

## 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

### 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 Baldi, 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 & Baldi, 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 emsienensis* (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, *Perotriletes caperatus* (McGregor) Steemans, 1989, *Triangulina aspera* Pöthe de Baldi, 1977, and *Cymbolithes 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  $\mu$ m mesh; the +10  $\mu$ m 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.

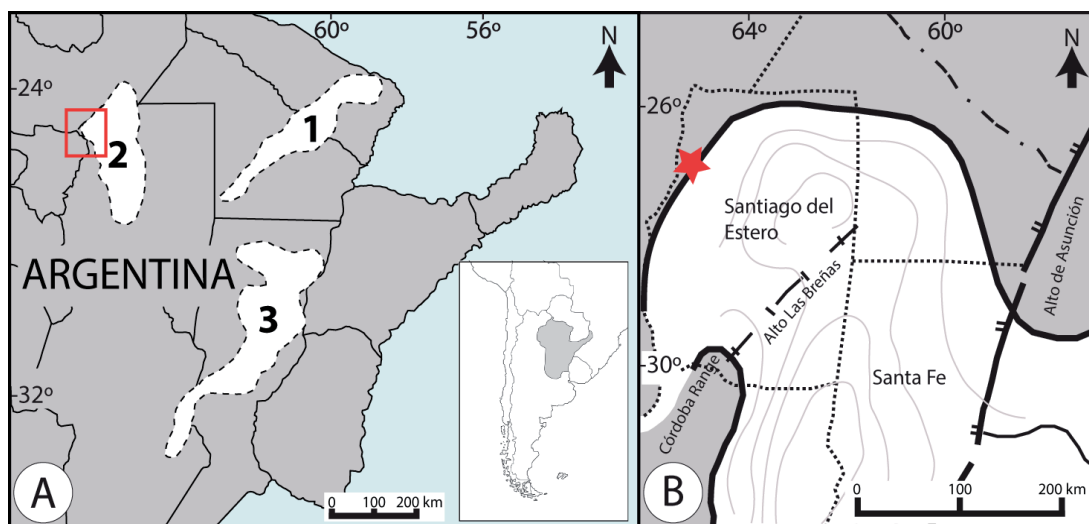


Fig. 1. A. Part of the Chacoparaná Basin, focused on NE Argentina and the location of the Paleozoic depocenters: (1) Lower Paleozoic, (2) Middle Paleozoic and (3) Upper Paleozoic. Modified from Reinante *et al.* (2014). B. Location of the studied locality.

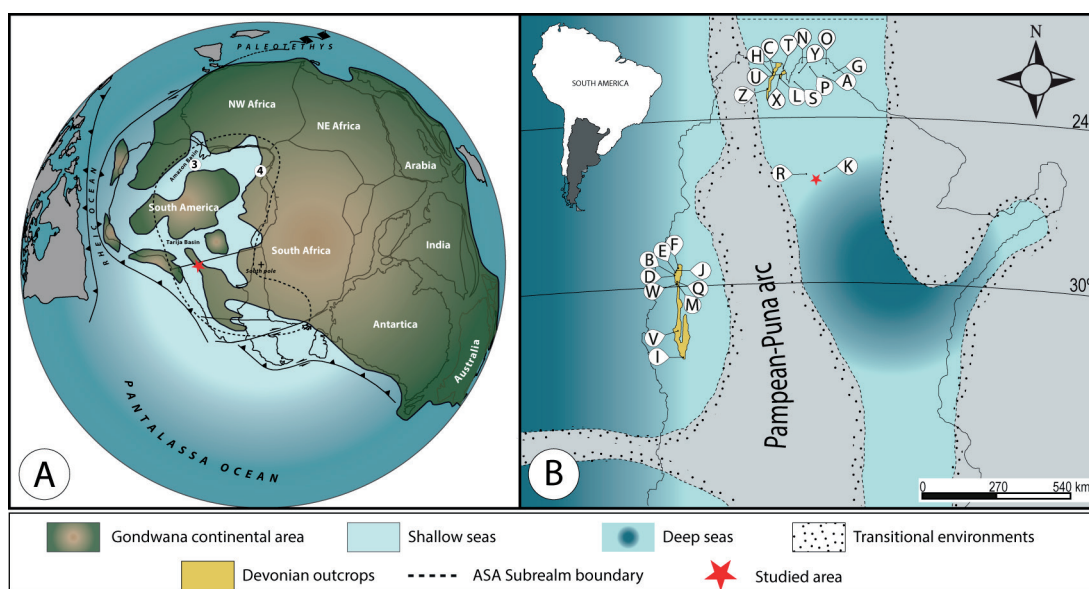


Fig. 2. A. Paleogeographical map featuring the Gondwana continent during the Middle Devonian (modified from Noetinger *et al.*, 2018). Dashed line encircles the Afrosouthamerican Subrealm (ASA) (after di Pasquo *et al.*, 2009, 2015). B. Paleoenvironmental map for late Eifelian/Givetian of Argentina (modified 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 (Grahns & 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 prasinophycean 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  $\mu\text{m}$ ; width of the vesicle 23.2  $\mu\text{m}$ ; wall thickness 2.5  $\mu\text{m}$ ; length of the processes 14–20  $\mu\text{m}$ ; width of the processes 3.5–5  $\mu\text{m}$ .

**Comparisons and remarks.** *Bimerga bensonii* Wood (1995) shows a bilaterally symmetrical vesicle with a minor length range 95(106)123  $\mu\text{m}$ . *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  $\mu\text{m}$ .

**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                                                                                           |               |
|           | •         |           |           |           |           | •         | •         |           |  | <i>Ammonidium garrasinoi</i> Ottone, 1996                                                      | ACRITARCHS    |
|           | •         |           |           |           |           |           |           |           |  | <i>Bimerga</i> sp.                                                                             |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Dactylofusa</i> ? sp.                                                                       |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Dupliciradiatum tenue</i> González, Moreno & Playford, 2005                                 |               |
| •         |           |           |           |           |           |           | •         |           |  | <i>Exochoderma arca</i> Wicander & Wood, 1981                                                  |               |
| •         |           |           |           |           |           |           |           |           |  | <i>Exochoderma triangulata</i> Wicander & Wood, 1981                                           |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Gorgonisphaeridium</i> sp.                                                                  |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Hapsidopalla sannemanni</i> (Deunff) emend. Playford, 1977                                  |               |
| •         |           |           |           |           |           |           |           |           |  | <i>Hoegklintia</i> cf. <i>H. longispina</i> Pöthé de Baldis, 1998                              |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Leiofusa</i> sp.                                                                            |               |
|           |           |           |           |           |           | •         |           |           |  | <i>Michystridium</i> sp.                                                                       |               |
|           |           |           |           |           |           |           |           |           |  | <i>Multiplicisphaeridium</i> sp.                                                               |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Navifusa bacilla</i> (Deunff) Playford, 1977                                                |               |
|           | •         |           |           |           |           |           | •         |           |  | <i>Palacanthus ledanoisii</i> Deunff emend. Playford, 1977                                     |               |
| •         |           |           |           |           |           |           |           |           |  | <i>Polyedryxium</i> sp. A                                                                      |               |
|           |           |           |           |           |           |           | •         |           |  | <i>Polyedryxium</i> sp. B                                                                      | SCOLECODONTS  |
| •         |           |           |           |           |           | •         | •         |           |  | <i>Veryhachium lairdii</i> group Servais, Li, Molyneux, Raevskaya & Rubinstein, 2007           |               |
| •         |           |           |           |           |           |           |           |           |  | <i>Veryhachium</i> sp. cf. <i>V. pastoris</i> Deunff, 1966                                     |               |
| •         |           |           |           |           |           |           |           |           |  | <i>Veryhachium trispinosum</i> group Servais, Li, Molyneux, Raevskaya & Rubinstein, 2007       |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Scolecodont</i> sp. A                                                                       |               |
|           |           |           |           |           |           | •         |           |           |  | <i>Scolecodont</i> sp. B                                                                       |               |
|           | •         |           | •         |           |           |           |           |           |  | <i>Ancyrochitina ancyrea</i> (Eisenack) Eisenack, 1955                                         | CHITINOZOANS  |
|           |           |           | •         |           |           |           |           |           |  | <i>Ancyrochitina cornigera</i> Collinson & Scott, 1958                                         |               |
|           |           |           | •         |           |           |           |           |           |  | <i>Ancyrochitina parisi</i> Volkheimer, Melendi & Salas, 1986                                  |               |
|           | •         |           | •         |           |           |           |           |           |  | <i>Ancyrochitina simplex</i> Grahn, Bergamaschi & Pereira, 2002                                |               |
|           | •         |           | •         |           |           |           |           |           |  | <i>Ancyrochitina</i> sp. A                                                                     |               |
|           |           |           | •         |           |           |           |           |           |  | <i>Ancyrochitina</i> sp. B                                                                     |               |
| •         | •         |           | •         |           |           |           |           |           |  | <i>Ancyrochitina</i> sp. C                                                                     |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Ancyrochitina</i> sp. D                                                                     |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Ancyrochitina</i> sp. E                                                                     |               |
|           | •         |           | •         |           |           |           |           |           |  | <i>Cyathochitina</i> sp. cf. <i>C. campanulis</i> Boneham & Masters, 1973                      |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Hercochitina</i> sp.                                                                        |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Hoegisphaera</i> sp. cf. <i>H. glabra</i> Staplin, 1961                                     |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Lagenochitina amottensis</i> Grignani & Mantovani, 1964                                     |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Lagenochitina postpirum</i> Camina, 2024                                                    |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Ramochitina autasmirimensense</i> Grahn & de Melo, 2004                                     | PRASINOPHYTES |
|           |           | •         |           | •         |           |           |           |           |  | <i>Cymatiosphaera canadensis</i> (Deunff) Deunff, 1954                                         |               |
|           |           |           |           |           |           |           |           |           |  | <i>Dictyotidium dictyotum</i> (Eisenack) Eisenack, 1955                                        |               |
|           |           |           |           |           |           | •         |           |           |  | <i>Dorsennidium</i> ( <i>Dorsennidium</i> ) <i>raczii</i> (Cramer) Sarjeant & Stancliffe, 1994 |               |
|           | •         |           |           |           |           | •         |           |           |  | <i>Pterospermella capitana</i> Wicander, 1974                                                  |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Pterospermella pernambucensis</i> (Brito) Eisenack, Cramer & Díez Rodríguez, 1973           | SPORES        |
| •         |           |           |           |           |           | •         |           |           |  | <i>Acinosporites lindlarensis</i> Riegel, 1968                                                 |               |
|           |           |           |           | •         |           |           |           |           |  | <i>Acinosporites parviornatus</i> Richardson, 1965                                             |               |
| •         | •         |           |           |           |           |           |           |           |  | <i>Apiculiretusispora plicata</i> (Allen) Stree, 1967                                          |               |
|           | •         |           | •         | •         |           | •         |           |           |  | <i>Corystisporites</i> sp. cf. <i>C. collaris</i> Tiwari & Schaarschmidt, 1975                 |               |
|           | •         |           | •         | •         | •         |           |           |           |  | <i>Corystisporites</i> sp. cf. <i>C. undulatus</i> Turnau, 1996                                |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Dibolisporites echinaceus</i> (Eisenack) Richardson, 1965                                   |               |
|           |           | •         |           |           |           |           |           |           |  | <i>Dibolisporites eifeliensis</i> (Lanninger) McGregor, 1973                                   |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Dibolisporites hystricosus</i> Hashemi & Playford, 2005                                     |               |
|           |           |           |           |           |           |           | •         |           |  | <i>Retusotrilites albarinii</i> di Pasquo & Noetinger, 2008                                    |               |
| •         |           | •         | •         |           |           | •         |           |           |  | <i>Cymbolithes rubinsteiniae</i> Noetinger, di Pasquo, Isaacson, Aceñolaza & Vergel, 2016      | CRYPTOSPORE   |
|           |           |           |           |           |           | •         |           |           |  | <i>Quadrisporites variabilis</i> (Cramer) Ottone & Rosello, 1996                               |               |
|           | •         |           |           |           |           |           |           |           |  | <i>Quadrisporites</i> sp. cf. <i>Q. granulatus</i> (Cramer) Ströther, 1991                     | ALGAE         |

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       |
|------------------------------------------------------------------------------------------------|--------------|
| <b>Marine palynomorphs</b>                                                                     |              |
| <b>Acritarchs</b>                                                                              |              |
| <i>Ammonidium garrasinoi</i> Ottone, 1996                                                      | 4. E.        |
| <i>Bimerga</i> sp.                                                                             | 4. A.        |
| <i>Dactylofusa</i> ? sp.                                                                       | 4. B.        |
| <i>Dupliciradiatum tenue</i> González, Moreno & Playford, 2005                                 | 4. F.        |
| <i>Exochoderma arca</i> Wicander & Wood, 1981                                                  |              |
| <i>Exochoderma triangulata</i> Wicander & Wood, 1981                                           |              |
| <i>Gorgonisphaeridium</i> sp.                                                                  | 4. G.; 6. J. |
| <i>Hapsidopalla sannemanni</i> Deunff emend. Playford, 1977                                    | 4. H.        |
| <i>Hoeghlintia</i> cf. <i>H. longispina</i> Pöthé de Baldi, 1998                               | 4. I.        |
| <i>Leiofusa</i> sp.                                                                            | 4. C.        |
| <i>Michystridium</i> sp.                                                                       | 4. J.        |
| <i>Multiplicisphaeridium</i> sp.                                                               | 4. K.        |
| <i>Navifusa bacilla</i> (Deunff) Playford, 1977                                                | 4. D.        |
| <i>Palacanthus ledanoisii</i> Deunff emend. Playford, 1977                                     |              |
| <i>Polyedryxium</i> sp. A                                                                      | 4. L.        |
| <i>Polyedryxium</i> sp. B                                                                      | 4. M.        |
| <i>Veryhachium lairdii</i> group Servais, Li, Molyneux, Raevskaya & Rubinstein, 2007           |              |
| <i>Veryhachium</i> sp. cf. <i>V. pastoris</i> Deunff, 1966                                     | 4. N.        |
| <i>Veryhachium trispinosum</i> group Servais, Li, Molyneux, Raevskaya & Rubinstein, 2007       |              |
| <b>Scolecodonts</b>                                                                            |              |
| Scolecodont sp. A                                                                              | 5. K.        |
| Scolecodont sp. B                                                                              | 5. L.        |
| <b>Chitinozoans</b>                                                                            |              |
| <i>Ancyrochitina ancyrea</i> (Eisenack) Eisenack, 1955                                         |              |
| <i>Ancyrochitina cornigera</i> Collinson & Scott, 1958                                         |              |
| <i>Ancyrochitina parisi</i> Volkheimer, Melendi & Salas, 1986                                  | 5. A.; 6. A. |
| <i>Ancyrochitina simplex</i> Grahn, Bergamaschi & Pereira, 2002                                | 5. B.        |
| <i>Ancyrochitina</i> sp. A                                                                     | 5. C.; 6. B. |
| <i>Ancyrochitina</i> sp. B                                                                     | 5. D.; 6. C. |
| <i>Ancyrochitina</i> sp. C                                                                     | 5. E.; 6. D. |
| <i>Ancyrochitina</i> sp. D                                                                     | 5. F.        |
| <i>Ancyrochitina</i> sp. E                                                                     | 5. G.        |
| <i>Cyathochitina</i> sp. cf. <i>C. campanulis</i> Boneham & Masters, 1973                      | 5. H.; 6. E. |
| <i>Hercochitina</i> sp.                                                                        | 5. I.        |
| <i>Hoegisphaera</i> sp. cf. <i>H. glabra</i> Staplin, 1961                                     | 5. M.; 6. I. |
| <i>Lagenochitina amottensis</i> Grignani & Mantovani, 1964                                     | 6. F.        |
| <i>Lagenochitina postpirum</i> Camina, 2024                                                    | 6. G.        |
| <i>Ramochitina autasmirimense</i> Grahn & Melo, 2004                                           | 6. H.        |
| <b>Prasinophytes</b>                                                                           |              |
| <i>Cymatiosphaera canadensis</i> (Deunff) Deunff, 1954                                         |              |
| <i>Dictyotidium dictyotum</i> (Eisenack) Eisenack, 1955                                        |              |
| <i>Dorsennidium</i> ( <i>Dorsennidium</i> ) <i>raczii</i> (Cramer) Sarjeant & Stancliffe, 1994 |              |
| <i>Pterospermella capitata</i> Wicander, 1974                                                  | 4. O.        |
| <i>Pterospermella pernambucensis</i> (Brito) Eisenack, Cramer & Diez Rodríguez, 1973           | 4. P.        |
| <b>Non-marine palynomorphs</b>                                                                 |              |
| <b>Spores</b>                                                                                  |              |
| <i>Acinosporites lindlarensis</i> Riegel, 1968                                                 |              |
| <i>Acinosporites parviornatus</i> Richardson, 1965                                             |              |
| <i>Apiculiretusispora plicata</i> (Allen) Stree, 1967                                          |              |
| <i>Corystisporites</i> sp. cf. <i>C. collaris</i> Tiwari & Schaarschmidt, 1975                 | 5. N.; 6. K. |
| <i>Corystisporites</i> sp. cf. <i>C. undulatus</i> Turnau, 1996                                | 5. O.        |
| <i>Dibolisporites echinaceus</i> (Eisenack) Richardson, 1965                                   |              |
| <i>Dibolisporites eifeliensis</i> (Lanning) McGregor, 1973                                     |              |
| <i>Dibolisporites hystriacus</i> Hashemi & Playford, 2005                                      |              |
| <i>Retusotrites albarinii</i> di Pasquo & Noetinger, 2008                                      |              |
| <b>Cryptospores</b>                                                                            |              |
| <i>Cymbolites rubinsteinae</i> Noetinger, di Pasquo, Isaacson, Aceñolaza & Vergel, 2016        |              |
| <b>Algae</b>                                                                                   |              |
| <i>Quadrifurcata variabilis</i> (Cramer) Ottone & Rosello, 1996                                |              |
| <i>Quadrifurcata</i> sp. cf. <i>Q. granulatus</i> (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  $\mu\text{m}$ ; width of the vesicle 60  $\mu\text{m}$ .

**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  $\mu\text{m}$ ; diameter of the vesicle 54  $\mu\text{m}$ ; width of the membrane 9  $\mu\text{m}$ .

**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  $\mu\text{m}$ ; wall thickness 2–3  $\mu\text{m}$ ; length of the processes 11–14  $\mu\text{m}$ ; space between processes 5–8  $\mu\text{m}$ ; diameter of the bases of the processes 4–5  $\mu\text{m}$ .

**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  $\mu\text{m}$ ), the wall thickness is thinner (1–2  $\mu\text{m}$ ) and processes are shorter (1.6–4.1  $\mu\text{m}$ ) with more narrow bases (0.8–1.6  $\mu\text{m}$ ). *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  $\mu\text{m}$ ) and circular to semicircular in outline, well-differentiated from the processes. Wall thickness is thinner (0.8–1.8  $\mu\text{m}$ ). Processes are solid, shorter (1.4–4.5  $\mu\text{m}$ ) and more widely spaced (0.4–4.5  $\mu\text{m}$ ), originating from smaller bases (0.5–2  $\mu\text{m}$ ), 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  $\mu\text{m}$ ; length of the processes 4–6  $\mu\text{m}$ , width of the processes 1–1.5  $\mu\text{m}$ ; space between processes 6–10  $\mu\text{m}$ .

**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 Baldi, 1998  
(Fig. 4I)

**Dimensions (1 specimen).** Total length of the vesicle 55  $\mu\text{m}$ ; length of the processes 11–25  $\mu\text{m}$ ; width of the processes 2.3–2.9  $\mu\text{m}$ .

**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 *Hoeghlintia* 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  $\mu\text{m}$ ; length of the vesicle 55  $\mu\text{m}$ ; width of the vesicle 17.21  $\mu\text{m}$ ; length of the processes 40.9–41.6  $\mu\text{m}$ ; width of the processes 4–5  $\mu\text{m}$ .

**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

*Micrhystridium* 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  $\mu\text{m}$ ; length of the processes 3.5–6.8  $\mu\text{m}$ .

**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  $\mu\text{m}$ ; diameter of the vesicle 36  $\mu\text{m}$ ; length of the processes 18–20  $\mu\text{m}$ ; diameter of the bases of the processes 7  $\mu\text{m}$ .

**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  $\mu\text{m}$ ) and shorter processes (10–14  $\mu\text{m}$ ). *Multiplicisphaeridium ampliatus* Playford (1977) has longer (22–35  $\mu\text{m}$ ) 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  $\mu\text{m}$ .

**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.

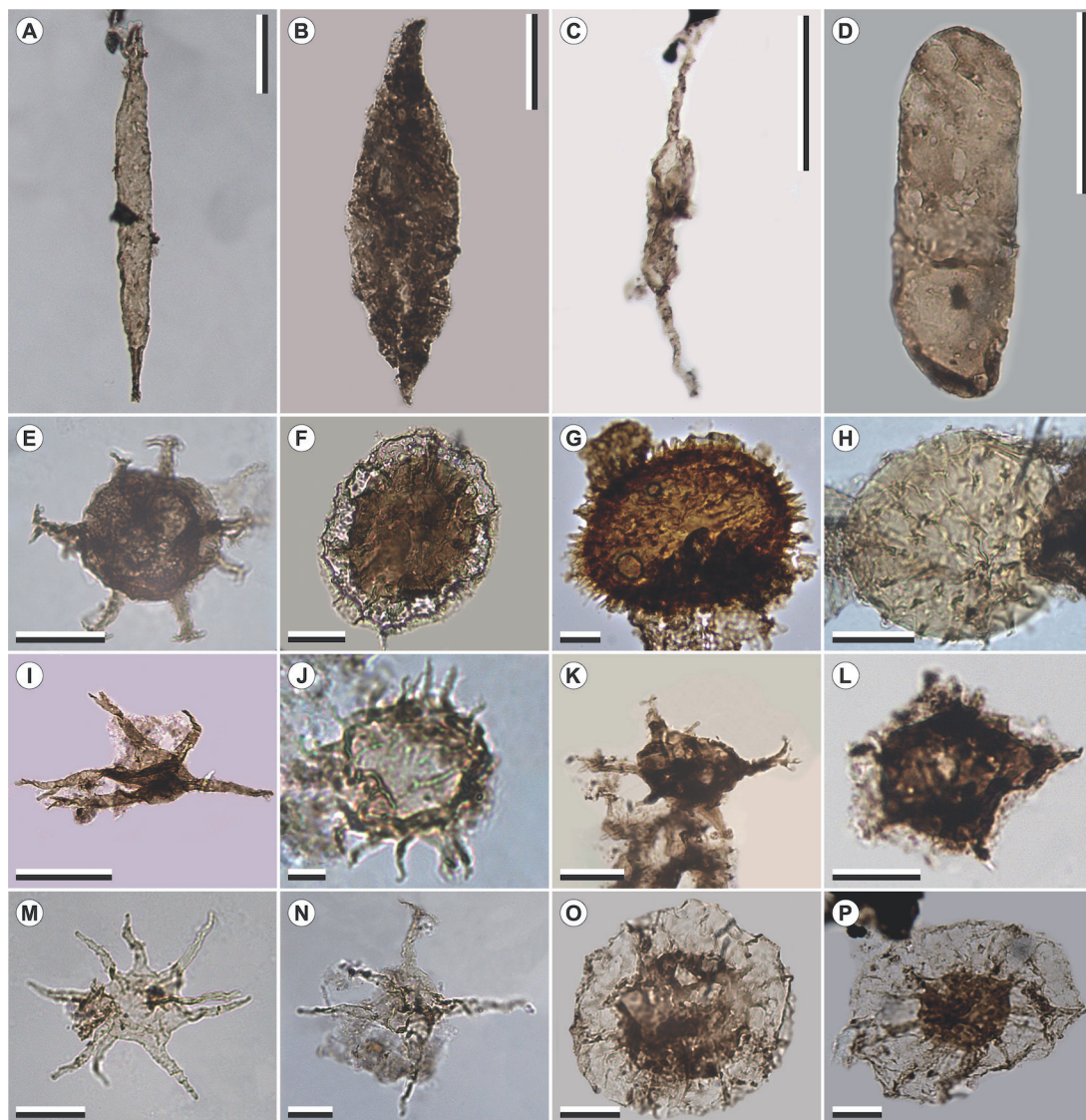


Fig. 4. Selected species. A. *Bimerga* sp., BA-Pal 5311 (1), C55/2. B. ?*Dactylofusa* sp. BA-Pal 5311 (1), M39. C. *Leiofusa* sp., BA-Pal 5311 (1), J29/3. D. *Navifusa bacilla* (Deunff) Playford, 1977, BA-Pal 5311 (1), O42/2. E. *Ammonidium garrasinoi* Ottone, 1996, BA-Pal 5330 (1), F39. F. *Dupliciradiatum 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 Baldi, 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 capitata* 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  $\mu$ m, J, N= 5  $\mu$ m, E–I, K–M, O–P= 10  $\mu$ m.

*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  $\mu$ m; diameter of the central body 26  $\mu$ m; length of the processes 20–28  $\mu$ m; width of the processes

4  $\mu\text{m}$ ; diameter of the bases of the processes 12  $\mu\text{m}$ .

**Remarks and comparisons.** In Noetinger (2010) *Polyedrixium pharaonis* Deunff (1961) is described with a larger (76  $\mu\text{m}$ ) 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  $\mu\text{m}$ ; length of the processes 35  $\mu\text{m}$ .

**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  $\mu\text{m}$ ; width of the plaque 43.7  $\mu\text{m}$ ; width of the teeth 8–15  $\mu\text{m}$ .

**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  $\mu\text{m}$ ; width of the plaque 25  $\mu\text{m}$ ; width of the teeth 5–7.5  $\mu\text{m}$ .

**Occurrence.** Level BA-Pal 5328.

## c) Chitinozoans

The principal measurements, recorded in micrometers ( $\mu\text{m}$ ), 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  $\mu\text{m}$  long with bases of 8 to 10  $\mu\text{m}$  wide.

**Dimensions (2 specimens).** L = 244–275  $\mu\text{m}$ ; ln = 127–137  $\mu\text{m}$ ; lc = 105–120  $\mu\text{m}$ ; D = 112–119  $\mu\text{m}$ ; dn = 40–45  $\mu\text{m}$ ; da = 45–47  $\mu\text{m}$ .

**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. campanulifera* 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  $\mu$ m, K–P = 10  $\mu$ m.

**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  $\mu\text{m}$  long with a 9  $\mu\text{m}$  wide base. The surface of the vesicle is smooth.

**Dimensions (2 specimens).** L= 160–222  $\mu\text{m}$ ; ln= 65–68  $\mu\text{m}$ ; lc= 85–165  $\mu\text{m}$ ; D= 83–98  $\mu\text{m}$ ; dn= 44–45  $\mu\text{m}$ ; da= 40–50  $\mu\text{m}$ .

**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  $\mu\text{m}$  long and bases of 6 to 15  $\mu\text{m}$  wide.

**Dimensions (6 specimens).** L= 115–250  $\mu\text{m}$ ; ln= 40–115  $\mu\text{m}$ ; lc= 80–165  $\mu\text{m}$ ; D= 46–103  $\mu\text{m}$ ; dn= 20–50  $\mu\text{m}$ ; da= 25–50  $\mu\text{m}$ .

**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  $\mu\text{m}$  long and 12  $\mu\text{m}$  wide at the base.

**Dimensions (1 specimen).** L= 196  $\mu\text{m}$ ; ln= 67.8  $\mu\text{m}$ ; lc= 125  $\mu\text{m}$ ; D= 74  $\mu\text{m}$ ; dn= 28  $\mu\text{m}$ ; da= 34  $\mu\text{m}$ .

**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  $\mu\text{m}$  long and with a 16  $\mu\text{m}$  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  $\mu\text{m}$ ; ln= 80  $\mu\text{m}$ ; lc= 188  $\mu\text{m}$ ; D= 60  $\mu\text{m}$ ; dn= 32  $\mu\text{m}$ ; da= 32  $\mu\text{m}$ .

**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  $\mu\text{m}$ ; ln= 80–112  $\mu\text{m}$ ; lc= 116–152  $\mu\text{m}$ ; D= 105–120  $\mu\text{m}$ ; dn= 40–50  $\mu\text{m}$ ; da= 32–55  $\mu\text{m}$ .

**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  $\mu\text{m}$ ; ln= 68  $\mu\text{m}$ ; lc= 210  $\mu\text{m}$ ; D= 73  $\mu\text{m}$ ; dn= 36  $\mu\text{m}$ ; da= 38  $\mu\text{m}$ .

**Remarks and comparisons.** *Hercochitina* sp. in Noetinger & di Pasquo (2011) has a smaller vesicle (145–209  $\mu\text{m}$ ). *Hercochitina crickmayi* Jansonius (1964) has a flat base and longitudinal membranes, up to 8  $\mu\text{m}$  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  $\mu\text{m}$ ; da= 45–47  $\mu\text{m}$ .

**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  $\mu\text{m}$ ; ln=80–108  $\mu\text{m}$ ; lc= 136–144  $\mu\text{m}$ ; D= 80–100  $\mu\text{m}$ ; dn= 43–49  $\mu\text{m}$ ; da= 31–40  $\mu\text{m}$ .

**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  $\mu\text{m}$  long and 3 to 6  $\mu\text{m}$  in width.

**Dimensions (1 specimen).** L= 222.8  $\mu\text{m}$ ; ln= 90  $\mu\text{m}$ ; lc= 130  $\mu\text{m}$ ; D= 70  $\mu\text{m}$ ; dn= 35.5  $\mu\text{m}$ ; da= 35.8  $\mu\text{m}$ .

**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  $\mu\text{m}$ ; length of the processes 7–24  $\mu\text{m}$ ; diameter of the bases of the processes 5–17  $\mu\text{m}$ .

**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  $\mu\text{m}$ ; length of the processes 12–30  $\mu\text{m}$ ; diameter of the bases of the processes 6.6–18  $\mu\text{m}$ ; processes 2.5–4  $\mu\text{m}$  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  $\mu\text{m}$ ; individual diameter 30  $\mu\text{m}$ .

**Remarks.** The only specimen found is poorly preserved and prevents more precise determination.

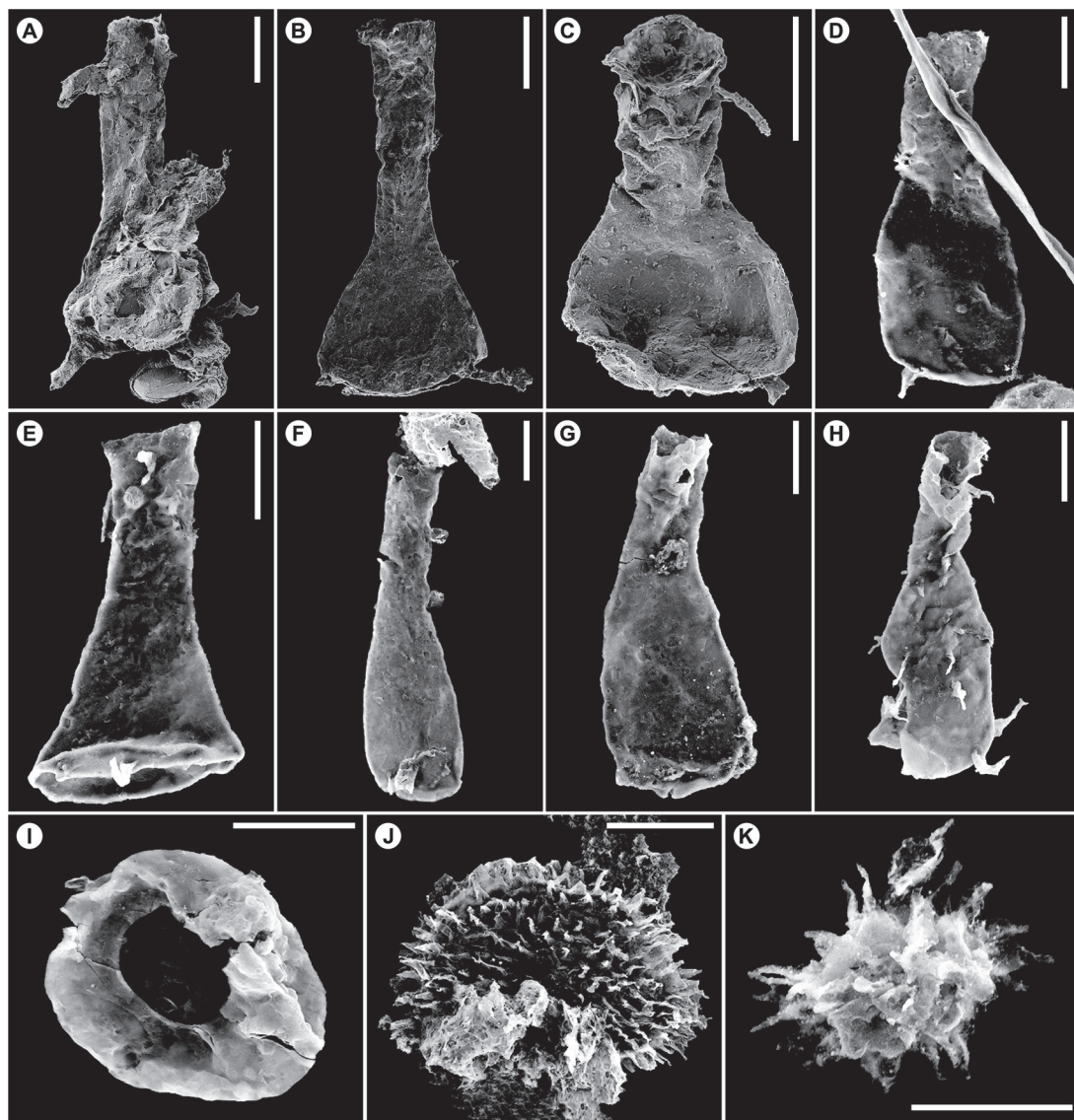


Fig. 6. Selected species. A. *Ancyrochitina parisi* (same specimen as in Fig. 5A), BA-Pal 5315 B. *Ancyrochitina* sp. A, BA-Pal 5315 C. *Ancyrochitina* sp. B, BA-Pal 5315 D. *Ancyrochitina* sp. C, BA-Pal 5311 E. *Cyathochitina* sp. cf. *C. campanulis* Boneham & Masters, 1973 (same specimen as in Fig. 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  $\mu$ m.

**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 *Pterospirmella capitata*, 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 *Quadriflorites*, 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. |
| <i>Ancyrochitina parisi</i> Volkheimer, Melendi & Salas, 1986             |          |       |      |        |      |       |      |
| <i>Ancyrochitina simplex</i> Grahn, Bergamaschi & Pereira, 2002           |          |       |      |        |      |       |      |
| <i>Ramochitina autasmirimense</i> Grahn & de Melo, 2004                   |          |       |      |        |      |       |      |
| <i>Ancyrochitina cornigera</i> Collinson & Scott, 1958                    |          |       |      |        |      |       |      |
| <i>Ammonidium garrasinoi</i> Ottone, 1996                                 |          |       |      |        |      |       |      |
| <i>Lagenochitina postpirum</i> Camina, 2024                               |          |       |      |        |      |       |      |
| <i>Cyathochitina</i> sp. cf. <i>C. campanulis</i> Boneham & Masters, 1973 |          |       |      |        |      |       |      |
| <i>Pterospermella capitata</i> 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

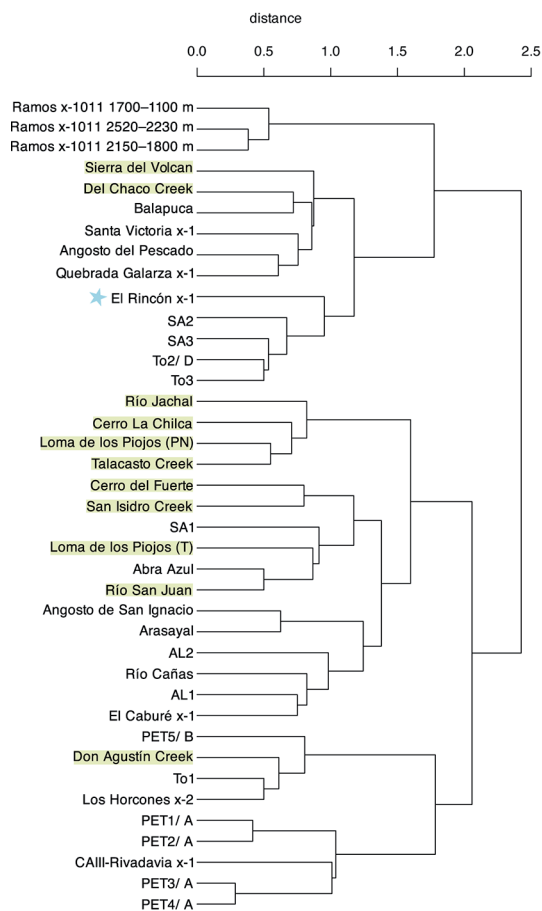


Fig. 7. Cluster analysis dendrogram (Jaccard index - Ward algorithm) showing the similarities between associations from the East and West (localities framed in yellow) on the basis of Supplementary material 1.

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 (Grahns & 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 superterraneas, Gondwana and Laurussia (Torsvik & Cocks, 2004). Several authors have studied the mega- and microfossils from this period (Marshall, 1996; Le Hérissé, 2001; Grahns, 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 cosmopolitanism. 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 cosmopolitanism, 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.

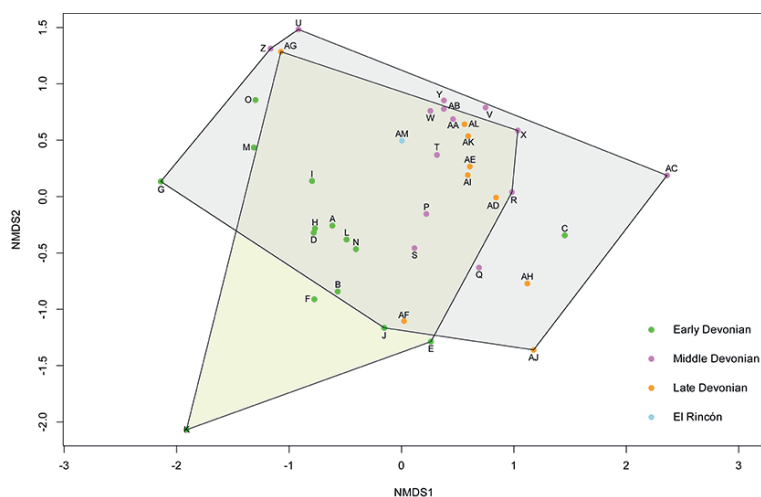


Fig. 8. NMDS ordination plot of selected 39 associations, spanning the Early to Late Devonian, based on Jaccard dissimilarities;  $k = 3$ , stress value = 0.1093696. Grey polygon represents associations to the east of the Pampean-Andean arc and yellow polygon includes associations towards the west. A. 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. (García Muro *et al.*, 2018). F. Cerro del Fuerte (Le Hérisse *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 (Grahns & 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 capitata*, *Cyathochitina* sp. cf. *C. campanulata* and *Ramochitina autsimirimensis*, suggests a minimum Givetian age for the section BA-Pal 5310-5311. While the presence

of *Ammonidium garrasinoi*, *Ancyrochitina 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>

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