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New palynological evidence from the Rincón Formation, Chacoparaná Basin, Argentina: implications for regional Devonian paleogeographic dynamics

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Abstract: The Chacoparaná Basin has long been recognized for its hydrocarbon potential due to its extensive Paleozoic sedimentary deposits. This study reexamines the palynological assemblage of the Rincón Formation, recovered from the "El Rincón" exploration well (YPF.SE.ER.x-1) in the Santiago del Estero Province, Argentina. By integrating taxonomic, biostratigraphic, and paleoecological analyses, we provide a refined age determination and paleoenvironmental reconstruction. The recovered assemblage comprises both marine and terrestrial palynomorphs, with a dominance of marine elements indicating a marginal marine depositional environment. Key identified species suggest an Eifelian to Givetian age. Hierarchical clustering and ordination analyses reveal regional and temporal affinities with other Devonian assemblages across Argentina, supporting the hypothesis of pronounced provincialism during the Early Devonian. This study highlights the importance of palynological analysis in refining stratigraphic correlations and enhancing our understanding of regional paleogeographical evolution, offering valuable insights for future hydrocarbon exploration in the area.

Key words: Eifelian–Givetian, biostratigraphy, paleoenvironment, hydrocarbon exploration, South America

Resumen: Nueva evidencia palinológica de la Formación Rincón, Cuenca Chacoparaná, Argentina: implicancias en la dinámica paleogeográfica regional durante el Devónico. La Cuenca Chacoparaná ha sido reconocida desde hace tiempo por su potencial hidrocarburífero debido a sus extensos depósitos sedimentarios del Paleozoico. Este estudio reexamina la asociación palinológica de la Formación Rincón, recuperada del pozo exploratorio "El Rincón" (YPF.SE.ER.x-1) en la provincia de Santiago del Estero, Argentina. La integración de análisis taxonómicos, bioestratigráficos y paleoecológicos proporciona una determinación de edad más precisa y una reconstrucción paleoambiental. La asociación recuperada incluye palinomorfos tanto marinos como terrestres, con un predominio de elementos marinos que indican un ambiente de depósito marino marginal. Las especies clave identificadas sugieren una edad entre el Eifeliano y el Givetiano. Los análisis de agrupamiento jerárquico y ordenación revelan afinidades regionales y temporales con otras asociaciones devónicas en Argentina, lo que respalda la hipótesis de un provincialismo pronunciado durante el Devónico Temprano. Este estudio resalta la importancia de los estudios palinológicos para refinar las correlaciones estratigráficas y mejorar la comprensión de la evolución paleogeográfica regional, ofreciendo valiosos aportes para futuras exploraciones de hidrocarburos en la zona.

Palabras clave: Eifeliano–Givetiano, bioestratigrafía, paleoambiente, exploración de hidrocarburos, Sudamérica

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INTRODUCTION

The Chacoparaná basin (Fig. 1A) is known for its potential to host hydrocarbons due to its sedimentary structure. It spans across parts of Argentina, Brazil, Paraguay and Uruguay, including both igneous and sedimentary beds deposited since the Paleozoic to the Cenozoic. Paleozoic rocks are distributed in three main depocenters (Reinante *et al.*, 2014): Lower, Middle and Upper Paleozoic (Fig. 1A). The Middle Paleozoic depocenter comprises the Silurian–Devonian and is expressed mainly in the Santiago del Estero Province subsoil (Fig. 1A, B). Most of the palynological information has been gathered from hydrocarbon exploration drilling, conducted by oil companies in Argentina, Paraguay, and Uruguay, which hold numerous unpublished reports in its archives from the mid-twentieth century. Additionally, there are various published studies based on material from the same explorations (e.g., Pöthe de Baldis, 1971, 1974; Volkheimer *et al.,* 1986; Grahn 2003; Noetinger & di Pasquo, 2013; Daners *et al.*, 2017; Rubinstein *et al.,* 2018; Camina *et al.,* 2024a, b). Currently, due to the ongoing interest in uncovering additional reserves, reassessing previously explored sections in light of the new available information is essential for the continued advancement of the energy industry. We present an assemblage (spores and phytoplankton) from the Rincón Formation recovered from the exploration well "El Rincón" (YPF.SE.ER.x-1), Santiago del Estero Province, Argentina (Fig. 1B). The taxonomic analysis enabled the reconstruction of the floristic composition. The palynological association is characterized in terms of genus/species composition and compared with those already known from localities and contemporaneous formations at a regional level to restrain the age of the Rincón Formation and to reconstruct the depositional environment. Finally, the studied association is integrated with assemblages from continental Argentina and analyzed to discern the dynamics of the palynological marine communities across the Devonian. This information is crucial for the establishment and interpretation of regional paleogeographical reconstructions.

Geological setting

The exploration well El Rincón (YPF.SE.ER.x-1), situated in the Santiago del Estero Province (Figs. 1B, 2), traverses a sedimentary sequence known as Santiago del Estero Group, which includes the Copo, Caburé and Rincón formations. In the Santiago del Estero Province and the eastern part of Salta Province, in the Puesto El Tigre x-1 well, the Rincón Formation overlies the quartzites of the Caburé Formation, which had been previously dated to the Pridolian and lower Pragian stages (Rubinstein, 2021). Overlying the latter, Permo-Carboniferous strata can be found. The thickness of the Rincón Formation ranges between 250 and 1300 meters, depending on the geographical location (Rubinstein, 2021) and the upper part can reach a thickness of approximately 1000 meters (Grahn & Gutiérrez, 2001). It is composed of black, laminar, micaceous shales that are partially fossiliferous (Chebli *et al.*, 1999). The fossiliferous strata within the formation include invertebrates such as *Metacryphaeus* sp., *Kozlowskiaspis subcesiva* Clarke 1913, *Australocoelia tourtelotti* Boucot & Gill 1956, among others, suggesting an Emsian–Givetian age (Cuerda & Baldis, 1971; Aceñolaza *et al.*, 1999). The palynological information gathered from Los Horcones x-2 well (Fig. 2B) in the northwestern part of the Santiago del Estero Province suggests a Givetian age for the formation (Grahn & Gutiérrez, 2001). Antonelli & Ottone (2006) studied material from the El Caburé x-1 well (Fig. 2B), located also in the former province and proposed a late Emsian to early Eifelian age based on the joint presence of *Dibolisporites echinaceus* (Eisenack) Richardson 1965, *Emphanisporites annulatus* McGregor, 1961, *Grandispora* spp., *Dictyotriletes emsiensis* (Allen) McGregor, 1973 and *Rhabdosporites langii* (Eisenack) Richardson 1960. Lastly, Noetinger & di Pasquo (2013) studied samples from the Puesto El Tigre x-1 well in Salta province (Fig. 2B) establishing an age range from the Pragian to the Emsian for the formation, based on the presence of key species such as *Ramochitina magnifica* Lange, 1967, *Perotrilites caperatus* (McGregor) Steemans, 1989, *Triangulina aspera* Pöthe de Baldis, 1977, and *Cymbohilates heteroverrucosus* Breuer, Al-Ghazi, Al-Ruwaili, Higgs, Steemans & Wellman, 2007.

MATERIAL AND METHODS

Nine cutting samples from the palynological collection of the Museo Argentino de Ciencias Naturales (MACN) were selected, corresponding to the interval between 1363 and 1689 meters below the wellhead (m.b.w.). The samples were chosen from a preliminary survey, representing the Devonian section. Due to the high crystal concentration, the residues were reprocessed. The mineral matrix was removed applying firstly HF (70%) to dissolve the silicates and HCl (33%) for the carbonates and, followed by a wash with distilled water to reach a neutral pH (Riding, 2021). The reprocessed, neutralized residues were filtered through a 10 μm mesh; the +10 μm fraction was mounted according to the Noetinger *et al.* (2017) protocol. The palynological slides were examined under transmitted light microscopy using a Leica DM2500 trinocular microscope, equipped with a Leica DFC290 camera. Additionally individual palynomorph specimens were selected from the residue, separated under a microscope, and mounted on coverslips attached to stubs for scanning electron microscopy (SEM). These were left to dry, then coated with a Pd-Au layer to be photographed with SEM Zeiss GeminiSEM 360. The metalized coverslips were remounted after SEM imaging to obtain pictures of the same individuals under light microscopy.

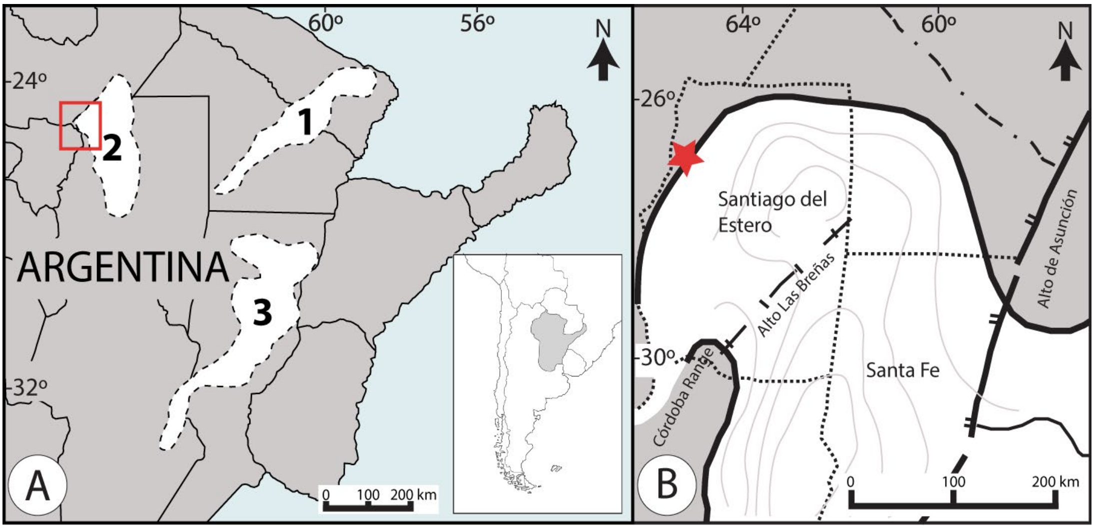

Fig. 1. A. Part of the Chacoparaná Basin, focused on NE Argentina and the location of the Paleozoic depocenters: (1) Lower Paleozoic, (2) Middle Paleozoic and (3) Upper Paleozoic. Modified from Reinante *et al.* (2014). B. Location of the studied locality.

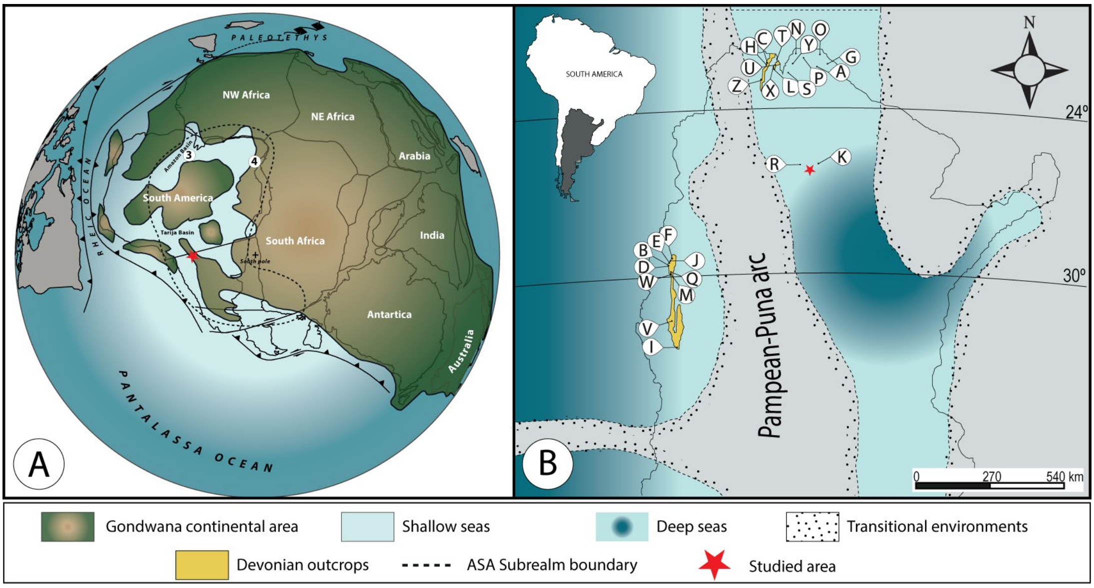

Fig. 2. A. Paleogeographical map featuring the Gondwana continent during the Middle Devonian (modified from Noetinger *et al.*, 2018). Dashed line encircles the Afrosouthamerican Subrealm (ASA) (after di Pasquo *et al.*, 2009, 2015). B. Paleoenvironmental map for late Eifelian/Givetian of Argentina (modified from Noetinger, 2015) and the location of Devonian localities. Early Devonian: A. Puesto El Tigre x-1 (Volkheimer *et al.*, 1986; Noetinger & di Pasquo, 2013). B. Río Jachal (García Muro & Rubinstein, 2015). C. Abra Límite (Noetinger & di Pasquo, 2010). D. Cerro La Chilca (García Muro *et al.*, 2017). E. Loma de los Piojos (García Muro *et al.*, 2018). F. Cerro del Fuerte (Le Hérissé *et al.*, 1996). G. Rivadavia x-1 (Camina *et al.*, 2024a). H. Abra Azul (Noetinger *et al.*, 2016). I. San Isidro Creek (Rubinstein & Steemans, 2007). J. Talacasto Creek (García Muro *et al.*, 2017). K. El Caburé x-1 (Antonelli & Ottone, 2006). L. Río Cañas (Pineda *et al.*, 2021; Le Hérissé *et al.*, 1996). M. Del Chaco Creek (Amenábar, 2009). N. San Antonio x-1 (Noetinger & di Pasquo, 2011). O. Santa Victoria x-1 (Barreda, 1986; Noetinger, 2015). P. Tonono x-1 (Noetinger, 2010). Q. Volcán Range (Amenábar *et al.*, 2006). R. Los Horcones x-2 (Grahn & Gutiérrez, 2001). S. Ramos x-1011 (Volkheimer *et al.*, 1986; Camina, 2024, García Muro *et al.*, 2025). T. Balapuca (di Pasquo, 2007a, b; Noetinger *et al.*, 2018). U. Angosto del Pescado (Noetinger *et al.*, 2018). V. San Juan River (Amenábar & di Pasquo, 2008). W. Don Agustín Creek (Amenábar, 2009). X. Angosto de San Ignacio (Noetinger *et al.*, 2018). Y. Quebrada Galarza x-1 (Ottone, 1996). Z. Arasayal (Noetinger *et al.*, 2018).

The program ImageJ® (Rueden *et al.,* 2017) was used to measure the specimens. The position of illustrated specimens in the respective slides is given in England-Finder coordinates. All the material (slides, residues, rock samples) is deposited in the Museo Argentino de Ciencias Naturales, Ciudad Autónoma de Buenos Aires, Argentina, under BA-Pal 5310, 5311, 5313, 5315, 5320, 5326, 5328, 5330 and 5331 accession numbers.

The depositional environment was inferred by the Palynological Marine Index [PMI= richness of marine palynomorphs (Rm)/ richness of terrestrial palynomorphs (Rt) + 1] 100, Helenes *et al.* (1998). Richness was calculated based on the number of genera. Low PMI values suggest brackish-water influence, while higher PMI values indicate marine depositional conditions.

For analyzing the similarities among various Devonian localities in the continental part of Argentina (Fig. 2), we constructed a presence/absence matrix (Supplementary data 1) including 39 associations, spanning the Early to Late Devonian: Barreda (1986), Volkheimer *et al.* (1986), Le Hérissé *et al.* (1996), Ottone (1996), Grahn & Gutiérrez (2001), Amenábar *et al.* (2006), Antonelli & Ottone (2006), di Pasquo (2007a, b), Rubinstein & Steemans (2007), Amenábar & di Pasquo (2008), Amenábar (2009), Noetinger (2010, 2015), Noetinger & di Pasquo (2010, 2011, 2013), García Muro & Rubinstein (2015), Noetinger *et al.* (2016, 2018), García Muro *et al.* (2017, 2018, 2025), Pineda *et al.* (2021), Camina (2024) and Camina *et al.* (2024a, b). The final data set lists 127 marine species from various taxa (chitinozoans, acritarchs and prasynophycean algae) that occur in at least two or more of these associations, thus, most species can be included. We chose to conduct the analyses only with marine taxa since floras from continental deposits are more likely to represent a local source compared to those from mixed and marine environments, where assemblages are often richer and have a broader representation, making it more difficult to establish correlations between them.

The statistical analyses were performed using R version 4.4.1 (R Development Core Team, 2024). Two coefficients recommended for binary data: the Jaccard index (Jaccard, 1908) and the modified Forbes index (Alroy, 2015a, b) were applied and later, the resulting distance matrices were subjected to hierarchical cluster analysis (Q mode) using the package vegan 2.6–8 (Oksanen *et al.*, 2024). Because clustering may impose hierarchies even when they do not exist (Hammer & Harper, 2006), additional tests were implemented in order to contrast the groupings achieved with the former method. Ordination processes, such as nMDS, are very useful to visualize trends and groupings. The scaling was performed with the package vegan 2.6–8 (Oksanen *et al.,* 2024).

RESULTS

Composition of the palynoflora

The assemblage comprises both marine and terrestrial elements. General preservation is poor, and the association is moderately diverse. Fifty-three species were identified, including those left in open nomenclature (Table 1, Fig. 3), distributed as follows: 19 acritarchs, 2 scolecodonts, 15 chitinozoans, 5 prasinophytes, 9 spores, 1 cryptospore and 2 chlorophycean algae (Figs. 4-6).

Systematic paleontology

Marine palynomorphs. Taxa left in open nomenclature are described or remarked upon below, organized by major groups and in alphabetical order. The complete list of recognized taxa, listed in alphabetical order for each major group of palynomorphs is included in Table 1.

a) Acritarchs

Fossil genus. *Bimerga* Wood, 1995
Type species. *Bimerga bensonii* Wood, 1995.

Bimerga sp.
(Fig. 4A)

Description. Elongated vesicle with one end opening into three processes, each with simple terminations.
Dimensions (1 specimen). Total length of the vesicle 249.16 μm; width of the vesicle 23.2 μm; wall thickness 2.5 μm; length of the processes 14–20 μm; width of the processes 3.5–5
Comparisons and remarks. *Bimerga bensonii* Wood (1995) shows a bilaterally symmetrical vesicle with a minor length range 95(106)123 μm. *Bimerga paulae* Le Hérissé (2011) displays a process at each end that bifurcates distally into a second or third order; the vesicle is smaller, ranging from 120 to 160 μm.
Occurrence. Level BA-Pal 5311.

Fossil genus. *Dactylofusa* Brito & Santos emend. Combaz, Lange & Pansart emend.

DEVONIAN									AGE	
EL RINCÓN									FORMATION	
1378-1381	1384-1387	1414-1417	1438-1441	1514-1517	1595-1598	1629-1632	1671-1674	1686-1689	Depth (m.b.w.)	
5310	5311	5313	5315	5320	5326	5328	5330	5331	SAMPLE	
									TAXA	
	●					●	●		*Ammonidium garrasinoi* Ottone, 1996	ACRITARCHS
	●								*Bimerga* sp.	
	●								*Dactylofusa*? sp.	
	●								*Dupliciradiatum tenue* González, Moreno & Playford, 2005	
●							●		*Exochoderma arca* Wicander & Wood, 1981	
●									*Exochoderma triangulata* Wicander & Wood, 1981	
	●								*Gorgonisphaeridium* sp.	
	●								*Hapsidopalla sannemanni* (Deunff) emend. Playford, 1977	
●									*Hoegklintia* cf. *H. longispina* Pöthé de Baldis, 1998	
	●								*Leiofusa* sp.	
						●			*Michystridium* sp.	
									Multiplicisphaeridium sp.	
	●								*Navifusa bacilla* (Deunff) Playford, 1977	
	●					●	●		*Palacanthus ledanoisii* Deunff emend. Playford, 1977	
●									*Polyedryxium* sp. A	
							●		*Polyedryxium* sp. B	
●						●	●		*Veryhachium lairdii* group Servais, Li, Molyneux, Raevskaya & Rubinsteink, 2007	
●									*Veryhachium* sp. cf. *V. pastoris* Deunff, 1966	
●									*Veryhachium trispinosum* group Servais, Li, Molyneux, Raevskaya & Rubinstein, 2007	
	●								Scolecodont sp. A	SCOLECODONTS
						●			Scolecodont sp. B	
	●		●						*Ancyrochitina ancyrea* (Eisenack) Eisenack, 1955	CHITINOZOANS
			●						*Ancyrochitina cornigera* Collinson & Scott, 1958	
			●						*Ancyrochitina parisi* Volkheimer, Melendi & Salas, 1986	
	●		●						*Ancyrochitina simplex* Grahn, Bergamaschi & Pereira, 2002	
	●		●						*Ancyrochitina* sp. A	
			●						*Ancyrochitina* sp. B	
●	●		●						*Ancyrochitina* sp. C	
	●								*Ancyrochitina* sp. D	
	●								*Ancyrochitina* sp. E	
	●		●						*Cyathochitina* sp. cf. *C. campanulis* Boneham & Masters, 1973	
	●								*Hercochitina* sp.	
	●								*Hoegisphaera* sp. cf. *H. glabra* Staplin, 1961	
	●								*Lagenochitina amottensis* Grignani & Mantovani, 1964	
	●								*Lagenochitina postpirum* Camina, 2024	
	●								*Ramochitina autasmirimense* Grahn & de Melo, 2004	
						●			*Cymatiosphaera canadensis* (Deunff) Deunff, 1954	PRASINOPHYTES
		●		●					*Dictyotidium dictyotum* (Eisenack) Eisenack, 1955	
						●			*Dorsennidium* (*Dorsennidium*) *raczii* (Cramer) Sarjeant & Stancliffe, 1994	
	●					●			*Pterospermella capitana* Wicander, 1974	
	●								*Pterospermella pernambucensis* (Brito) Eisenack, Cramer & Diez Rodríguez, 1973	
●						●			*Acinosporites lindlarensis* Riegel, 1968	SPORES
				●					*Acinosporites parviornatus* Richardson, 1965	
●	●								*Apiculiretusispora plicata* (Allen) Streel, 1967	
	●		●	●		●			*Corystisporites* sp. cf. *C. collaris* Tiwari & Schaarschmidt, 1975	
	●		●	●	●				*Corystisporites* sp. cf. *C. undulatus* Turnau, 1996	
	●								*Dibolisporites echinaceus* (Eisenack) Richardson, 1965	
		●							*Dibolisporites eifeliensis* (Lanninger) McGregor, 1973	
	●								*Dibolisporites hystricosus* Hashemi & Playford, 2005	
							●		*Retusotriletes albarinii* di Pasquo & Noetinger, 2008	
●		●	●			●			*Cymbohilates rubinsteinae* Noetinger, di Pasquo, Isaacson, Aceñolaza & Vergel, 2016	CRYPTOSPORE
						●			*Quadrisporites variabilis* (Cramer) Ottone & Rosello, 1996	ALGAE
	●								*Quadrisporites* sp. cf. *Q. granulatus* (Cramer) Ströther, 1991	

Fig. 3. Stratigraphic distribution of the taxa in the studied section.

Table 1. Complete list of taxa identified in the El Rincón Formation from the exploration well "El Rincón" (YPF.SE.ER.x-1), Santiago del Estero Province.

Taxa identified in this study	Figure
Marine palynomorphs	
Acritarchs	
Ammonidium garrasinoi Ottone, 1996	4. E.
Bimerga sp.	4. A.
Dactylofusa? sp.	4. B.
Dupliciradiatum tenue González, Moreno & Playford, 2005	4. F.
Exochoderma arca Wicander & Wood, 1981	
Exochoderma triangulata Wicander & Wood, 1981	
Gorgonisphaeridium sp.	4. G.; 6. J.
Hapsidopalla sannemanni Deunff emend. Playford, 1977	4. H.
Hoegklintia cf. *H. longispina* Pöthé de Baldis, 1998	4. I.
Leiofusa sp.	4. C.
Michystridium sp.	4. J.
Multiplicisphaeridium sp.	4. K.
Navifusa bacilla (Deunff) Playford, 1977	4. D.
Palacanthus ledanoisii Deunff emend. Playford, 1977	
Polyedryxium sp. A	4. L.
Polyedryxium sp. B	4. M.
Veryhachium lairdii group Servais, Li, Molyneux, Raevskaya & Rubinsteink, 2007	
Veryhachium sp. cf. *V. pastoris* Deunff, 1966	4. N.
Veryhachium trispinosum group Servais, Li, Molyneux, Raevskaya & Rubinstein, 2007	
Scolecodonts	
Scolecodont sp. A	5. K.
Scolecodont sp. B	5. L.
Chitinozoans	
Ancyrochitina ancyrea (Eisenack) Eisenack, 1955	
Ancyrochitina cornigera Collinson & Scott, 1958	
Ancyrochitina parisi Volkheimer, Melendi & Salas, 1986	5. A.; 6. A.
Ancyrochitina simplex Grahn, Bergamaschi & Pereira, 2002	5. B.
Ancyrochitina sp. A	5. C.; 6. B.
Ancyrochitina sp. B	5. D.; 6. C.
Ancyrochitina sp. C	5. E.; 6. D.
Ancyrochitina sp. D	5. F.
Ancyrochitina sp. E	5. G.
Cyathochitina sp. cf. *C. campanulis* Boneham & Masters, 1973	5. H.; 6. E.
Hercochitina sp.	5. I.
Hoegisphaera sp. cf. *H. glabra* Staplin, 1961	5. M.; 6. I.
Lagenochitina amottensis Grignani & Mantovani, 1964	6. F.
Lagenochitina postpirum Camina, 2024	6. G.
Ramochitina autasmirimense Grahn & Melo, 2004	6. H.
Prasinophytes	
Cymatiosphaera canadensis (Deunff) Deunff, 1954	
Dictyotidium dictyotum (Eisenack) Eisenack, 1955	
Dorsennidium (*Dorsennidium*) *raczii* (Cramer) Sarjeant & Stancliffe, 1994	
Pterospermella capitana Wicander, 1974	4. O.
Pterospermella pernambucensis (Brito) Eisenack, Cramer & Diez Rodríguez, 1973	4. P.
Non-marine palynomorphs	
Spores	
Acinosporites lindlarensis Riegel, 1968	
Acinosporites parviornatus Richardson, 1965	
Apiculiretusispora plicata (Allen) Streel, 1967	
Corystisporites sp. cf. *C. collaris* Tiwari & Schaarschmidt, 1975	5. N.; 6. K.
Corystisporites sp. cf. *C. undulatus* Turnau, 1996	5. O.
Dibolisporites echinaceus (Eisenack) Richardson, 1965	
Dibolisporites eifeliensis (Lanninger) McGregor, 1973	
Dibolisporites hystricosus Hashemi & Playford, 2005	
Retusotriletes albarinii di Pasquo & Noetinger, 2008	
Cryptospores	
Cymbohilates rubinsteinae Noetinger, di Pasquo, Isaacson, Aceñolaza & Vergel, 2016	
Algae	
Quadrisporites variabilis (Cramer) Ottone & Rosello, 1996	
Quadrisporites sp. cf. *Q. granulatus* (Cramer) Ströther, 1991	5. P.

Cramer, 1970
Type species. *Dactylofusa maranhensis* Brito & Santos, 1965.

?*Dactylofusa* sp.
(Fig. 4B)

Description. Vesicle boat-shaped or fusiform, with acuminate distal ends. Vesicle wall is ornamented with granules along its total length.
Dimensions (1 specimen). Total length of the vesicle 205 μm; width of the vesicle 60 μm.
Remarks. Due to poor preservation, the characteristics defining the genus are not observable, leaving the classification uncertain.
Occurrence. Level BA-Pal 5311.

Fossil genus. *Dupliciradiatum* González, Moreno & Playford, 2005
Type species. *Dupliciradiatum crassum* González, Moreno & Playford, 2005.

Dupliciradiatum tenue González, Moreno & Playford, 2005
(Fig. 4F)

Dimensions (1 specimen). Total diameter 74 μm; diameter of the vesicle 54 μm; width of the membrane 9 μm.
Remarks. The specimen is well-preserved. The species has not been previously documented for the Givetian period. The specimen found in this study could potentially extend its known stratigraphic range, however, given that only a single specimen was found, this hypothesis remains uncertain.
Occurrence. Level BA-Pal 5311.

Fossil genus. *Gorgonisphaeridium* Staplin, Jansonius & Pocok emend. Kiryanov, 1978
Type species. *Gorgonisphaeridium winslowii* Staplin, Jansonius & Pocok, 1965.

Gorgonisphaeridium sp.
(Fig. 4G, 6J)

Description. Semi-spherical vesicle with an irregular outline defined by the processes. The surface is finely scabrated and densely adorned with processes distributed evenly around the vesicle. The processes are solid and cylindrical, with slight bifurcations towards the tip; in some cases, the bifurcations are sharp, while in others they are blunter.
Dimensions (1 specimen). Diameter of the vesicle 135 μm; wall thickness 2–3 μm; length of the processes 11–14 μm; space between processes 5–8 μm; diameter of the bases of the processes 4–5 μm.
Remarks and comparisons. *Gorgonisphaeridium* sp. is similar to *G. inflatum* Wicander & Wood (1981) in terms of the vesicle structure and the arrangement and morphology of processes. Nevertheless, *G. inflatum* vesicle is smaller in diameter (30–49 μm), the wall thickness is thinner (1–2 μm) and processes are shorter (1.6–4.1 μm) with more narrow bases (0.8–1.6 μm). *Gorgonisphaeridium discissum* Playford (1981) is similar to *G.* sp. B, but differs on its measurements and the morphology of processes. Vesicle is spherical (36–42 μm) and circular to semicircular in outline, well-differentiated from the processes. Wall thickness is thinner (0.8–1.8 μm). Processes are solid, shorter (1.4–4.5 μm) and more widely spaced (0.4–4.5 μm), originating from smaller bases (0.5–2 μm), ending in pointed apices or occasionally bifurcated. Species with similar characteristics and size were not found for the Gondwana region.
Occurrence. Level BA-Pal 5311.

Fossil genus. *Hapsidopalla* Playford emend. Wicander & Wood,1981
Type species. *Hapsidopalla sannemannii* Deunff emend. Playford, 1977.

Hapsidopalla sannemannii Deunff emend. Playford, 1977
(Fig. 4H)

Dimensions (1 specimen). Diameter of the vesicle 60 μm; length of the processes 4–6 μm, width of the processes 1–1.5 μm; space between processes 6–10 μm.
Remarks. This is the first record for the species in Argentina.
Occurrence. Level BA-Pal 5311.

Fossil genus. *Hoegklintia* Dorning, 1981
Type species. *Hoegklintia visbyensis* Eisenack, 1959.

Hoegklintia sp. cf. *H. longispina* Pöthe de Baldis, 1998
(Fig. 4I)

Dimensions (1 specimen). Total length of the vesicle 55 μm; length of the processes 11–25 μm; width of the processes 2.3–2.9 μm.
Remarks. Although the species is cited for the

Silurian in Rubinstein & García Muro (2011), García Muro *et al.* (2018) mentions the species for the Devonian Period as *Hoegklintia* cf. *H. longispina*.
Occurrence. Level BA-Pal 5310.

Fossil genus. *Leiofusa* Eisenack emend. Eisenack emend. Combaz, Lange & Pansart emend. Cramer,1970
Type species. *Leiofusa fusiformis* Eisenack *ex* Eisenack,1938.

Leiofusa sp.
(Fig. 4C)

Description. Fusiform vesicle with a cylindrical central body. Each end tapers abruptly into a simple, long and distinct process.
Dimensions (1 specimen). Total length of the vesicle 131.3 μm; length of the vesicle 55 μm; width of the vesicle 17.21 μm; length of the processes 40.9–41.6μm; width of the processes 4–5 μm.
Remarks and comparisons. *Leiofusa banderillae* Cramer (1964) is similar in its measurements but differs from *L.* sp. in the morphology of the vesicle, which is subcircular to oval in the former. *L. pyrena* Wicander & Wood (1981) displays a similar morphology but differs on having a larger vesicle and shorter processes. *Leiofusa* sp. in Ottone (1996) shares similar dimensions but differs slightly in the morphology of the vesicle, where each end tapers gradually to a thin process. Species with similar characteristics and size were not found for the Gondwana region.
Occurrence. Level BA-Pal 5311.

Fossil genus. *Micrhystridium* Deflandre emend. Sarjeant & Stancliffe, 1994
Type species. *Micrhystridium inconspicuum* Deflandre, 1937

Michystridium sp.
(Fig. 4J)

Description. Vesicle with circular outline from which numerous, spiny, relatively short processes emerge.
Dimensions (1 specimen). Diameter of the vesicle 23.5 μm; length of the processes 3.5–6.8 μm.
Remarks and comparisons. *Micrhystridium* genre was originally described by Deflandre (1937) and includes a large number of species. The morphological simplicity of the genre makes it difficult to distinguish between species (Wicander & Wood, 1981).
Occurrence. Level BA-Pal 5328.

Fossil genus. *Multiplicisphaeridium* Staplin emend. Sarjeant & Vavrdová, 1997
Type species. *Multiplicisphaeridium ramispinosum* Staplin emend. Sarjeant & Vavrdová, 1997.

Multiplicisphaeridium sp.
(Fig. 4K)

Description. Vesicle spherical, circular to subcircular outline. Processes communicate freely with the vesicle; processes branch in a first and second order (only discernible in one case).
Dimensions (1 specimen). Total length 82 μm; diameter of the vesicle 36 μm; length of the processes 18–20 μm; diameter of the bases of the processes 7 μm.
Remarks and comparisons. *Multiplicisphaeridium ramusculosum* Deflandre emend. Lister (1970) in Pineda *et al.* (2021) has a larger number of processes. *Multiplicisphaeridium segregatum* Wicander & Wood (1997) has a smaller vesicle (18–24 μm) and shorter processes (10–14 μm). *Multiplicisphaeridium ampliatum* Playford (1977) has longer (22–35 μm) and more numerous (10–14) processes.
Occurrence. Level BA-Pal 5313.

Fossil genus. *Polyedryxium* Deunff emend. Deunff, 1971
Type species. *Polyedryxium deflandrei* Deunff *ex* Deunff, 1961.

Polyedryxium sp. A
(Fig. 4L)

Description. Polyhedral vesicle with outlines marked by ridges that extend beyond the vesicle and end in blunt tips.
Dimensions (1 specimen). Diameter of the vesicle 55 μm.
Remarks. *Polyedryxium decorum* Deunff (1955) is comparable in size and features ridges that extend beyond the vesicle. However, the vesicle consists of 6 to 9 concave faces, which are not observable. The only specimen studied is poorly preserved, which prevents a more precise identification.
Occurrence. Level BA-Pal 5310.

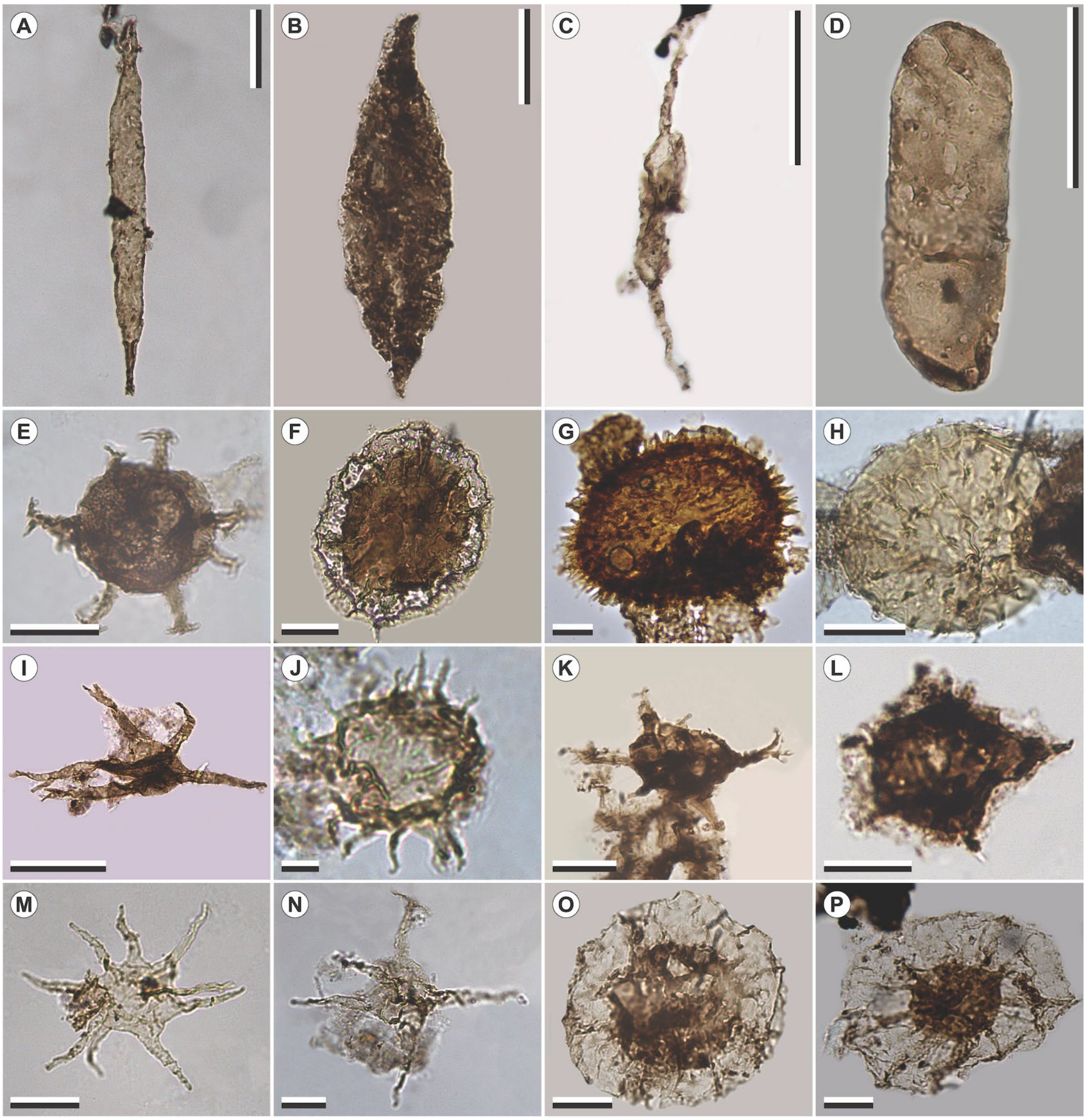

Fig. 4. Selected species. A. *Bimerga* sp., BA-Pal 5311 (1), C55/2. B. ?*Dactylofusa* sp. BA-Pal 5311 (1), M39. C. *Leiofusa* sp., BA-Pal 5311 (1), J29/3. D *Navifusa bacilla* (Deunff) Playford, 1977, BA-Pal 5311 (1), O42/2. E. *Ammonidium garrasinoi* Ottone, 1996, BA-Pal 5330 (1), F39. F. *Dupliciradiatum tenue* González, Moreno & Playford, 2005, BA-Pal 5311 (1), O42/4. G. *Gorgonisphaeridium* sp., BA-Pal 5311 (1), U44/3. H. *Hapsidopalla sannemannii* (Deunff) emend. Playford, 1977, BA-Pal 5311 (1), F49/4. I. *Hoegklintia* sp. cf. *H. longispina* Pöthé de Baldis, 1998, BA-Pal 5310 (4), B61/1. J. *Michystridium* sp. BA-Pal 5328 (1), B60/2. K. *Multiplicisphaeridium* sp., BA-Pal 5313 (1), A22. L. *Polyedryxium* sp. A, BA-Pal 5310 (1), J39/2. M. *Polyedryxium* sp. B, BA-Pal 5330 (1), A39/2. N. *Veryhachium* sp. cf. *V. pastoris* Deunff, 1966, BA-Pal 5310 (4), F48/2. O. *Pterospermella capitana* Wicander, 1974, BA-Pal 5311 (1), A39/2. P. *Pterospermella pernambucensis* (Brito) Eisenack, Cramer & Diez Rodriguez, 1973, BA-Pal 5311 (1). Scale bar A–D= 50 μm, J, N= 5 μm, E–I, K–M, O–P= 10 μm.

Polyedryxium sp. B
(Fig. 4M)

Description. The vesicle is amorphous, with nine homomorphic processes that emerge from wide bases and narrow into acuminate tips. Surface of processes is apparently granulated.

Dimensions (1 specimen). Total diameter 70 μm; diameter of the central body 26 μm; length of the processes 20–28 μm; width of the processes

4 μm; diameter of the bases of the processes 12 μm.

Remarks and comparisons. In Noetinger (2010) *Polyedrixium pharaonis* Deunff (1961) is described with a larger (76 μm) and cubic-shaped vesicle.

Occurrence. Level BA-Pal 5330.

Fossil genus. *Veryhachium* Deunff emend. Sarjeant & Stancliffe 1994

Type species. *Veryhachium trisulcum* (Deunff) Deunff 1954, subsequent designation by Downie (1959) (see Loeblich & Tappan, 1976).

Veryhachium sp. cf. *V. pastoris* Deunff, 1966
(Fig. 4N)

Description. Rectangular vesicle with 4 processes that emerge from each corner in one single plane, one of which bifurcates on its tip. A fifth process projects perpendicularly from the center of the vesicle.

Dimensions (1 specimen): Total length of the vesicle 28.8 μm; length of the processes 35 μm.

Remarks and comparisons: *Veryhachium pastoris* Deunff (1966) features seven processes arranged in two perpendicular planes: five in one plane and two in the other. The specimen found is similar in dimensions and morphology, but the number of processes described originally is not observed, leaving the species classification uncertain.

Occurrence. Level BA-Pal 5310.

b) Scolecodonts

Scolecodont sp. A
(Fig. 5K)

Description. Jaw consists of an elongated, curved plaque with eight teeth, each having a robust base and rounded tips. These gradually diminish in size towards the posterior end and are uniformly directed backwards.

Dimensions (1 specimen). Total length 127 μm; width of the plaque 43.7 μm; width of the teeth 8–15 μm.

Occurrence. Level BA-Pal 5311.

Scolecodont sp. B
(Fig. 5L)

Description. Jaw consists of a short, slightly curved plaque, with a total of eight teeth. Seven of these are equal in size, while at one end, a larger, hook-shaped tooth can be observed. The tips are acuminate.

Dimensions (1 specimen). Total length 55 μm; width of the plaque 25 μm; width of the teeth 5–7.5 μm.

Occurrence. Level BA-Pal 5328.

c) Chitinozoans

The principal measurements, recorded in micrometers (μm), are: L = total length; ln = length of the neck; lc = length of the chamber; D = maximum diameter of the chamber; dn = diameter of the neck, and da = diameter of the aperture.

Fossil genus. *Ancyrochitina* Eisenack,1955

Type species. *Ancyrochitina ancyrea* (*Conochitina ancyrea*) (Eisenack) Eisenack,1955.

Ancyrochitina sp. A
(Figs. 5C, 6B)

Description. The vesicle chamber is conical, and the base is slightly convex with rounded edges. The shoulders are slightly developed, and the flexure is pronounced. The neck is cylindrical and occupies approximately 50% of the total height. The surface of the vesicle is smooth. The base displays bifurcating processes that extend up to 47 μm long with bases of 8 to 10 μm wide.

Dimensions (2 specimens). L= 244–275 μm; ln= 127–137 μm; lc= 105–120 μm; D= 112–119 μm; dn= 40–45 μm; da= 45–47μm.

Remarks and comparisons. *Ancyrochitina* sp. A is similar to *A. parisi* Volkheimer, Melendi & Salas (1986) in terms of the morphology of the chamber, neck, and overall measurements. However, *A. parisi* features processes on the neck similar to those on its base, while *A.* sp. A lacks processes on the neck. *Ancyrochitina postdesmea* Grahn (2002) also has processes on both the base and the neck, like *A. parisi*. *Ancyrochitina ancyrea* (Eisenack) Laufeld (1974) has a conical vesicle with a smooth surface, a subtly marked flexure and shoulders, a cylindrical neck that gradually widens toward the aperture, and a convex to flat base bearing 8 to 10 long processes that bifurcate or trifurcate. Despite these similarities, *A.* sp. A has a greater total length range than *A. ancyrea.*

Occurrence. Level BA-Pal 5311/ 5315.

Ancyrochitina sp. B
(Figs. 5D, 6C)

Fig. 5. Selected species. A. *Ancyrochitina parisi*, BA-Pal 5315 (4), S38/4. B. *Ancyrochitina simplex* Grahn, Bergamaschi & Pereira, 2002, BA-Pal 5311 (1), A36/2. C. *Ancyrochitina* sp. A, BA-Pal 5311 (1), D40. D. *Ancyrochitina* sp. B, BA-Pal 5315 (1), E37. E. *Ancyrochitina* sp. C, BA-Pal 5311 (1), Q36/4. F. *Ancyrochitina* sp. D, BA-Pal 5311 (1), F33/3. G. *Ancyrochitina* sp. E, BA-Pal 5311 (1), D37. H. *Cyathochitina* sp. cf. *C. campanulis* Boneham & Masters, 1973, BA-Pal 5311 (2), J53/4. I. *Hercochitina* sp. BA-Pal 5311 (1), A42/1. J. *Lagenochitina postpirum* Camina, 2024, BA-Pal 5311 MEB (1), BA-Pal 5311 (2), L53. K. *Scolecodont* sp. A, BA-Pal 5311 (1), N30/3. L. *Scolecodont* sp. B, BA-Pal 5328 (1), O56/3. M. *Hoegisphaera* sp. cf. *H. glabra* Staplin, 1961, BA-Pal 5311 (4), G43/1. N. *Corystisporites* sp. cf. *C. collaris* Tiwari & Schaarschmidt, 1975, BA-Pal 5315 (1), B55/3. O. *Corystisporites* sp. cf. *C. undulatus* Turnau, 1996, BA-Pal 5315 (1), A33/1. P. *Quadrisporites* sp. cf. *Q. granulatus* (Cramer) Ströther, 1991, BA-Pal 5311 (1), J50/2. Scale bar A–J= 50 μm, K–P= 10 μm.

Description. The vesicle is ovoid to conical, and the base is convex to flat, the margins are slightly rounded. The shoulders are poorly developed, and the flexure is only slightly marked. The neck is short and cylindrical, occupying approximately 35% of the total height, and features one simple process up to 35 μm long with a 9 μm wide base. The surface of the vesicle is smooth.

Dimensions (2 specimens). L= 160–222 μm; ln= 65–68 μm; lc= 85–165 μm; D= 83–98 μm; dn= 44–45 μm; da= 40–50 μm.

Remarks and comparisons. *Ancyrochitina taouratinensis* Boumendjel (1985) has a conical vesicle with rounded margins and poorly developed shoulders and flexure. The neck/body ratio is the same in both species (40%). However, *A. taouratinensis* features processes on the base as well as small spines decorating the wall of the chamber and neck. *Ancyrochitina* aff. *A. langei* Sommer & Van Boekel (1964) has a short, cylindrical neck with spines near the aperture, but differs in the shape of the vesicle and has processes on the base. *Ancyrochitina paranaensis* Grahn, Pereira & Bergamaschi (2000) has a similar vesicle appearance and a total length within the same size range. However, the vesicle of *A. paranaensis* is covered with spines and has a base bearing a crown of up to eight branching processes.

Occurrence. Level BA-Pal 5315.

Ancyrochitina sp. C
(Figs. 5E, 6D)

Description. Vesicle with a subconical to ovoid shape, a convex to flat base, and slightly rounded margins. The shoulders are only slightly developed, and the flexure is marked. The neck is cylindrical and expands at the opening, representing approximately 40% of the total length. The base features simple processes of 18 to 40 μm long and bases of 6 to 15 μm wide.

Dimensions (6 specimens). L= 115–250 μm; ln= 40–115 μm; lc= 80–165 μm; D= 46–103 μm; dn= 20–50 μm; da= 25–50 μm.

Remarks and comparisons. *Ancyrochitina arirambaense* Grahn & Melo (2005), shows certain similarities with *A.* sp. C, featuring simple processes on the base, a cylindrical neck without processes, and a smooth vesicle. However, they differ in vesicle shape, similar to *A. simplex* Grahn (2002). *Ancyrochitina morzadeci* Paris (1981) has a vesicle with rounded margins, a straight cylindrical neck, a mostly smooth surface, and a base with processes. However, in *A. morzadeci*, the shoulders are absent, the vesicle is mostly conical, the neck is covered with spines, and the base processes are bifurcated, whereas those of *Ancyrochitina* sp. C are simple.

Occurrence. Level BA-Pal 5310/5311/5315.

Ancyrochitina sp. D
(Fig. 5F)

Description. The vesicle is conical to ovoid with a convex to rounded base and rounded margins. Shoulders are slightly marked, and the flexure is pronounced. The neck is short, occupying 35% of the total length, and expands at the opening. A simple process is observed at the base, 60 μm long and 12 μm wide at the base.

Dimensions (1 specimen). L= 196 μm; ln= 67.8 μm; lc= 125 μm; D= 74 μm; dn= 28 μm; da= 34 μm.

Remarks and comparisons. *Ancyrochitina fragilis* Eisenack (1955) features an elongated conical-ovoid body with a rounded base and a cylindrical neck that expands towards the opening. It has 4 to 6 simple, robust processes on its base, while *A.* sp. D shows only a single simple process, lacking the characteristic curvature. *Ancyrochitina* sp. D*,* as described by Grahn & Melo (2005), has an ovoid vesicle, a cylindrical neck, and a smooth surface. However, it has 8 simple appendages on the base and a proportionally shorter neck (2/5).

Occurrence. Level BA-Pal 5311.

Ancyrochitina sp. E
(Fig. 5G)

Description. The vesicle is cylindrical with a constriction approximately in the middle of the chamber. The base ranges from convex to flat and has simple processes that extend up to 47 μm long and with a 16 μm wide base. Shoulders are poorly developed, and the flexure is slightly marked. The neck is short, straight, and cylindrical, occupying 30% of the total length. The base features a simple process and two broken bases can be seen.

Dimensions (1 specimen). L= 271 μm; ln= 80 μm; lc= 188 μm; D= 60 μm; dn= 32 μm; da= 32 μm.

Remarks and comparisons. *Ancyrochitina* sp. E shares some characteristics with *A. biconstricta* Lange (1949), such as its dimensions, shape and proportions of the neck, and the overall shape of the vesicle, described as “cylindroconical.” Additionally, *A. biconstricta* features a crown of 6 to 8 simple processes, when complete. However, the distinguishing feature of *A. biconstricta is* a constriction above the margin, while *A.* sp. E has a constriction approximately in the middle of the chamber. Furthermore, *A.* sp. E has a slightly developed flexure and shoulders, whereas *A. biconstricta* has a slightly marked flexure and lacks shoulders. *Ancyrochitina* sp. B, as described by Camina (2024), has an elongated ovoid to subcylindrical vesicle, with poorly developed shoulders and flexure, a cylindrical neck occupying 30% of the total length, and a smooth surface. Despite these similarities, *A.* sp. B has a base with a crown that displays up to 8 simple and branched processes, whereas *A.* sp. E has a single simple process and two broken bases. Additionally, *A.* sp. E has a characteristic constriction in the vesicle, which is not present in *A.* sp. B. *Ancyrochitina* sp. C in Gaugris & Grahn (2006) has a similar appearance, with an elongated body, a cylindrical neck and a crown of four simple appendices at the base. However, the appendices are much longer and the vesicle does not exhibit the characteristic constriction as seen in *A.* sp. E.

Occurrence. Level BA-Pal 5311.

Fossil genus. *Cyathochitina* Eisenack, 1955

Type species. *Conochitina campanulaeformis* Eisenack, 1931.

Cyathochitina cf. *campanulis* Boneham & Masters, 1973

1973 *Cyathochitina campanulis*; Boneham & Masters p.94, figs 8–9.

Cyathochitina sp. cf. *C. campanulis* Boneham & Masters, 1973
(Figs. 5H, 6E)

Description. The vesicle chamber is conical to bell-shaped, with a concave to flat base. The flanks are straight to concave, and the flexure is slightly marked. The neck is cylindrical and occupies, on average, 42% of the total length. The wall is unornamented.

Dimensions (4 specimens). L= 215–240 μm; ln= 80–112 μm; lc= 116–152 μm; D= 105–120 μm; dn= 40–50 μm; da= 32–55 μm.

Remarks and comparisons. Although *Cyathochitina campanulis* has only been recorded in Euramerica for the Silurian (Boneham & Masters, 1973), Camina *et al.* (2024b) registered *Cyathochitina* sp. cf. *C. campanulis* for the first time for the Devonian and suggested that a revision of the species is necessary. The specimens found in this study have a morphology comparable with those described by Camina *et al.* (2024b), although a carina at the base is mentioned, which is not observed here. In the original description, Boneham & Masters (1973) detailed that a few specimens have a narrow carina but most do not.

Occurrence. Level BA-Pal 5311/5315.

Fossil genus. *Hercochitina* Jansonius, 1964

Type species. *Hercochitina crickmayi* Jansonius,1964.

Hercochitina sp.
(Fig. 5I)

Description. The vesicle chamber is claviform, shoulders and flexure are absent. The base is convex to rounded. The vesicle surface is ornamented with longitudinally arranged ridges. The neck is cylindrical and flares at the aperture.

Dimensions (1 specimen). L= 287 μm; ln= 68 μm; lc= 210 μm; D= 73 μm; dn= 36 μm; da= 38 μm.

Remarks and comparisons. *Hercochitina* sp. in Noetinger & di Pasquo (2011) has a smaller vesicle (145–209 μm). *Hercochitina crickmayi* Jansonius (1964) has a flat base and longitudinal membranes, up to 8 μm height, that arise abruptly from the wall. This species is cited from the Ordovician to the early Gothlandian and is predominantly found in Laurentia, with additional records from Baltica, Avalonia, and Gondwanan margins.

Occurrence. Level BA-Pal 5311.

Fossil genus. *Hoegisphaera* Staplin emend. Paris, Grahn, Nestor & Lakova, 1999

Type species. *Hoegisphaera glabra* Staplin,1961.

Hoegisphaera sp. cf. *H. glabra* Staplin, 1961
(Figs. 5M, 6I)

Description. The vesicle is semispherical to discoidal, and the diameter of the aperture represents half of the total length.

Dimensions (3 specimens). L= 108–118 μm; da= 45–47 μm.

Remarks and comparisons. *Hoegisphaera* sp. cf. *H. glabra* Staplin (1961) is characterized by the lack of a defined collar and a wide aperture, a feature that distinguishes it from the specimens of *Hoegisphaera glabra* from the Frasnian.

Occurrence. Level BA-Pal 5311.

Fossil genus. *Lagenochitina* Eisenack, 1931 emend. Paris, Grahn, Nestor & Lakova, 1999
Type species. *Lagenochitina baltica* Eisenack, 1931.

Lagenochitina postpirum Camina, 2024
(Fig. 6G)

Dimensions (3 specimens). L=216–250 μm; ln=80–108 μm; lc= 136–144 μm; D= 80–100 μm; dn= 43–49 μm; da= 31–40 μm.
Remarks. The specimen is originally described in Camina (2024) with a shorter neck (25% of the total length).
Occurrence. Level BA-Pal 5311.

Fossil genus. *Ramochitina* Sommer & Van Boekel, 1964 emend. Paris, Grahn, Nestor & Lakova, 1999
Type species. *Ramochitina ramosi* Sommer & Van Boekel, 1964.

Ramochitina autasmirimense Grahn & Melo, 2004
(Fig. 6H)

Description. The vesicle chamber is conical, with rounded margins and a convex base. The neck is short, occupying approximately 35% of the total length, and cylindrical. The shoulders are well developed and the flexure is weak. The surface of the vesicle is covered with simple and bifurcated spines, up to 33 μm long and 3 to 6 μm in width.
Dimensions (1 specimen). L= 222.8 μm; ln= 90 μm; lc= 130 μm; D= 70 μm; dn= 35.5 μm; da= 35.8 μm.
Remarks. When originally described in Grahn & Melo (2004), bifurcated spines were not mentioned or described. Camina *et al.* (2024b) reported clearly developed bifurcated spines on the studied material and suggested that bifurcated spines, as well as simple spines, should be added as diagnostic features of the species. The specimen found in this study supports this claim.
Occurrence. Level BA-Pal 5311.

Non-marine palynomorphs

a) Spores

Fossil genus. *Corystisporites* Richardson, 1965
Type species. *Corystisporites multispinosus* Richardson,1965.

Corystisporites sp. cf. *C.collaris* Tiwari & Schaarschmidt, 1975
(Fig. 5N)

Description. Trilete spore of circular to subcircular outline, with a large number of processes placed densely on the vesicle surface. The processes are short, have a wide base and taper abruptly to a pointed apex.
Dimensions (5 specimens). Diameter of the vesicle 50–72 μm; length of the processes 7–24 μm; diameter of the bases of the processes 5–17 μm.
Remarks. The poor state of preservation of the studied material prevents a more precise determination.
Occurrence. Level BA-Pal 5315/ 5320/ 5328.

Corystisporites sp. cf. *C. undulatus* Turnau, 1996
(Figs. 5O, 6K)

Description. Trilete spore of circular to subcircular outline. Bares numerous long processes that emerge from a wide base and narrow into a pointed apex.
Dimensions (8 specimens). Total diameter 60–95 μm; length of the processes 12–30 μm; diameter of the bases of the processes 6.6–18 μm; processes 2.5–4 μm wide.
Remarks. The poor state of preservation of the studied material prevents a more precise determination.
Occurrence. Level BA-Pal 5311/5315/5320/5326.

b) Algae

Fossil genus. *Quadrisporites* Henelly *ex* Potonié & Lele emend. Amenábar, di Pasquo, Carrizo & Azcuy, 2006
Type species. *Quadrisporites horridus* Hennelly *ex* Potonié & Lele, 1961.

Quadrisporites sp. cf. *Q. granulatus* (Cramer) Ströther, 1991
(Fig. 5P)

Description. Colony formed by 4 members joined by ridges. The surface of the wall can be smooth, scabrate or finely granulated.
Dimensions (1 specimen). Total diameter 60 μm; individual diameter 30 μm.
Remarks. The only specimen found is poorly preserved and prevents more precise determination.

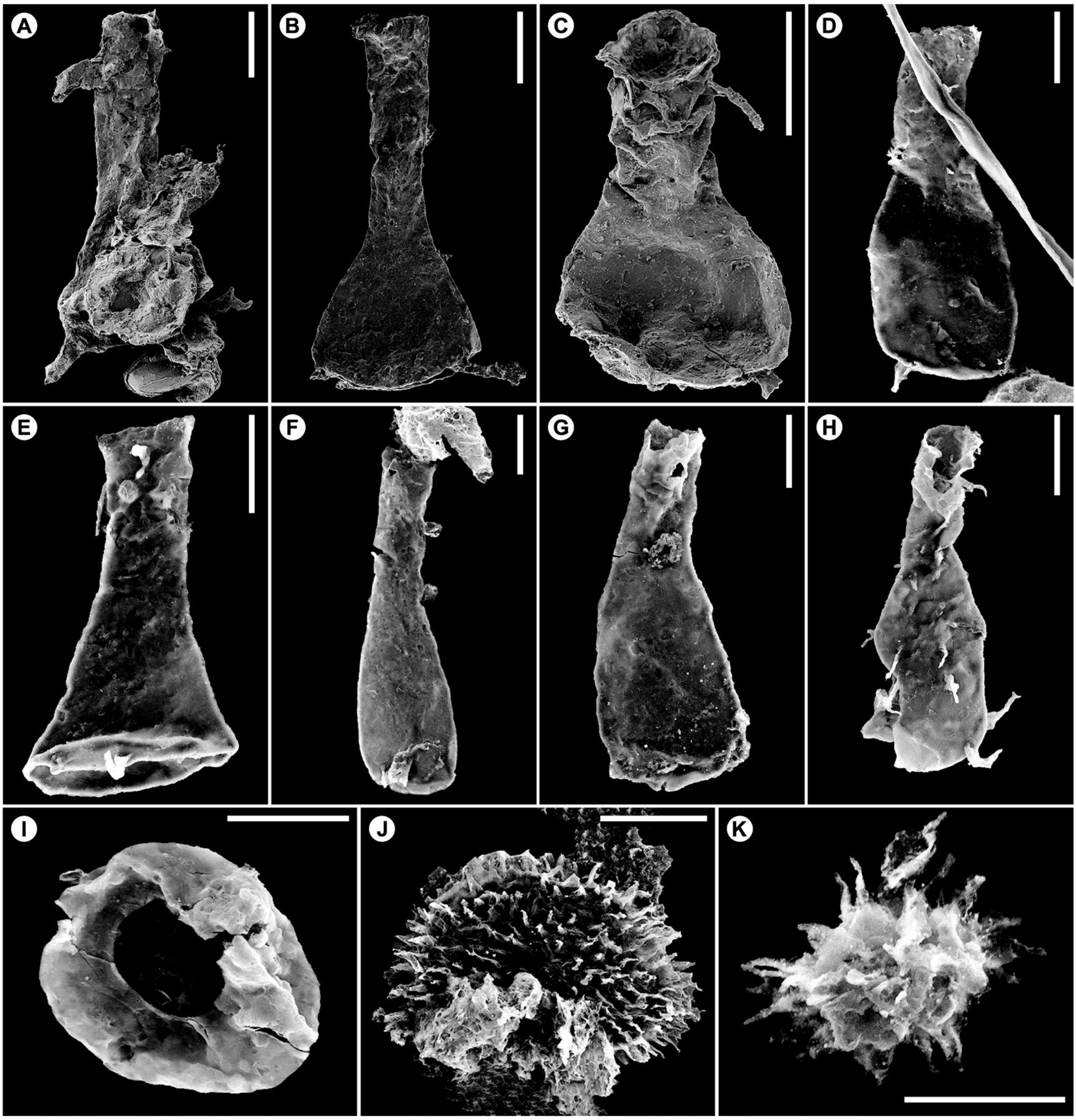

Fig. 6. Selected species. A. *Ancyrochitina parisi* (same specimen as in Fig. 5A), BA-Pal 5315 B. *Ancyrochitina* sp. A, BA-Pal 5315 C. *Ancyrochitina* sp. B, BA-Pal 5315 D. *Ancyrochitina* sp. C, BA-Pal 5311 E. *Cyathochitina* sp. cf. *C. campanulis* Boneham & Masters, 1973 (same specimen as in Fig. 5H), BA-Pal 5311 F. *Lagenochitina amottensis* Grignani & Mantovani, 1964, BA-Pal 5311 G. *Lagenochitina postpirum* Camina, 2024, BA-Pal 5311 H. *Ramochitina autasmirimense* Grahn & Melo, 2004, BA-Pal 5311 I. *Hoegisphaera* sp. cf. *H. glabra* Staplin, 1961, BA-Pal 5311 J. *Gorgonisphaeridium* sp. (same specimen as in Fig. 4G), BA-Pal 5311 K. *Corystisporites* sp. cf. *C. collaris* Tiwari & Schaarschmidt, 1975, BA-Pal 5311. Scale bar = 50 μm.

Occurrence. Level BA-Pal 5311.

Ordination analysis

From the hierarchical cluster (HC) analysis of the 39 Devonian localities based on the Jaccard index, four main groups can be observed (Fig. 7). The first group includes associations from the Chaco-Salteño and Chaco-Pampean plains, the Subandean Range, and the Precordillera, covering the Middle to Late Devonian. The association studied here is part of this group.

The second group contains mainly Early Devonian assemblages from the Precordillera, with exceptions including SA1 from the Subandean Range and Middle Devonian, Abra Azul also from the Subandean Range, and Río

San Juan, which belongs to the Late Devonian in the Precordillera.

The third group includes Middle and Late Devonian assemblages from the Chaco-Salteño and Chaco-Pampean plains, as well as the Subandean Range, except for AL1, which is from the Early Devonian.

The fourth group primarily consists of Early Devonian associations from the Chaco-Salteño and Chaco-Pampean plains, as well as the Subandean Range. Exceptions include Don Agustín Creek from the Precordillera and Late Devonian, and To1 and Los Horcones x-2 from the Chaco-Salteño and Chaco-Pampean plains, both dated to the Middle Devonian.

Regarding the HC based on the Forbes index (Supplementary material 2), the associations are arranged similarly to those in Fig. 7. However, it is worth noting that in the case of the Jaccard index, the Rincón assemblage is placed on the same cluster with 4 associations that range from the Middle to Late Devonian and are located in the Chaco-Salteño plain and Subandean Range. In contrast, the Forbes analysis groups it with only two of these associations, both from the Middle Devonian and situated in the same regions.

Lastly, the nMDS analysis (Fig. 8) reveals that the studied assemblage shows a closer relationship with the Ramos x-1 and Santa Victoria x-1 associations from the Subandean and Chaco-Salteño Plain, respectively.

DISCUSSION

Age and Correlation

The recovered assemblage contains both continental and marine species, mainly with long-known stratigraphic ranges (Table 2). However, some species occur on a more restricted range, which allows for a more precise determination of the assemblage's age. Among the latter, the presence of *Lagenochitina postpirum* (Fig. 6G) on the level BA-Pal 5311 (Fig. 3), species known for the early Givetian (Camina, 2024), along with *Pterospermella capitana,* recorded from the Givetian to Famennian (Ottone, 1996; Filipiak, 2005; Amenábar *et al.*, 2009; Noetinger, 2010), *Cyathochitina* sp. cf. *C. campanulis, a* species recorded for the early Givetian (Camina *et al.*, 2024b), and *Ramochitina autasmirimense* with a maximum Givetian age (Grahn & Melo, 2004; di Pasquo *et al.*, 2015; Noetinger *et al.*, 2018; Camina *et al.*, 2024b), suggests a ?late Givetian age for the top of the well (Levels BA-Pal 5310–5311). The occurrence of *Ammonidium garrasinoi* at level BA-Pal 5328 and 5330, with an Eifelian–Famennian range (Ottone, 1996; Noetinger, 2010; Noetinger & di Pasquo, 2010; di Pasquo *et al.*, 2015), *Ancyrochitina simplex*, ranging from Eifelian to Givetian (Grahn & Melo, 2004, 2005; Grahn *et al.*, 2006, 2008; Noetinger, 2010), *A. cornigera,* with an Eifelian–Frasnian (Lange, 1967; Wicander & Wood, 1997; Paris *et al.*, 2000; Grahn & Melo, 2004, 2005; Grahn *et al.*, 2006; Camina *et al.*, 2024b) and *A. parisi,* key species for the homonymous Biozone as defined by Volkheimer *et al.* (1986), representing the late Early Devonian, points to a maximum Eifelian age for the lower section of the well (BA-Pal 5313–5331). It is worth mentioning that the species *Hoegklintia* sp. cf. *H. longispina* was not considered in the age assessment. García Muro *et al.* (2018) reported this species for the first time in the Devonian Period, assigning a late Pragian–Emsian age, though the number of specimens found was not specified. Since only one specimen was identified in this study, the evidence is insufficient to revise the age of the assemblage or to extend the species known age.

It should be noted that the state of preservation, along with the diversity of the assemblage's samples are consistent with those typical of the Early Devonian. However, no preserved species that could support this conjecture were found. Given the above discussion, the biostratigraphic and ordination analyses (Figs. 7, 8) suggest an age ranging from the Eifelian to the Givetian, corresponding to the Middle Devonian. The stratigraphic distribution of the identified elements indicates that contamination from caving is not significant in the studied section, yet caving cannot be entirely excluded.

Paleoecology

The assemblage studied in this work is predominantly composed of marine palynoflora, with a significantly lower proportion of spores when compared to the chitinozoans and marine phytoplankton observed. This claim is supported by the PMI, which shows a value of 471. This value indicates a marine environment, with continental elements carried to the final deposition environment by fluvial input. This hypothesis is supported by the presence of the algae *Quadrisporites,* which is considered as an indicator of freshwater to marginal marine environments (Pineda *et al.*, 2021). Additionally, the morphology of the acritarchs is mainly simple and does not display a complex ornamentation. This kind of format is interpreted as an indicator

Table 2. Known stratigraphic ranges of palynomorph taxa identified at El Rincón Formation, based on selected literature: Amenábar *et al.*, 2009; Camina, 2024; Camina *et al.*, 2024b; di Pasquo *et al.*, 2015; Filipiak, 2005; Grahn, 2002; Grahn *et al.*, 2002; Grahn & Melo, 2004; Grahn, 2005; Grahn & Melo, 2005; Grahn *et al.*, 2006, 2008, 2013; Lange, 1967; Martin, 1981; Mendlowicz Mauller *et al.*, 2009; Noetinger, 2010; Noetinger & di Pasquo, 2010, 2011, 2013, 2018; Ottone, 1996; Paris *et al.*, 2000; Tonarová *et al.*, 2017; Valenzuela *et al.*, 1990; Volkheimer *et al.*, 1986; Wicander, 1974, 1975, 1983; Wicander & Wood, 1997.

	Devonian						
	Lower			Middle		Upper	
	Loch.	Prag.	Ems.	Eif.	Giv.	Fras.	Fam.
Ancyrochitina parisi Volkheimer, Melendi & Salas, 1986			■	■	■		
Ancyrochitina simplex Grahn, Bergamaschi & Pereira, 2002				■	■		
Ramochitina autasmirimense Grahn & de Melo, 2004				■	■		
Ancyrochitina cornigera Collinson & Scott, 1958				◀	■		
Ammonidium garrasinoi Ottone, 1996				■	■	■	■
Lagenochitina postpirum Camina, 2024					■		
Cyathochitina sp. cf. *C. campanulis* Boneham & Masters, 1973					■		
Pterospermella capitana Wicander, 1974					■	■	▶

of unstable paleoenvironments (e.g. variations on salinity, temperature, nutrient availability), features corresponding to a marginal marine environment (Amenábar, 2009). Scolecodonts, jaws of polychaete worms, are typically associated with shallow marine environments. Suttner & Hints (2010) studied a scolecodont assemblage from Devonian limestones and concluded that the jaws were deposited in back-reef or lagoonal settings. Lastly, although the paleoecology of chitinozoans remains uncertain, they have mainly been reported in shallow water deposits, with no evidence of abyssal occurrence (Paris, 2006). Taken together, these findings suggest a marginal marine depositional environment for the studied locality.

Paleobiogeography

The results obtained from the different ordination analyses show a common pattern within the different methods: the associations tend to cluster by both age and region. Two main regional groupings can be identified, on one hand, assemblages from the East of the Pampean-Puna arc (Fig. 2), including both the Chaco-Salteño and Chaco-Pampean plains, and the Subandean Range, and on the other, the assemblages from Precordillera, towards the West. Nevertheless, there are some exceptions that are worth noting.

The first group in the Jaccard analysis aligns with the proposed hypothesis, consisting exclusively of East and West assemblages from the Middle and Late Devonian. The assemblage under study is included in this cluster. The second cluster is mostly composed of Early Devonian associations from the West, except for SA1, Abra Azul and Río San Juan assemblages. Certain characteristics of the previously mentioned assemblages may explain why they are present in the cluster. Regarding SA1, this one is composed mostly of continental elements (93%) with only 6 marine species (Noetinger & di Pasquo, 2011). The Abra Azul assemblage is also dominated by continental specimens, with only 2 marine species (Noetinger *et al.*, 2016). Lastly, Río San Juan is very poor, having only one marine species (Amenábar & di Pasquo, 2008). Within the third cluster, the assemblage apparently inconsistent would be AL1, where only 4 species were identified (Noetinger & di Pasquo, 2010). The fourth and final group is dominated by associations from the Early Devonian, belonging to the East. Exceptions in this group include the Don Agustín Creek assemblage, To1, and Los Horcones x-2. Don Agustín Creek assemblage is poor, with only two identified species (Amenábar, 2009). Assemblage To 1 is characterized by low values of PMI and high terrestrial input, with only 2 marine species (Noetinger, 2010). Los Horcones x-2 consist of only one identified marine species (Grahn & Gutiérrez, 2001). On the other hand, the first cluster in the Forbes analyses mainly contains assemblages dated to the Early Devonian from the West. Exceptions include Río San Juan, with only 1 marine species (Amenábar & di Pasquo, 2008), and Abra Azul with only 2 marine species (Noetinger *et al.*, 2016). The second cluster groups associations from the Early Devonian, all located in the East. Exceptions are AL2 (Middle Devonian), with 1 marine species (Noetinger & di Pasquo, 2010), and Angosto de San Ignacio and Arasayal, both

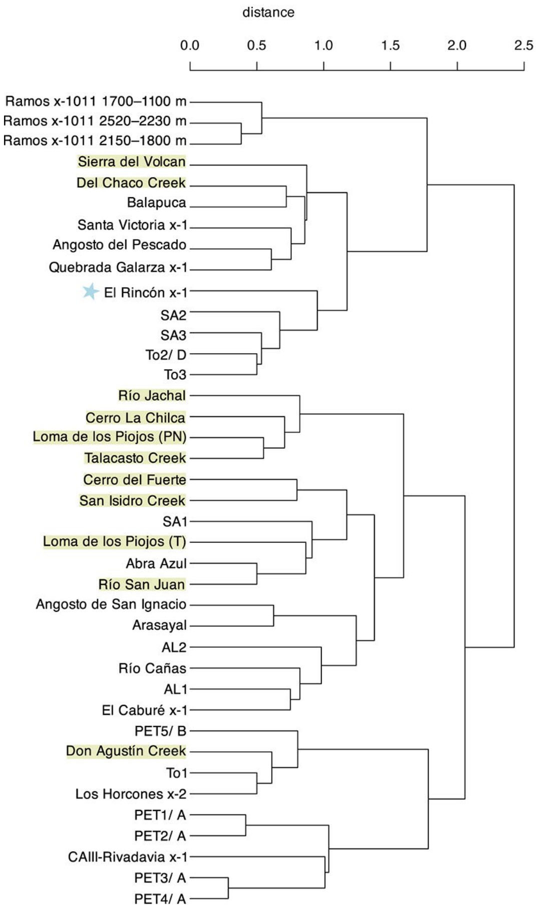

Fig. 7. Cluster analysis dendogram (Jaccard index - Ward algorithm) showing the similarities between associations from the East and West (localities framed in yellow) on the basis of Supplementary material 1.

dated Late Devonian (Noetinger *et al.*, 2018). There are two possible explanations for these irregularities: one pertains to the sample size, while the other relates to the inherent nature of the hierarchical clustering method, which may impose hierarchical structures even in the absence of true hierarchies, as previously discussed. In the third cluster, the studied assemblage is grouped with Middle Devonian assemblages from the East. Exceptions in this group are Don Agustín Creek, with 2 identified species (Amenábar, 2009), Los Horcones x-2, with one identified marine species (Grahn & Gutiérrez, 2001), and three associations from the PET well (Volkheimer *et al.*, 1986; Noetinger & di Pasquo, 2013). Finally, the fourth cluster consists exclusively of assemblages from the Middle and Late Devonian, from both the East and West.

Setting aside the exceptions mentioned above, the remaining groups provide valuable paleobiogeographical evidence when considered within the time frame. Between the Early and part of Middle Devonian, the Earth's geography was dominated by two major superterranes, Gondwana and Laurussia (Torsvik & Cocks, 2004). Several authors have studied the mega- and microfossils from this period (Marshall, 1996; Le Hérissé, 2001; Grahn, 2002; Steemans *et al.*, 2007; Noetinger, 2010; di Pasquo *et al.*, 2015) noticing a marked provincialism within taxa. This endemism was likely driven by paleoenvironmental factors such as climate and latitude, rather than paleogeographic barriers (Noetinger, 2010; Capel *et al.*, 2023). During this period, in the Argentinian region, the assemblages denominated as from the East and West in this study, were physically separated by an emerged area known as the Pampean Puna arc.

Notably, the ordination analyses reveal that Early Devonian associations are grouped together but in two distinct branches: one containing the assemblages from the East, and the other from the West. This organizational structure supports the concept of provincialism during the Early Devonian, with the division of branches likely explained by the physical barrier represented by the Pampean Puna arc.

From the Givetian onward, a decline in provincialism is observed, with a tendency towards cosmopolitism. This was favored by specific paleogeographic and paleoclimatic conditions, most notably the northward migration of Gondwana and its eventual collision with Euramerica, which culminated in the formation of the supercontinent Pangea (Torsvik & Cocks, 2017). Some authors (McGregor, 1979; McGregor & Playford, 1992; Capel *et al.*, 2023) argue that some degree of provincialism may have still existed. However, the results of the ordination analyses support the idea of cosmopolitism, where associations belonging from the Middle to Late Devonian are grouped together on the same branch, regardless of geographical region. The Puna Arc functioned as a regulatory structure for the deposition of Devonian sediments, as originally noted by Bonarelli (1921). A more comprehensive assessment of its influence requires an expanded collection of palynofloras, particularly from the Middle Devonian of the Precordillera, where the current scarcity of well-defined assemblages limits a thorough analysis. Enhancing the dataset will support the refinement of a more robust paleogeographic framework.

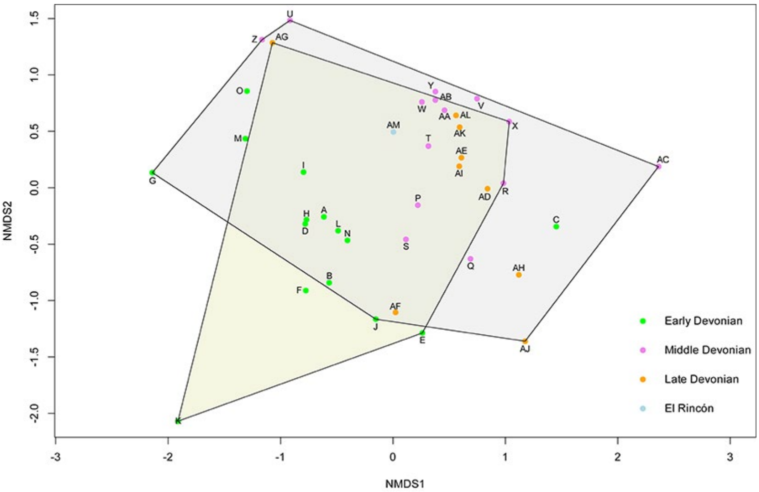

Fig. 8. NMDS ordination plot of selected 39 associations, spanning the Early to Late Devonian, based on Jaccard dissimilarities; k = 3, stress value = 0.1093696. Grey polygon represents associations to the east of the Pampean-Andean arc and yellow polygon includes associations towards the west. A. PET1/ Assemblage A (Volkheimer *et al.*, 1986; Noetinger & di Pasquo, 2013). B. Río Jáchal (García Muro & Rubinstein, 2015). C. AL1 (Noetinger & di Pasquo, 2010) D. Cerro La Chilca (García Muro *et al.*, 2017). E. Loma de los Piojos - Talacasto Fm. (Garcia Muro *et al.*, 2018). F. Cerro del Fuerte (Le Hérissé *et al.*, 1996). G. CAIII-Rivadavia x-1 (Camina *et al.*, 2024a). H. PET2/ Assemblage A (Volkheimer *et al.*, 1986; Noetinger & di Pasquo, 2013). I. PET3/ Assemblage A (Volkheimer *et al.*, 1986; Noetinger & di Pasquo, 2013). J. Abra Azul (Noetinger *et al.*, 2016). K. San Isidro Creek (Rubinstein & Steemans, 2007). L. Loma de los Piojos - Punta Negra Fm. (García Muro *et al.*, 2018). M. PET4/ Assemblage A (Volkheimer *et al.*, 1986; Noetinger & di Pasquo, 2013). N. Talacasto Creek (García Muro *et al.*, 2017). O. PET5/ Assemblage B (Volkheimer *et al.*, 1986; Noetinger & di Pasquo, 2013). P. El Caburé x-1 (Antonelli & Ottone, 2006). Q. Río Cañas (Pineda *et al.*, 2021). R. Del Chaco Creek (Amenábar, 2009). S. SA1 (Noetinger & di Pasquo, 2011). T. Santa Victoria x-1 (Barreda, 1986; Noetinger, 2015). U. To1 (Noetinger, 2010). V. To2/ Assemblage D (Noetinger, 2010). W. Ramos x-1011 - 2520-2230 m (Camina, 2024; García Muro *et al.*, 2025). X. Sierra del Volcán (Amenábar, 2009). Y. Ramos x-1011 - 2150-1800 m (Camina, 2024; García Muro *et al.*, 2025). Z. Los Horcones x-2 (Grahn & Gutiérrez, 2001). AA. Ramos x-1011 - 1700-1100 m (Camina, 2024; García Muro *et al.*, 2025). AB. SA2 (Noetinger & di Pasquo, 2011). AC. AL2 (Noetinger & di Pasquo, 2010). AD. Balapuca (Noetinger *et al.*, 2018). AE. Angosto del Pescado (Noetinger *et al.*, 2018). AF. Río San Juan (Amenábar & di Pasquo, 2008). AG. Don Agustín Creek (Amenábar, 2009). AH. Angosto de San Ignacio (Noetinger *et al.*, 2018). AI. Quebrada Galarza x-1 (Ottone, 1996). AJ. Arasayal (Noetinger *et al.*, 2018). AK. To3 (Noetinger, 2010). AL. SA3 (Noetinger & di Pasquo, 2011). AM. El Rincón x-1.

CONCLUSIONS

The studied palynological assemblage from the Rincón Formation, obtained from the exploration well 'El Rincón' (YPF.SE.ER.x-1), Santiago del Estero Province, Argentina, has provided valuable insights into its age, depositional environment, and paleobiogeographical significance. The assemblage is dominated by marine phytoplankton, with the presence of some spores and cryptospores. The particular features of the examined biodiversity suggest a marginal marine depositional environment. The stratigraphic analysis, based on the distribution range of key species such as *Lagenochitina postpirum,* together with *Pterospermella capitana, Cyathochitina* sp. cf. *C. campanulis* and *Ramochitina autasmirimense*, suggests a minimum Givetian age for the section BA-Pal 5310-5311. While the presence of *Ammonidium garrasinoi*, *Ancyorchitina simplex*, *Ancyrochitina cornigera* and *Ancyrochitina parisi,* suggests an Eifelian age for the lower section of the well (BA-Pal 5313-5331), representing the Middle Devonian.

The paleobiogeographic analysis supports the hypothesis of marked provincialism during the Early Devonian, with associations clustering into two main groups, separated by the physical barrier of the Pampean-Puna Arc. The studied assemblage falls within the Middle Devonian eastern group, reinforcing its regional affinity and contributing to broader paleogeographic reconstructions of Devonian marine environments in South America. Future research integrating additional palynological records will further refine these interpretations and advance our comprehension of Devonian marine communities and their environmental dynamics.

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Supplementary material

http://revista.macn.gob.ar/ojs/index.php/RevMus/rt/suppFiles/917/0

REFERENCES

Aceñolaza, F.G., G.F. Aceñolaza & García, G. 1999. El Silúrico-Devónico del Noroeste Argentino. In: R. Caminos (ed.), *Geología Argentina,* Instituto de Geología y Recursos Minerales, Buenos Aires, Argentina, Anales. vol. 9. pp. 205–214.

Alroy, J. 2015a. A simple way to improve multivariate analyses of paleoecological data sets. *Paleobiology* 41: 377–386.

Alroy, J. 2015b. A new twist on a very old binary similarity coefficient. *Ecology* 96: 575–586.

Amenábar, C.R. 2009. Middle Devonian microfloras from the Chigua Formation, Precordillera region, northwestern Argentina. *Geological Society, London, Special Publications* 314: 177–192.

Amenábar, C.R. & M. di Pasquo. 2008. Nuevos aportes a la palinología, cronología y paleoambiente de la Precordillera Occidental de Argentina: formaciones El Planchón, Codo (Devónico) y El Ratón (Mississippiano). *Acta Geológica Lilloana* 21: 3–20.

Amenábar, C.R., M. di Pasquo, H.A. Carrizo & C.L. Azcuy. 2006. Palynology of the Chigua (Devonian) and Malimán (Carboniferous) formations in the Volcán Range, San Juan Province, Argentina. Part I. Paleomicroplankton and acavate smooth and ornamented spores. *Ameghiniana* 43: 339–375.

Amenábar, C.R., M. di Pasquo & C.L. Azcuy. 2009. Palynofloras of the Chigua (Devonian) and Malimán (Mississippian) formations from the Precordillera Argentina: Age, correlation and discussion of the D/C boundary. *Revista Española de Micropaleontología* 41: 217–239.

Antonelli, J. & E.G. Ottone 2006. Palinología de coronas del Devónico y Carbonífero Superior del Pozo YPF.SE.EC.X-1, El Caburé, provincia de Santiago del Estero, Argentina. *Revista Del Museo Argentino de Ciencias Naturales* 8: 111–117.

Barreda, V.D. 1986. Acritarcos Givetiano-Frasnianos de la Cuenca del Noroeste, Provincia de Salta. Argentina. *Revista Española de Micropaleontología* 18: 229–245.

Bonarelli, G. 1921. Tercera Contribución al Conocimiento Geológico de Las Regiones Petrolíferas Subandinas Del Norte (Provincias de Salta y Jujuy). Ministerio de Agricultura de la Nación, Buenos Aires, Argentina, pp. 169.

Boneham, R.F. & W.R. Masters. 1973. Silurian Chitinozoa of Indiana II: The Waldron Shale and Osgood Member of the Salamonie Dolomite. *American Midland Naturalist 90(1):* 87-96.

Boumendjel, K. 1985. Nouvelles espèces de Chitinozoaires dans le Silurien et le Dévonien du Bassin d'Illizi (S.E. du Sahara algérien). *Revue de Micropal*eontologie 28(3): 155-166.

Brito, I.M. & A. da S. Santos. 1965. Contribuição ao conhecimento dos microfósseis Silurianos e Devonianos da Bacia do Maranhão. Part I. *Notas Preliminares e Estudos/ Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Brasil* 129: 1–29.

Camina, S.C. 2024. *Quitinozoos de las cuencas devónicas del noroeste argentino y del sur de Bolivia: bioestratigrafía, paleobiogeografía y paleoambientes. Un enfoque hacia la exploración de hidrocarburos*. PhD. Thesis, Universidad Nacional de San Luis, San Luis, Argentina, 202 pp.

Camina, S.C., C.V. Rubinstein, A. Butcher & J.P. Lovecchio. 2024a. Middle–Late Silurian and Early Devonian Chitinozoans from the Chacoparaná Basin, Salta Province, Argentina. *Ameghiniana* 61: 93–117.

Camina, S.C., C.V. Rubinstein, A. Butcher, V.J. García Muro, G. Vergani & M. Pereira. 2024b. A new chitinozoan assemblage from the Middle Devonian Los Monos Formation (sub-Andean basin, southern Bolivia) and its biozonal implications for Western Gondwana. *PLOS ONE* 19: e0297233.

Capel, E., C.J. Cleal, T. Servais & B. Cascales-Miñana. 2023. New insights into Silurian–Devonian palaeophytogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology* 613: 111393.

Chebli, G., M. Mozetic, E.A. Rosello & M. Bühler. 1999. Cuencas sedimentarias de la llanura Chacopampeana. In: *Geología Argentina,* Instituto de Geología y Recursos Minerales, Buenos Aires, Argentina, Anales. pp. 627–644.

Cramer, F.H. 1964. Microplankton from three Palaeozoic formations in the province of Leon, NW-Spain. *Leidse Geologische Mededelingen* 30: 253–361.

Cramer, F.H. 1970. Distribution of selected Silurian acritarchs. An account of the palynostratigraphy and paleogeography of selected Silurian acritarch taxa. *Revista Española de Micropaleontologia*, Número extraordinario 1: 1–203.

Cuerda, A.J. & B.A. Baldis. 1971. Silúrico-Devónico de la Argentina. *Ameghiniana* 8: 128–164.

Daners, G., A. Le Hérissé, P. Breuer & G. Veroslavsky. 2017. Pragian–Emsian palynomorphs from the Cordobés Formation, Norte Basin, Uruguay: stratigraphically restricted and regionally correlative palynological events in the cool-water Malvinokaffric Realm. *Palynology* 41: 121–137.

Deflandre, G. 1937. Microfossiles des Silex crétacés. Deuxième partie: Flagellés incertae sedis, Hystrichosphaeridés, Sarcodinés, Organismes divers. *Annales de Paléontologie* 26: 51–103.

Deunff, J. 1955. Un microplancton fossile dévonien à Hystrichosphères du continent Nord-Américain. *Bulletin de Microscopie appliquée* 2: 11–12.

Deunff, J. 1961. Quelques précisions concernant les Hystrichosphaeridées de Dévonien du Canada. *Compte rendu sommaire des séances de la Société geóloique de France* 8: 216–218.

Deunff, J. 1966. *Recherches sur les microplanctons du Dévonien (Acritarches et Dinophycae)*. PhD. Thesis, Université Rennes, 168 pp.

Deunff, J. 1971. Le genre *Polyedryxium* Deunff. Revision et observations. *Microfossiles organiques du Paleozoique* 3: 7–49.

di Pasquo, M. 2007a. Asociaciones palinológicas en las formaciones Los Monos (Devónico) e Itacua (Carbonífero Inferior) en Balapuca (Cuenca Tarija), sur de Bolivia. Parte 2. Asociaciones de la Formación Itacua e interpretación estratigráfica y cronología de las formaciones Los Monos e Itacua. *Revista Geológica de Chile* 34: 163–198.

di Pasquo, M. 2007b. Asociaciones palinológicas en las formaciones Los Monos (Devónico) e Itacua (Carbonífero Inferior) en Balapuca (Cuenca Tarija), sur de Bolivia. Parte 1. Formación Los Monos. *Revista Geológica de Chile* 34: 97–137.

di Pasquo, M., C.R. Amenábar & S. Noetinger. 2009. Middle Devonian microfloras and megafloras from western Argentina and southern Bolivia: their importance in the palaeobiogeographical and palaeoclimatic evolution of western Gondwana. *Geological Society, London, Special Publications* 314(1): 193–213.

di Pasquo, M., S. Noetinger, P. Isaacson, G. Grader, D. Starck, E. Morel & H.A. Folnagy. 2015. Mid-Late Devonian assemblages of herbaceous lycophytes from northern Argentina and Bolivia: Age assessment with palynomorphs and invertebrates and paleobiogeographic importance. *Journal of South American Earth Sciences* 63: 70–83.

Dorning, K.J. 1981. Silurian acritarchs from the type Wenlock and Ludlow of Shropshire, England. *Review of Palaeobotany and Palynology* 34(2): 175–203.

Downie, C. 1959. Hystrichospheres from the Silurian Wenlock Shale of England. *Palaeontology* 2(1): 56–71.

Eisenack, A. 1931. Neue Mikrofossilien des baltischen Silurs. I. *Palaeontologische Zeitschrift* 13: 74–118.

Eisenack, A. 1938. Neue Mikrofossilien des baltischen Silurs. IV. *Palaeontologische Zeitschrift* 19: 217–243.

Eisenack, A. 1955. Chitinozoen, Hystrichosphären und andere mikrofossilien aus dem Beyrichia-kalk. *Senckenbergiana lethaea* 36: 157–188.

Eisenack, A. 1959. Chitinöse Hüllen aus Silur und Jura des Baltikums als Foraminiferen. *Paläontologische Zeitschrift* 33: 90–95.

Filipiak, P. 2005. Late Devonian and Early Carboniferous acritarchs and prasinophytes from the Holy Cross Mountains (central Poland). *Review of Palaeobotany and Palynology* 134: 1–26.

García Muro, V.J. & C.V. Rubinstein. 2015. New Biostratigraphic Proposal for the Lower Palaeozoic Tucunuco Group (San Juan Precordillera, Argentina) Based on Marine and Terrestrial Palynomorphs. *Ameghiniana* 52: 265–285.

García Muro, V.J., C.V. Rubinstein & J.J. Rustán. 2017. Early Devonian organic-walled phytoplankton and miospores from the Precordillera Basin of San Juan, Argentina: biostratigraphic and paleobiogeographic implications. *Palynology* 41: 138–157.

García Muro, V.J., C.V. Rubinstein, J.J. Rustán & P. Steemans. 2018. Palynomorphs from the Devonian Talacasto and Punta Negra Formations, Argentinean Precordillera: New biostratigraphic approach. *Journal of South American Earth Sciences* 86: 110–126.

García Muro, V.J., C.V. Rubinstein, S.C. Camina, G. Vergani & M. Pereira. 2025. Late Early to Middle Devonian palynology of the Ramos x-1011 borehole from the Tarija Basin, northwestern Argentina. *Review of Palaeobotany and Palynology* 334: 105278.

Gaugris, K.D.A. & Y. Grahn. 2006. New chitinozoan species from the Devonian of the Paraná Basin, south Brazil, and their biostratigraphic significance. *Ameghiniana* 43: 293–310.

Grahn, Y. 2002. Upper Silurian & Devonian Chitinozoa from central and southern Bolivia, central Andes. *Journal of South American Earth Sciences* 15: 315–326.

Grahn, Y. 2003. Silurian and Devonian chitinozoan assemblages from the Chaco-Paraná Basin, northeastern Argentina and central Uruguay. *Revista Española de Micropaleontología* 35: 1–8.

Grahn, Y. 2005. Devonian chitinozoan biozones of Western Gondwana. *Acta Geologica Polonica* 55(3): 211–227.

Grahn, Y. & P.R. Gutiérrez. 2001. Silurian and Middle Devonian chitinozoa from the Zapla and Santa Bárbara ranges, Tarija Basin, northwestern Argentina. *Ameghiniana* 38: 35–50.

Grahn, Y. & J.H.G. Melo. 2004. Integrated Middle Devonian chitinozoan and miospore zonation of the Amazonas Basin, northern Brazil. *Revue de Micropaléontologie* 47: 71–85.

Grahn, Y. & J.H.G. Melo. 2005. Middle and Late Devonian Chitinozoa and biostratigraphy of the Parnaíba and Jatobá Basins, northeastern Brazil. *Palaeontographica. Abteilung B, Palaophytologie* 272: 1–50.

Grahn, Y., E. Pereira & S. Bergamaschi. 2000. Silurian and Lower Devonian chitinozoan biostratigraphy of the Paraná Basin in Brazil and Paraguay. *Palynology* 24: 147–176.

Grahn, Y., S. Bergamaschi & E. Pereira. 2002. Middle and Upper Devonian chitinozoan biostratigraphy of the Paraná Basin in Brazil and Paraguay. *Palynology* 26: 135–165.

Grahn, Y., S. Loboziak & J.H.G. Melo. 2003. Integrated correlation of Late Silurian (Pridoli *s.l.*)–Devonian chitinozoans and miospores in the Solimões Basin, northern Brazil. *Acta Geologica Polonica* 53: 283–300.

Grahn, Y., J.H.G. Melo & S. Loboziak. 2006. Integrated Middle and Late Devonian miospore and chitinozoan zonation of the Parnaíba Basin, Brazil: an update. *Revista Brasileira de Paleontologia* 9: 283–294.

Grahn, Y., C. Young & L. Borghi. 2008. Middle Devonian chitinozoan biostratigraphy and sedimentology in the eastern outcrop belt of the Parnaíba Basin, northeastern Brazil. *Revista Brasileira de Paleontologia* 11: 137–146.

Grahn, Y., P.M. Mauller, S. Bergamaschi & E.P. Bosetti. 2013. Palynology and sequence stratigraphy of three Devonian rock units in the Apucarana Subbasin (Paraná Basin, south Brazil): additional data and correlation. *Review of Palaeobotany and Palynology* 198: 27–44.

Hammer, Ø. & D.A.T. Harper. 2006. *Paleontological Data Analysis*. Blackwell Publishing, Malden, 351 pp.

Helenes, J., C. De Guerra & J. Vasquez. 1998. Palynology and Chronostratigraphy of the Upper Cretaceous in the Subsurface of the Barinas Area, Western Venezuela. *AAPG Bulletin* 82: 1308–1328.

Jaccard, P. 1908. Nouvelles recherches sur la distribution florale. *Bulletin de la Societe Vaudoise des Sciences Naturelles* 44: 223–270.

Jansonius, J. 1964. Morphology and classification of some Chitinozoa. *Bulletin of Canadian Petroleum Geology* 12: 901–918.

Lange, F.W. 1949. Novos microfósseis devonianos do Paraná. *Arquivos do Museu Paranaense* 7: 287–298.

Lange, F.W. 1967. Biostratigraphic subdivision and correlation of the Devonian in the Paraná Basin. *Boletim Paranaense de Geociências* 21 (22): 63–98.

Laufeld, S. 1974. Silurian chitinozoa from Gotland. Fossils and Strata 5: 1–130.

Le Hérissé, A. 2001. Evolution of Devonian phytoplanctonic assemblages in the upper Eréré Formation and Curua Group (Barreirinha and lower Curiri formations), Tapajos river area, Amazon Basin, northern Brazil. In: J.H.G. Melo & G.J.S. Terra (eds.), *Correlaçao de sequencias palaeozoicas sul-americanas,* Cienca-Tecnica-Petroleo 20, pp. 117–124.

Le Hérissé, A. 2011. A reappraisal of F.W. Lange's 1967 algal microfossil studies. In: *Essays in Honour of Frederico Waldemar Lange,* pp. 151–179.

Le Hérissé, A., C.V. Rubinstein & P. Steemans. 1996. Lower Devonian palynomorphs from the Talacasto Formation, Cerro del Fuerte Section, San Juan Precordillera, Argentina. In: O. Fatka, O. & T. Servais (eds.), *Acritarcha in Praha,* Acta Universitatis Carolinae, Geologica, pp. 497–515.

Lister, T.R. 1970. The acritarchs and chitinozoa from the Wenlock and Ludlow Series of the Ludlow and Nillichope areas, Shorpshire. *Monograph of the Palaeontographical Society of London* 124: 1–100.

Loeblich, A.R.Jr. & H. Tappan. 1976. Some new and revised organic-walled phytoplancton microfossil genera. *Journal of Paleontology* 50(2): 301–308.

Marshall, J.E.A. 1996. Vegetational history of Devonian spores. In: J. Jansonius, & D.C. McGregor (eds.), *Palynology principles and applications,* AASP Foundation 1, pp. 1133–1141.

Martin, F. 1981. Acritarches du Famennien Infé□rieur à Villers-sur-Lesse (Belgique). B*ulletin de l'Institut Royal des Sciences Naturelles de Belgique 52(2): 1–55.*

McGregor, D.C. 1979. Devonian miospores of North America. *Palynology* 3: 31–52.

McGregor, D.C. & G. Playford. 1992. *Canadian and Australian Devonian Spores: Zonation and Correlation*. Geological Survey of Canada, Ottawa, 125 pp.

Mendlowicz Mauller, Y. Grahn & T.R. Machado Cardoso. 2009. Palynostratigraphy from the lower Devonian of the Paraná Basin, south Brazil, and a revision of contemporary chitinozoan biozones from Western Gondwana. *Stratigraphy* 6: 313–332.

Noetinger, S. 2010. Middle-Upper Devonian palynoflora from the Tonono x-1 borehole, Salta Province, northwestern Argentina. *Ameghiniana* 47: 165–184.

Noetinger, S. 2015. Spore diversity trends in the Middle Devonian of the Chaco-Salteño Plain, northwestern Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology* 417: 151–163.

Noetinger, S. & M. di Pasquo. 2010. Palynomorphs from Abra Límite, Zenta Range, Eastern Cordillera, Northwestern Argentina. *Revista Brasileira de Paleontologia* 13: 13–20.

Noetinger, S. & M. di Pasquo. 2011. Devonian palynological assemblages from the San Antonio x-1 borehole, Tarija Basin, northwestern Argentina. *Geologica Acta* 9: 199–216.

Noetinger, S. & M. di Pasquo. 2013. New palynological information from the subsurface Copo, Caburé and Rincón formations (upper Lochkovian–Emsian), Salta Province, Argentina. *Memoirs of the Association of Australasian Palaeontologists* 44: 107–121.

Noetinger, S., M. di Pasquo, P. Isaacson, G. Aceñolaza & M.del M.Vergel. 2016. Integrated study of fauna and microflora from the Early Devonian (Pragian–Emsian) of northwestern Argentina. *Historical Biology* 28: 913–929.

Noetinger, S., R.R. Pujana, A. Burrieza & H.P. Burrieza. 2017. Use of UV-curable acrylate gels as mounting media for palynological samples. *Revista Del Museo Argentino de Ciencias Naturales n.s.* 19: 19–23.

Noetinger, S., M. di Pasquo & D. Starck. 2018. Middle-Upper Devonian palynofloras from Argentina, systematic and correlation. *Review of Palaeobotany and Palynology* 257: 95–116.

Oksanen, J., F.G. Blanchet, R. Kindt, P. Legendre, P.R. Minchin, R.B. O'Hara, G. Simpson, P. Solymos, M.H.H. Stevens & H. Wagner. 2022. Package 'vegan'. https://github.com/vegandevs/vegan

Ottone, E.G. 1996. Devonian palynomorphs from the Los Monos Formation, Tarija Basin, Argentina. *Palynology* 20: 105–155.

Paris, F. 1981 Les Chitinozoaires dans le Paléozoïque du sudouest de l'Europe. *Mémoires de la Société* *géologique et mineralogique de Bretagne* 26: 1–412.

Paris, F. 2006. Chitinozoans: A Fascinating and Mysterious Microfossil-Group. Université de Rennes, Rennes-cedex, 81 pp.

Paris, F., Y. Grahn, V. Nestor & I. Lakova. 1999. A revised chitinozoan classification. *Journal of Paleontology* 73: 549–570.

Paris, F., T. Winchester-Seeto, K. Boumendjel & Y. Grahn. 2000. Toward a global biozonation of Devonian chitinozoans. *Courier-Forschungsinstitut Senckenberg 220:* 39–55.

Pineda, J., S. Noetinger & E.G. Ottone. 2021. Palynology of the Early to Middle Devonian Pescado Formation, Subandean Range, Salta Province, Argentina. *Ameghiniana* 58: 301–317.

Playford, G. 1977. Lower to Middle Devonian acritarchs of the Moose River Basin, Ontario. *Geological Survey of Canada*, *Bulletin* 279: 1–87.

Playford, G. 1981. Late Devonian acritarchs from the Gneudna Formation in the western Carnarvon Basin, Western Australia. *Geobios* 14: 145–171.

Pöthe de Baldis, E.D. 1971. Microplancton del Silúrico Superior de Santiago del Estero, República Argentina. *Ameghiniana* 8: 282–290.

Pöthe de Baldis, E.D. 1974. El microplancton del Devónico Medio de Paraguay. *Revista Española de Micropaleontología* 6: 367–379.

Potonié, R. & K.M. Lele. 1961. Studies in the Talchir Flora of India. I. Sporae dispersae from the Talchir Beds of South Rewa Gondwana Basin. *The Palaeobotanist* 8: 22–37.

R Development Core Team 2022. R: A language and environment for statistical computing.

Reinante, S.M., G. Olivieri, A. Salinas, J.P. Lovecchio & Y. Basile. 2014. La Cuenca Chacoparaná: estratigrafía y recursos de hidrocarburos. In: *Geología y recursos naturales de la provincia de Córdoba,* Córdoba, Argentina, Relatorio del XIX Congreso Geológico Argentino, pp. 895–912.

Riding, J.B. 2021. A guide to preparation protocols in palynology. *Palynology* 45: 1–110.

Rubinstein, C.V. 1997. Silurian acritarchs from South America: a review. *Acta Universitatis Carolinae Geologica* 40: 603–629.

Rubinstein, C.V. 2021. *Léxico Estratigráfico de La Argentina: Devónico*. Asociación Geológica Argentina, Buenos Aires, 189 pp.

Rubinstein, C.V. & P. Steemans. 2007. New palynological data from the Devonian Villavicencio Formation, Precordillera of Mendoza, Argentina. *Ameghiniana* 44: 3–9.

Rubinstein, C.V. & V.J. García Muro. 2011. Fitoplancton marino de pared orgánica y mioesporas silúricos de la Formación Los Espejos, en el perfil del Río de Las Chacritas, Precordillera de San Juan, Argentina. *Ameghiniana* 48(4): 618-641.

Rubinstein, C.V., J. Lovecchio & I. Gebhard. 2018. Early Devonian marine and terrestrial palynomorphs from the Chacoparana Basin, Uruguay. *Ameghiniana* 55: 277–302.

Rueden, C.T., J. Schindelin, M.C. Hiner, B.E. De Zonia, A.E. Walter, E.T. Arena & K.W. Eliceiri. 2017. ImageJ2: ImageJ for the next generation of scientific image data. *BMC Bioinformatics* 18: 529 pp.

Sarjeant, W.A.S. & M. Vavrdová. 1997. Taxonomic reconsideration of *Multiplicisphaeidium* Staplin, 1961 and other acritarch genera with branching processes. *Geolines 5: 1–52.*

Sommer, F.W. & N.M. Van Boekel. 1964. Quitinozoarios do Devoniano de Goiás. *Anais da Academia Brasileira de Ciências* 36: 423–431.

Staplin, F.L. 1961. Reef-controlled distribution of Devonian microplankton in Alberta. *Palaeontology* 4(3): 392–424.

Staplin, F.L., J. Jansonius & S.A.J. Pocock. 1965. Evaluation of some Acritarchous Hystrichosphere Genera. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen* 123: 167–201.

Steemans, P., C.H. Wellman & J. Filatoff. 2007. Palaeophytogeographical and palaeoecological implications of a miospore assemblage of earliest Devonian (Lochkovian) age from Saudi Arabia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 250: 237–254.

Suttner, T.J. & O. Hints. 2010. Devonian scolecodonts from the Tyrnaueralm, Graz Palaeozoic, Austria. *Memoirs of the Association of Australasian Palaeontologists* 39: 139–145.

Tonarová, P., S. Vodrážková, L. Ferrová, G.S. de la Puente, O. Hints, J. Frýda & M. Kubajko. 2017. Palynology, microfacies and biostratigraphy across the Daleje Event (Lower Devonian, lower to upper Emsian): new insights from the offshore facies of the Prague Basin, Czech Republic. *Palaeobiodiversity and Palaeoenvironments* 97: 419–438.

Torsvik, T.H. & L.R.M. Cocks. 2004. Earth geography from 400 to 250 Ma: a palaeomagnetic, faunal and facies review. *Journal of the geological society 161(4):* 555–572.

Torsvik, T.H. & L.R.M. Cocks. 2017. Earth history and palaeogeography. *Cambridge University Press, Cambridge, 317 pp.*

Valenzuela, J.M.G., T. Palacios Medrano & M.J. Palacios González. 1990. Aspects of the paleoecology of the Santos de Maimona Basin; Acritarchs and spores. *Geogaceta 8:* 118–121.

Volkheimer, W., D.L. Melendi & A. Salas. 1986. Devonian chitinozoans from northwestern Argentina. *Palaeontographica. Abteilung B* 173: 229–251.

Wicander, E.R. 1974. Upper Devonian-Lower Mississippian acritarchs and prasinophycean algae from Ohio, USA. *Palaontographica*, Abt. B 148: 9–43.

Wicander, E.R. 1975. Fluctuations in a late Devonian-Early Mississippian phytoplankton flora of Ohio, USA. *Palaeogeography, Palaeoclimatology, Palaeoecology* 17(2): 89–108.

Wicander, E.R. 1983. A catalog and biostratigraphic distribution of North American Devonian acritarchs. *American Association of Stratigraphic Palynologists Foundation, Contribution series 10: 1–133.*

Wicander, E.R. & G. Wood. 1981. Systematics and biostratigraphy of the organic-walled microphytoplankton from the Middle Devonian (Givetian) Silica Formation, Ohio, U.S.A. *American Association of Stratigraphic Palynologists*, Contribution Series Number, 8: 1–137.

Wicander, E.R. & G.D. Wood. 1997. The use of microphytoplankton and chitinozoans for interpreting transgressive/regressive cycles in the Rapid Member of the Cedar Valley Formation (Middle Devonian), Iowa. *Review of Palaeobotany and Palynology* 98(1-2): 125–152.

Wood, G.D. 1995. The gondwanan acritarch *Bimerga bensonii* gen. et sp. nov.: Paleogeographic and biostratigraphic importance in the Devonian malvinokaffric realm. *Palynology* 19: 221–231.

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