine is indicated by a black arrow. 13. Focus through to the nexine. The nexine is indicated by the black arrow. 14. *A. capitata* Srivastava on undeterminate gymnosperm pollen grain, MPEF-PALIN122: D41/0. 15. *A. capitata* Srivastava on *Podocarpidites* spp., MPEF-PALIN123 (SEM).

forest soils has been a focus of numerous studies during the last decade (e.g., Letcher & Powell 2001; Czczuga & Muszynska 2001; Wurzbacher et al. 2014). In these environments, aquatic fungi grow on pollen grains and produce exo-enzymes that can decompose the pollen wall (Czczuga & Muszynska 2001). Wurzbacher et al. (2014) concluded that fungal attack on wind-distributed pollen (mainly pine pollen) is very important in various freshwater ecosystems, perhaps especially acidic dystrophic lakes.

The assemblages containing *A. capitata* infection were recorded from lacustrine sediments, particularly those from coal seams. Based on the palynofacies analysis of the Cañadón Lahuincó 'A' section (Figures 1–2), it is inferred that the Cañadón Asfalto succession cropping out in Cañadón Lahuincó creek accumulated in an extensive littoral zone with fluvial influence, as shown by the high degree of terrestrial input, woody remains and gymnosperm pollen (Olivera 2012). In such a setting, sporomorphs can arrive via different routes and processes. A considerable proportion of the spores and pollen grains that reach streams or rivers are carried by surface runoff (Holmes 1994, p. 10), while others are deposited directly from the atmosphere by winds.

Fluvial transport is often intermittent and sporomorphs can become partially degraded whilst temporarily exposed on various substrates such as leaves, small branches and particularly the soil, where they are subject to microbial attack (Holmes 1994). The MPEF-PALIN122 sample, which contains high percentages of pollen grains that have adhered spores of *A. capitata*, is from a thin coal seam. This horizon is interpreted as a mire deposit related to a transgressive event (Olivera et al. 2013).

The palynological assemblages recognized in the different horizons show a high proportion of Cheirolepidiaceae and Araucariaceae, and the presence of upland forest components (mainly Podocarpaceae and Pinaceae) indicates that warm-temperate and relatively humid conditions prevailed in the region surrounding the depocentre (Olivera 2012). The other components of the palynoflora (bryophyte, lycophytes and filicopsida spores, and pollen grains of Corytospermaceae and Caytoniaceae families) (Figure 3) suggest a seasonal, sub-tropical palaeoclimate for the Cañadón Asfalto region during late Early to mid Middle Jurassic time (Olivera 2012).

The highest frequencies of *A. capitata* were recorded on Cheirolepidiaceae (*Classopollis*), but it also occurs on specimens of Araucariaceae (*Inaperturopollenites* and *Callialasporites*) and Podocarpaceae (*Podocarpidites*) pollen grains, especially from coal seams. Many authors mention that the fungi occur in

significant quantities and diversities in peat deposits (Schof 1946; Van Geel 1978, Cook et al. 2011; O'Keefe & Hower 2011; O'Keefe et al. 2011; Hower et al. 2013; O'Keefe et al. 2013). Although *A. capitata* is more frequent in coal seams in the Cañadón Asfalto Formation, it is also present in samples from other facies, such as proximal prodelta sediments (e.g., MPEF-PALIN123, Olivera et al. 2013).

Srivastava (1976) originally described *A. capitata* from marine palynofloral assemblages. It is important to emphasize the continental character of the present palynoflora. There is no published information about the ecological requirements of *A. capitata*. However, following the approach of Van Geel (1979), its ecological preferences can be inferred through comparison with known palynomorphs recorded from the same sample.

6. Conclusions

- Spherical spores assigned to *Annella capitata* show the same characteristics (shape, size, exine wall) regardless of the pollen taxa they are associated with. This is the main criterion for distinguishing them from ubish bodies, as the latter differ in ultrastructure, size and morphology according to the taxa on which they occur. The presence of hyphae and fungal germlings reinforce a fungal origin of these spherules, as does the intense bio-corrosion recognized in many of the palynomorphs observed in this study.
- *A. capitata* was identified on pollen grains of the Cheirolepidiaceae (*Classopollis*), Araucariaceae (*Inaperturopollenites* and *Callialasporites*) and Podocarpaceae (*Podocarpidites*) families. This fungus was not observed on the few lycophyte and fern spores identified in the assemblages.
- Numerous *A. capitata* spores were identified on different conifer pollen grains; however, hyphae were only recognized in a few specimens, suggesting a greater degree of ontogenetic maturity in most of the identified fungal spores.
- Based on palynofacies and sedimentological analyses, and the ecological preferences of the different plant families recognized in the Cañadón Asfalto palynoflora, it is suggested that *A. capitata* may have developed in low-energy environments, under warm-temperate and humid conditions, such as in forest humid soils, peats and lakes.

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Author biographies

DANIELA E. OLIVERA is a postdoctoral fellow at the Consejo Nacional de Investigaciones Científicas y Técnicas (CCT-CONICET) in Bahía Blanca, Argentina, and a teaching assistant in palaeontology at the Universidad Nacional del Sur, Bahía Blanca, Argentina. She obtained a PhD during 2012 from the Universidad Nacional del Sur. Daniela's current research interests include the palynofacies and palynostratigraphy of the Mesozoic and Cenozoic of Argentina

MIRTA E. QUATTROCCHIO specialises in marine and terrestrial palynology applied to projects on Mesozoic and Cenozoic biostratigraphy and basin analysis throughout Argentina. She is a researcher for the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Bahía Blanca, Argentina.

ANA M. ZAVATTIERI holds both Masters and PhD degrees, and specialises in palaeontology. She is an independent researcher with the National Research Council of Argentina, and works on the biostratigraphy, palaeontology and palynology of the Early Permian to Early Jurassic of Argentina and adjacent areas.

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