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# Middle-Upper Devonian palynofloras from Argentina, systematic and correlation

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ABSTRACT

This investigation documents the first palynoassemblage spanning the Middle-Upper Devonian from four outcropping sections located in northwestern Argentina. The recovered material includes fairly well-preserved palynomorphs, both from marine and continental origin, including acritarchs, prasinophytes, cryptospores, spores and chlorophytes. In two of the four studied localities chitinozoans were encountered, whilst only one of them have yielded scolecodonts. Five new species are described including one acritarch specimen: *Gorgonisphaeridium impexus* sp. nov., two prasinophytes: *Cymatiosphaera robusta* sp. nov. and *Pterospermella simplex* sp. nov., one chitinozoan: *Angochitina plicata* sp. nov. and one miospore species: *Apiculatasporites ruptus* sp. nov. Hierarchical cluster analysis recognize two well-differentiated palynofloras in Argentina for the Early and Middle-Late Devonian. A poor correlation with known Devonian biostratigraphical schemes from Gondwanan and peri Gondwanan regions, support the theory of an endemic flora in northwestern and eastern Gondwana even during the Middle and Late Devonian. The palynoassemblage studied here provides an important source of reference to improve former strata correlation in the Tarija and neighbouring basins.


## 1. Introduction

Devonian sediments throughout Argentina are mostly centred in western and northwestern regions (Fig. 1A, B). They have undergone several geological processes that ended up modifying the organic content, resulting in high thermal maturity and the consequential poor recovery of organic material. However, there are several Devonian sections that have yielded palynological assemblages spanning the Lower to Upper Devonian. They comprise material from different sources such as outcrops and exploration boreholes including cuttings and core samples. In western Argentina, the studies include the Talacasto (Le Hérissé et al., 1996; García-Muro et al., 2014); Chigua (Amenábar et al., 2006, 2007), Villavicencio (Rubinstein and Steemans, 2007) and Codo formations (Amenábar and di Pasquo, 2008) (Fig. 2). In northwestern Argentina (NOA), Devonian deposits crop out in the eastern part of the Eastern Cordillera (*Cordillera Oriental*) and the Subandean Ranges, extending also in the subsurface of both, the latter and the Chaco-Salteño Plain (Starck et al., 1993). These deposits are included in the Tarija Basin, shared with Bolivia. Palynological studies in these regions are for the most part based on subsurface samples (Barreda 1986; Volkheimer et al., 1986; Ottone, 1996; Grahn and Gutiérrez, 2001; Noetinger, 2010, 2015; Noetinger and Di Pasquo, 2011), product of oil exploration surveys of the renowned source rocks from the producing basins of Bolivia and northwestern Argentina (Illich et al., 1981). These units include the top of the Copo, Caburé, Rincón and Tonono formations in the Chaco-Salteño plain and the Los Monos Formation in Eastern Cordillera (Fig. 2). There is also a small exposure of the Ventana Group (Fig. 2) in the Buenos Aires province, eastern Argentina, which have yielded lycophytes, but no palynomorphs were reported (Cingolani et al., 2003).

Palynostratigraphical schemes based only in ditch cutting samples have limitations. Caving and mud contamination can affect the distribution of elements within a column, resulting in inaccurate palynomorph ranges. Therefore, the use of controls such as subsurface cores and outcrop samples are essential. The Pescado and Piedras formations, exposed in the Eastern Cordillera (Fig. 2), have yielded poor Early Devonian assemblages (Noetinger and Di Pasquo, 2010; Noetinger et al., 2016). Close to the Argentinian-Bolivian boundary there were two studied localities where Early to Middle Devonian palynofloras were recovered (Di Pasquo, 2007; Di Pasquo and Noetinger, 2008). Studied cores spanning the Early Devonian in Noetinger and Di Pasquo (2013) have served as controls in the Chaco-Salteño Plain. Even less numerous are the cases of reliable

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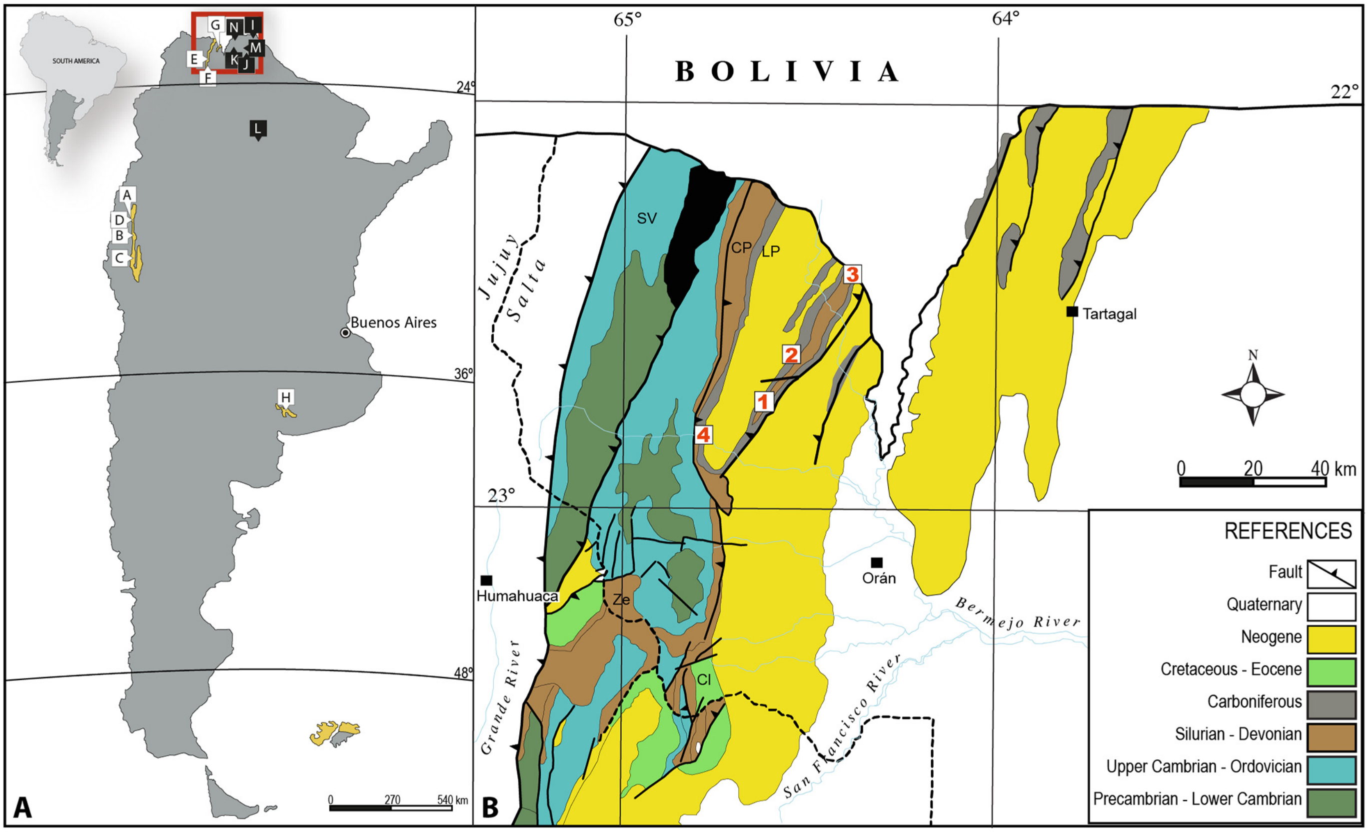


**Fig. 1.** (A) Devonian outcrops in Argentina and its related studies. Western Argentina: A, Le Hérissé et al. (1996). B, Amenábar et al. (2006, 2007). C, Rubinstein and Steemans (2007). D, García Muro et al. (2014). Northwestern Argentina: E, Noetinger and di Pasquo (2010). F, Noetinger et al. (2016). G, di Pasquo et al. (2015). Eastern Argentina: H, Cingolani et al. (2003). Studies based in subsurface material: I, Barreda (1986), Noetinger (2015). J, Volkheimer et al. (1986), Noetinger and di Pasquo (2013). K, Ottone (1996). L, Grahn and Gutierrez (2001). M, Noetinger (2010). N, Noetinger and di Pasquo (2011). (B) Geologic map of northern Argentina (modified from Kley and Monaldi, 1999) with the locations studied herein: (1) Angosto de San Ignacio, (2) Angosto del Pescado, (3) Balapuca (sections in both margins of the Bermejo river, political boundary between Argentina and Bolivia), (4) Arasayal.

references for the Middle Devonian in the southern portion of the basin, taking into account only few core samples in Ottone (1996) and Noetinger (2010).

This investigation documents the first palynoassemblage spanning the Middle-Upper Devonian from four outcropping sections located in the Argentinian Subandean (Fig. 1B). The recovered material includes fairly well-preserved palynomorphs, both from marine and continental origin. A taxonomic detail together with the stratigraphical distribution of the species is presented here, providing a well-supported reference section that will help improve former strata correlation in this basin and neighbouring regions. In addition, a correlation analysis with other Devonian palynofloras from Argentina is addressed.

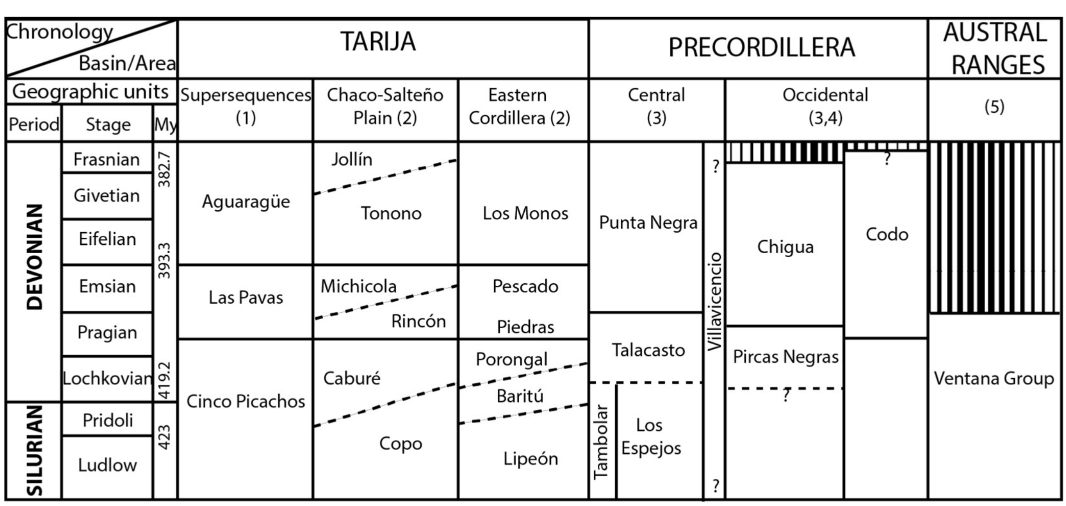


**Fig. 2.** Chronostratigraphy of Argentine Devonian units. References: (1, 2) Starck et al. (1993), Starck (1999); (3) Baldis and Peralta (1999); (4) Amenábar and di Pasquo (2008); (5) Limarino et al. (1999).

## 2. Geological setting

The siluro-devonian succession analysed comprises sandstone-dominated packages alternating with finer-grained shales and siltstones arranged in three supersequences: Cinco Picachos, Las Pavas and Aguaragüe (Fig. 2). The Las Pavas Supersequence is composed of five progradational cycles (I–V, Fig. 3). Each cycle is initiated by grey pelites bearing abundant invertebrates, overlaid by sandstones with hummocky structure finalising, upwards into cross-stratification. Each depositional sequence is bounded by a large-scale flooding surface (Starck et al., 1993). The Supersequence includes the Piedras and Pescado formations (Starck et al., 1993). The Pescado Formation involves fine-grained, dark green–grey greywackes and grey, whitish and yellowish micaceous sandstones with abundant cross-stratification structures interbedded with finer silt- and claystones (Cuerda and Baldis, 1971; Antelo Pérez, 1983). The finely laminated dark shales and siltstones with minor sandstone layers interbedded of the Los Monos Formation follow upward and is part of the overlying Aguaragüe Supersequence.

## 3. Materials and methods

### 3.1. Studied localities

Four localities were sampled for palynologic studies in the Argentinean portion of the Subandean Ranges. In the case of the Angosto del Pescado and Balapuca, the sections were surveyed and measured with a Jacob's staff (also known as cross-staff, pole with length marks). The Angosto de San Ignacio and Arasayal section were not measured, and the stratigraphic columns (Fig. 3) are schematic.

#### 3.1.1. Angosto de San Ignacio

Corresponds to an isolated outcrop of shales located in the left margin of the Iruya River, where it cuts across the Cinco Picachos Range at Eastern Cordillera—Subandean boundary (S 22° 45′ 57″; W 65° 12′ 14″ Fig. 1B). According to the local geology, this outcrop involves high levels within the Devonian section. Two samples were extracted from this section but only one was palynological productive (Fig. 3).

#### 3.1.2. Angosto del Pescado

The Pescado river cuts a narrow valley across the structure of the Pescado Range, the Angosto del Pescado section (S 22° 41.20., W 64° 34.40. Fig. 1B), where 20 samples for palynology (Fig. 3), from the Pescado and Los Monos formations, together with well-preserved lycophyte remains and invertebrates, were collected (Di Pasquo et al., 2015). The fauna of this area is known since the beginning of the twentieth century (e.g. Feruglio, 1933) but the recent collection is still under study.

#### 3.1.3. Arasayal

Four samples were studied from this section (Fig. 3), located in the central part of the Pescado Range (S 22°38′40.68″; W 64°31′24.55″. Fig. 1B). The sampled interval corresponds to a finer-grained shales and siltstones section resting above conglomeratic quartzites. This contact seems to be the flooding surface that separates the Las Pavas and Aguaragüe supersequences. According to the lithological correlation, these levels correspond to the basal section of the Pescado Formation.

#### 3.1.4. Balapuca

This section is located where the Bermejo River cuts the Pescado Range, at the Argentinean-Bolivian border (S 22°30′3.96″; W 64°27′ 37.29″. Fig. 1B). Twenty three samples were studied from this section (Fig. 3). Geological, including palaeontological, descriptions are included in di Pasquo (2005, 2007) and di Pasquo et al. (2009, 2015).

### 3.2. Methods

Shale and siltstone and fine-grained sandstone levels were sampled from each of the four localities detailed above. The samples from Angosto del Pescado and Balapuca were processed at the Laboratory of Palynostratigraphy and Palaeobotany CICYTTP (CONICET- Entre Ríos - UADER) in Diamante (Entre Ríos province, Argentina). Standard methodology was performed (Traverse, 2007) with the exception of the use of HCl since the samples did not react to it. Productive samples were improved using other treatments (i.e. HF second time, boiled HCl, KOH, ZnCl), then sieved through a 25 μm mesh and mounted with glycerine jelly. The other two localities were processed at the Laboratory of Palaeopalynology (Palaeontology Section, Museo de Ciencias Naturales "Bernardino Rivadavia"- MACN-) following conventional methods (Playford, 1977). Organic residues were then sieved through a 20 μm mesh and mounted on standard microscope slides with acrylate (Noetinger et al., 2017). Samples were analysed and illustrated with a trinocular transmitted light microscopes Nikon Eclipse E200 and Leica DM500 both bearing video cameras Amuscope 14 MB at the CICYTTP, and Leica DM2500 with Leica DFC290 camera at MACN. Measurements were carried out through the software ImageJ 1.49v. (Schneider et al., 2012). The position of illustrated specimens in the respective slides is given in England–Finder coordinates, and the materials (slides, residues, rocks) are quoted with the CICYTTP-Pl acronym (Repository).

A palynological marine index (PMI) was introduced by Helenes et al. (1998), with the purpose of detecting changes in the depositional environment in adjacent samples, with the following formula (PMI = Marine Richness (Rm)/(Terrestrial Richness (Rt) + 1) * 100). Samples without marine palynomorphs would have a PMI = 0, low values of PMI are interpreted as indicative of brackish-water influence, and higher PMI values are interpreted as indicative of marine deposition. Considering that the samples contained fairly well-preserved elements, the marine and terrestrial richness were expressed as number of species per sample rather than genera, as stipulated in de Araujo Carvalho et al. (2006). Because the PMI is based on the palynomorph diversity of terrestrial and marine species, it is therefore used as a substitute for the typical terrestrial/marine ratio.

In order to asses the similarity between the different Devonian localities in Argentina a presence/absence matrix (Supplementary material) was constructed following Barreda (1986), Volkheimer et al. (1986), Le Hérissé et al. (1996), Ottone (1996), Grahn and Gutiérrez (2001), Amenábar et al. (2006, 2007), Rubinstein and Steemans (2007), Noetinger (2010, 2015), Noetinger and Di Pasquo (2010, 2011, 2013), García-Muro et al. (2014) and Noetinger et al. (2016). The total data set comprises 16 localities, spanning the Lower to Upper Devonian and, the list of species representing different taxa (e.g., Phytoplankton, spores, algae, chitinozoans) were taken in consideration, accounting a total of 347. Species left in open nomenclature were not contemplated.

Hierarchical cluster analyses were performed using R version 3.0.1 (R development Core Team 2013). Two dissimilarity matrices were calculated through the package vegan 2.3–5 (Oksanen et al., 2016), using two different coefficients recommended for binary data, Jaccard (see Shi, 1993) and Raup-Crick (Raup and Crick, 1979). The latter were then subjected to hierarchical cluster analysis (Q mode), with the R base package. Since their approaches and assumptions are particular, testing two different algorithms (UPMGA and Complete Linkage) was important in order to weigh the robustness of the groups.

## 4. Results

### 4.1. Composition of the palynoflora

The palynological composition of the studied localities present fairly well-preserved, both marine and terrestrial elements. The Angosto de San Ignacio locality provided 31 species: 23

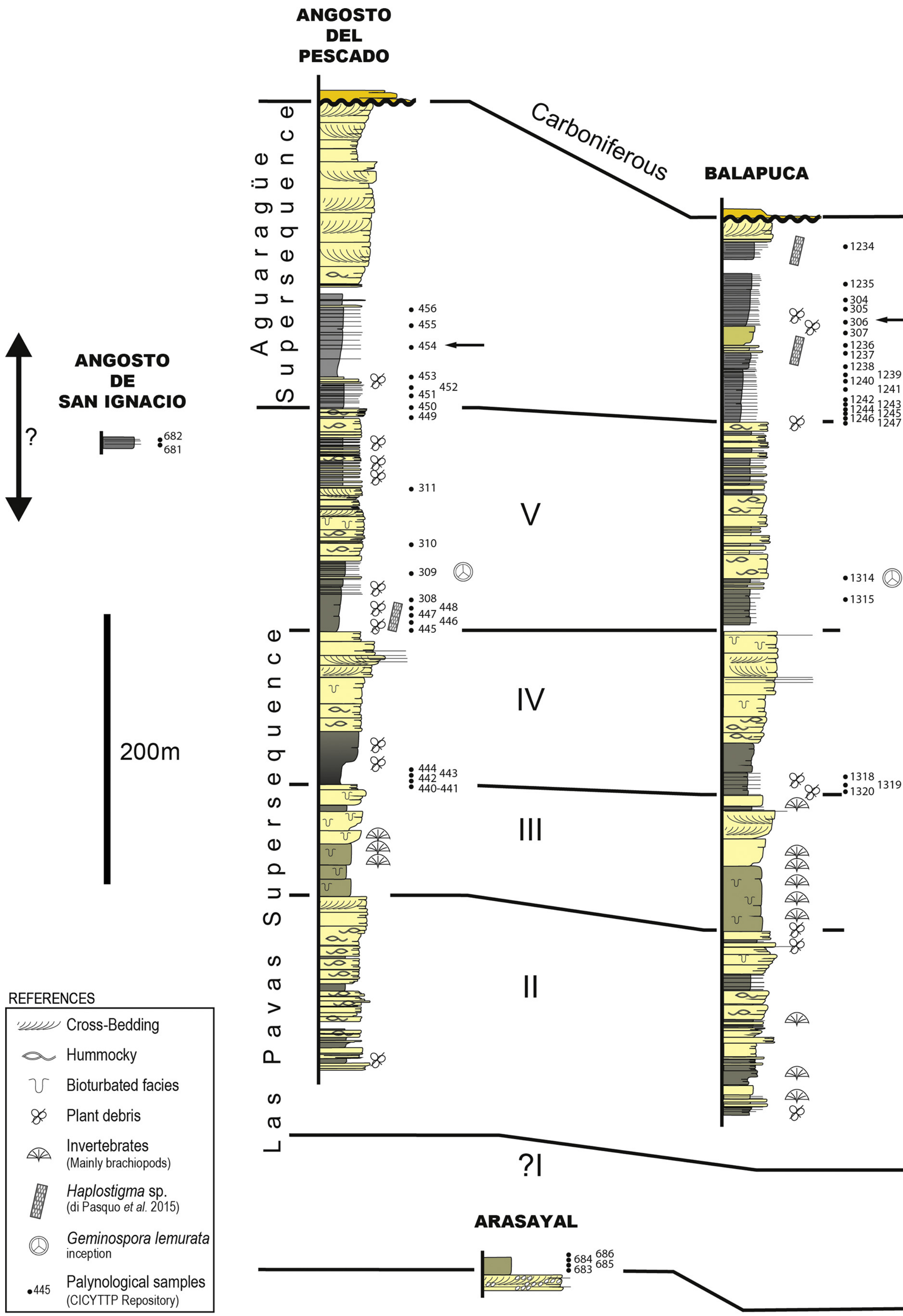


**Fig. 3.** Composite lithologic logs of the studied sections: Angosto de San Ignacio, Angosto del Pescado, Arasayal and Balapuca with sampling levels. I-V sequences in the Las Pavas Supersequence. The arrow marks the transition to the Frasnian in the Angosto del Pescado and Balapuca logs.

representatives of microplankton (15 acritarch and 8 prasinophyte species), 6 spores, 1 cryptospore and 1 chlorophyte species. The Angosto del Pescado locality comprises a very diverse assemblage with different palynological groups, 35 acritarch species, 13 prasinophytes, 8 chitinozoans, 3 chlorophytes, 6 cryptospores and 75 spore species. The Arasayal section yielded a total of 24 species including 12 acritarchs, 6 prasinophytes, 1 cryptospore and 5 spores, and the Balapuca section produced 13 acritarch species, 8 prasinophytes, 4 chitinozoans, 3 chlorophytes, 1 cryptospore, 59 spore species and 3 unidentified scolecodonts (Plates I–V).

### 4.2. Systematic palaeontology

The complete list of recognized taxa are listed by major groups and in alphabetical order in the Appendix. New, left in open nomenclature and species that justify additional remarks are described in the section

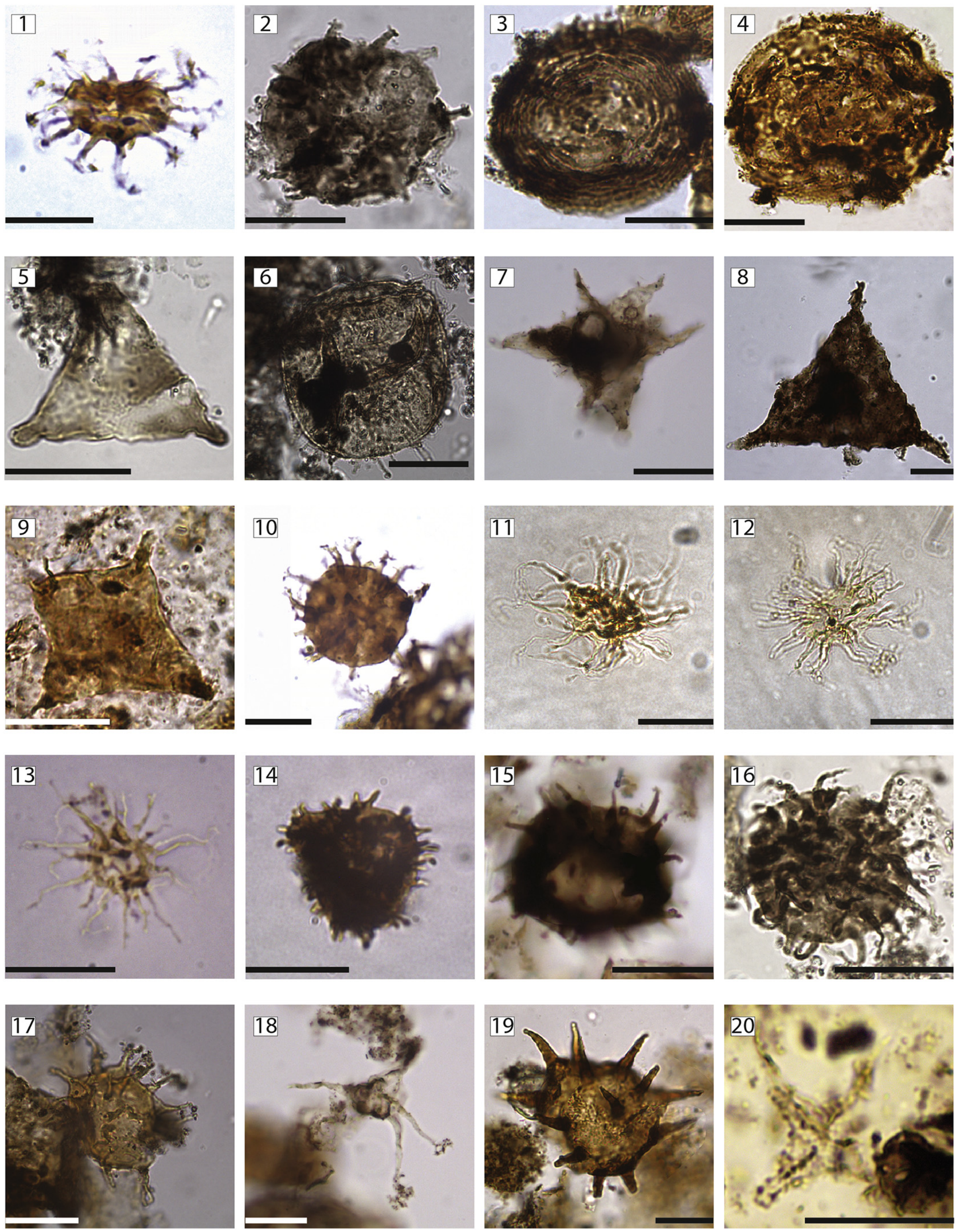

**Plate I.** Selection of taxa from the studied sections. Each illustration has the sample number and England Finder coordinates specified. Scale = 20 μm. 1. *Ammonidium loriferum* – *Ammonidium garrasinoi* (morphon). CICYTTP-Pl 682 (2), C55/4. 2. *Baltisphaeridium juliae*. CICyTTP-Pl 1314(1), K53/1. 3. *Chomotriletes bistchoensis*. CICyTTP-Pl 454(1), N59. 4. *Chomotriletes vedugensis*. CICyTTP-Pl 451(1), G28. 5. *Crassiangulina* sp. 1. CICyTTP-Pl 443(1), X59/3. 6. *Elektoriskos* sp. 1 CICyTTP-Pl 441(1), B46/2. 7. *Estiastra* sp. cf. *E. culcita*. CICyTTP-Pl 445(1), C56/4. 8. *Estiastra* sp. cf. *E. rhytidoa*. CICyTTP-Pl 446(1), P39. 9. *Evittia* sp. cf. *E. sommeri*. CICyTTP-Pl 308(2), T61. 10. *Gorgonisphaeridium furcillatum*. CICyTTP-Pl 682(2), F56/4. 11. *Gorgonisphaeridium impexus* sp. nov. Holotype. CICyTTP-Pl 682(1), K50/2. 12. *Gorgonisphaeridium impexus* sp. nov. Paratype. CICyTTP-Pl 682(1), D43. 13. *Gorgonisphaeridium impexus* sp. nov. CICyTTP-Pl 682(2), D45. 14. *Gorgonisphaeridium* sp. cf. *G. absitum*. CICyTTP-Pl 682(1), Q24/2. 15. *Gorgonisphaeridium* sp. 1. CICyTTP-Pl 445(1), D56/2. 16. *Gorgonisphaeridium* sp. 2. CICyTTP-Pl 443(1), N35/3. 17. *Michrystridium flexibile*. CICyTTP-Pl 454(1), Q48. 18, *Ozotobrachion furcillatus*. CICyTTP-Pl 445(1), B43. 19. Sp. B in Noetinger and di Pasquo, 2011. CICyTTP-Pl 451(1), T44/2. 20. *Stellinium oppidum* (Deunff) in Quadros 1999. CICyTTP-Pl 1320(2), D29.

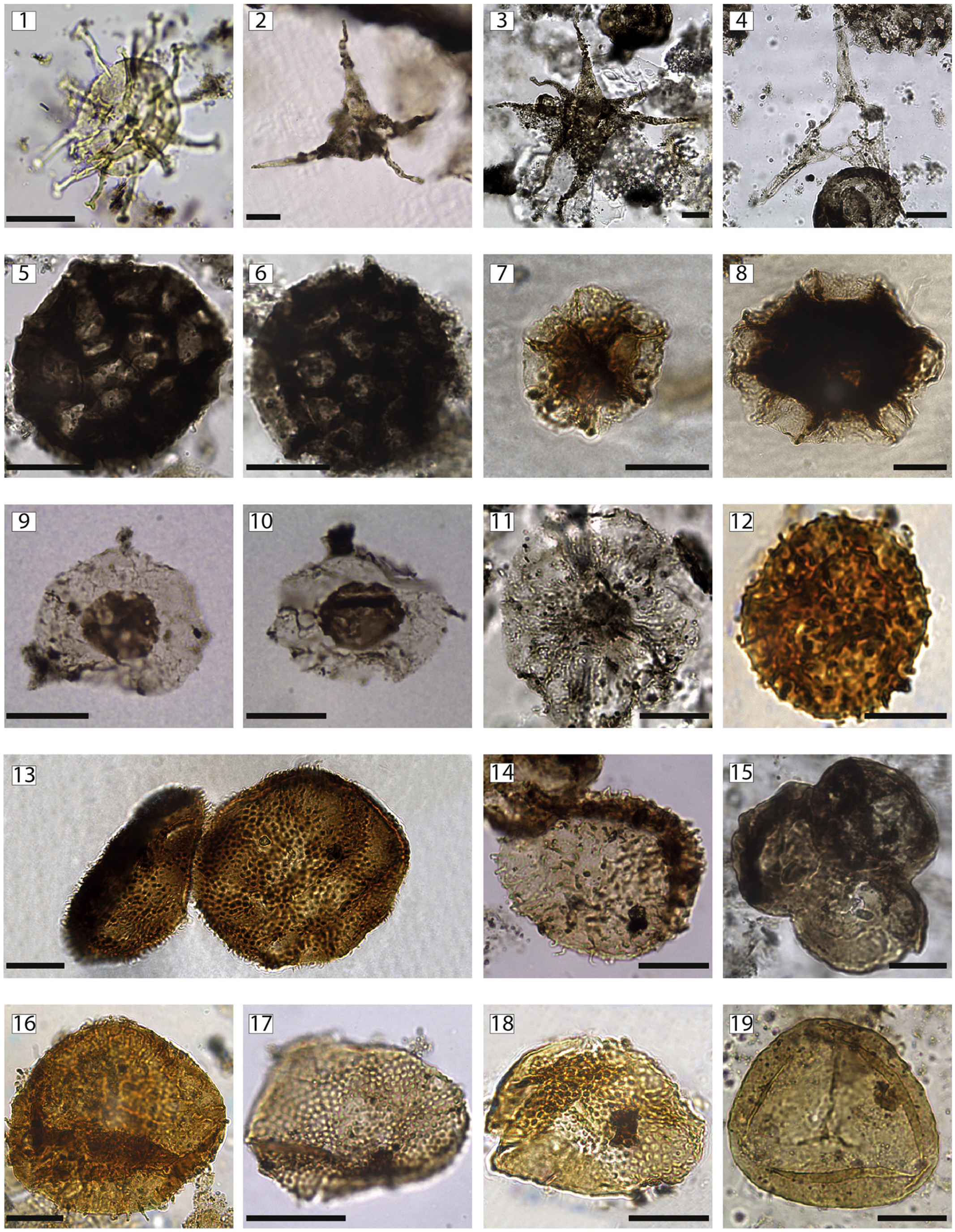


**Plate II.** Selection of taxa from the studied sections. Each illustration has the sample number and England Finder coordinates specified. Scale = 20 μm. 1. *Umbellasphaeridium* sp. cf. *U. deflandrei*. CICyTTP-Pl 1239(1), H60/3. 2. *Veryhachium europaeum*. CICyTTP-Pl 682(2), L29. 3. *Veryhachium pastoris*. CICyTTP-Pl 444(1),U45/1. 4. *Deflandrastrum*? sp. 1 CICyTTP-Pl 440 (1), W27/2. 5. *Cymatiosphaera robusta* sp. nov. Holotype. CICyTTP-Pl 443(1), S46/2. 6. *Cymatiosphaera robusta* sp. nov. Paratype. CICyTTP-Pl 444(1), E47. 7. *Cymatiosphaera turbinata*. CICyTTP-Pl 682(1), H36/2. 8. *Duvernaysphaera radiata*. CICyTTP-Pl 682(1), Q30/4. 9. *Pterospermella simplex* sp. nov. Holotype. CICyTTP-Pl 684(1), X47. 10. *Pterospermella simplex* sp. nov. Paratype. CICyTTP-Pl 684(1), O29/1. 11. *Pterospermella* sp. 1. CICyTTP-Pl 444(1), L38. 12. *Cymbohilates* sp. 1. CICyTTP-Pl 450(1), U37. 13 *Cymbohilates rubinsteinae*. CICyTTP-Pl 682(1), B30/2. 14. *Cymbohilates* sp. 2. CICyTTP-Pl 451(1), M26/4. 15. *Rimosotetras problematica*. CICyTTP-Pl 452(1), J38/4. 16. *Anapiculatisporites petilus*. CICyTTP-Pl 450(1) J38/4. 17. *Apiculatasporites ruptus* sp. nov. Holotype. CICyTTP-Pl 311(4), D42. 18. *Apiculatasporites ruptus* sp. nov. Paratype. CICyTTP-Pl 454(1), X34/1. 19. *Archaeozonotriletes* sp. 1. CICyTTP-Pl 451 (1), X52/2.

below. Species are organized by major groups and following alphabetical order. Morphological terminology related to spores and cryptospores follows the concepts in Punt et al. (2007). The lowest and highest measurements of the spore and cryptospores main axis are detailed, together with the mode in the cases that was possible to calculate. Extra measurements for different variables were also taken in consideration. Stratigraphical important species, new elements and species quoted for the first time in NOA are illustrated.

*4.2.1. Systematic descriptions*

*4.2.1.1. Acritarchs. Crassiangulina* sp. 1

Plate I, 5

*Description*: Vesicle triangular in shape with straight or slightly concave sides. Eilyma laevigate. There is one process in each of the vertices of the vesicle. The latter are short homomorphic and are apparently a thickening of the eilyma,

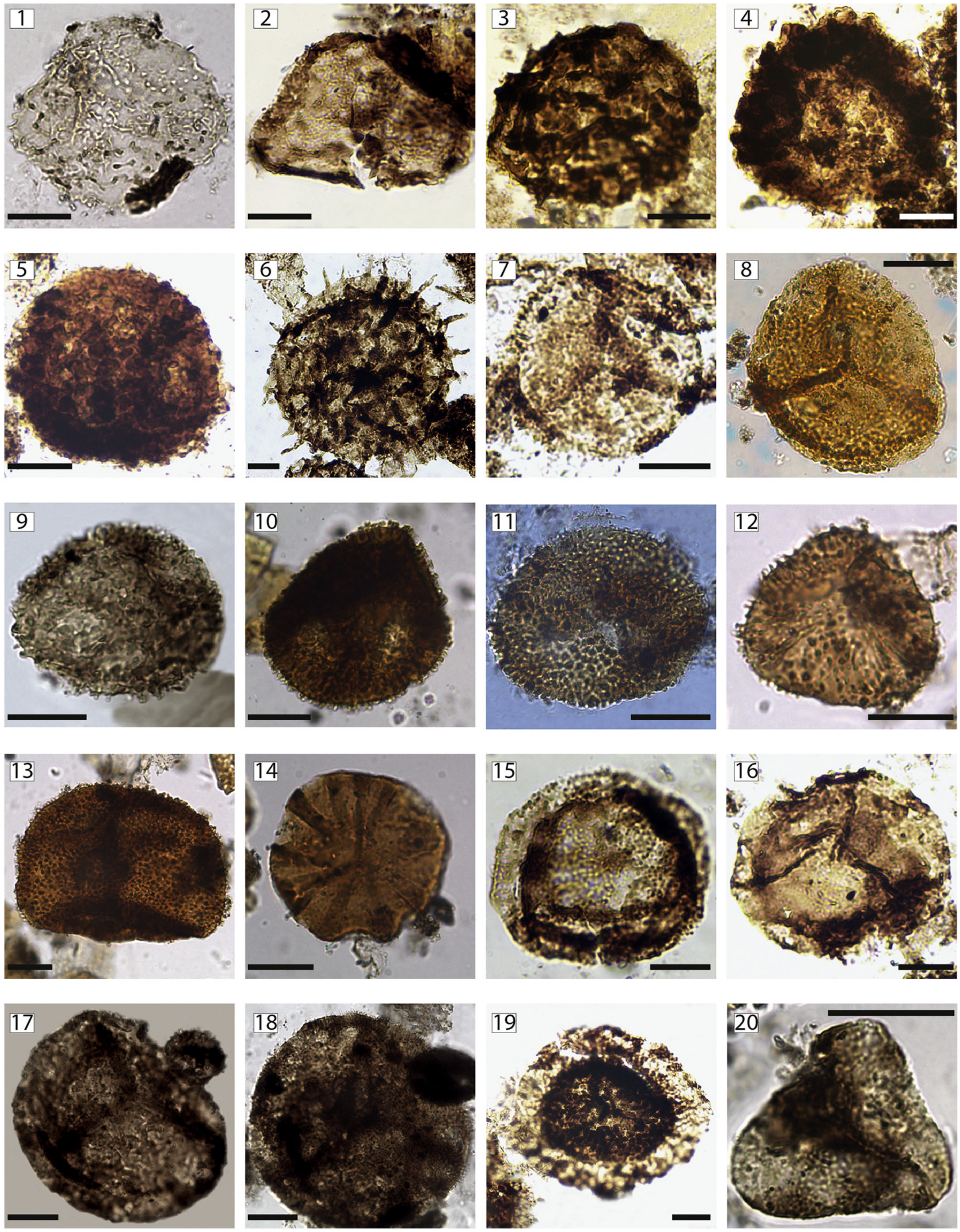


**Plate III.** Selection of taxa from the studied sections. Each illustration has the sample number and England Finder coordinates specified. Scale = 20 μm. 1. *Biornatispora* sp. cf. *B. dubia*. CICyTTP-Pl 311(4), D45. 2. *Camarozonotriletes rugulosus*. CICyTTP-Pl 1239(1), E13. 3. *Chelinospora concinna*. CICyTTP-Pl 304(2), G44/2. 4. *Chelinospora ligurata*. CICyTTP-Pl 306(1), H41. 5. *Convolutispora tegula*. CICyTTP-Pl 1240(1), O45/3. 6. *Corystisporites* sp. cf. *Acanthotriletes horridus* in McGregor and Camfield, 1982. CICyTTP-Pl 306(2), S24. 7. *Craspedispora paranaensis*. CICyTTP-Pl 306(2), Z34/3. 8. *Cymbosporites variegatus*. CICyTTP-Pl 450(1), U55/4. 9. *Dibolisporites* sp. cf. *D. uncatus*. CICyTTP-Pl 446(1), W51/2. 10. *Dibolisporites* sp. 1. CICyTTP-Pl 451(1), K47. 11. *Dibolisporites* sp. 1 in Breuer and Steemans, 2013. CICyTTP-Pl 311(4), D29/4. 12. *Dibolisporites tuberculatus*. CICyTTP-Pl 454(1), F47. 13. *Dibolisporites turriculatus*. CICyTTP-Pl 454(1), G55/4. 14. *Emphanisporites robustus*. CICyTTP-Pl 454(1), N52. 15. *Endoculeospora altobellii*. CICyTTP-Pl 1245(1), T54/4. 16. *Endosporites longiradiatus*. CICyTTP-Pl 306(2), E37. 17. *Geminospora antaxios*. CICyTTP-Pl 443(1), Z31. 18. *Geminospora* sp. 1. CICyTTP-Pl 444(1), U62/4. 19. *Grandispora megaformis*. CICyTTP-Pl 307(1), V55. 20. *Granulatisporites concavus*. CICyTTP-Pl 443(1), W55/2.

*Dimensions (one specimen)*: Overall: 35 μm. Eilyma thickness: 0.9 μm; vesicle side: 27.5–28.2-30.5 μm; process length: 4.8–5.8 μm; process base width: 3.3–4.1 μm.

*Occurence*: Angosto del Pescado.

*Comparisons*: The specimen resembles *Veryhachium improcerum*Wicander and Loeblich 1977 but the latter has shorter processes (3 μm) and is smaller overall (19–20 μm). *Crassiangulina tessellita* Jardiné et al., *emend*. Wauthoz et al. 2003. has three to eight processes always verrucate. *C. grotesca* Cramer et al. emend. Wauthoz et al. 2003 bears filamentous elements in each apex and *C. variacornuta* Wauthoz et al. 2003 has complex processes.

*Elektoriskos* sp. 1

Plate I, fig. 6

*Description*: Vesicle spherical. Wall thin, laevigate. Numerous stiff, hairlike homomorphic processes (>30) with acuminated or blunt tips that are regularly distributed on the vesicle.

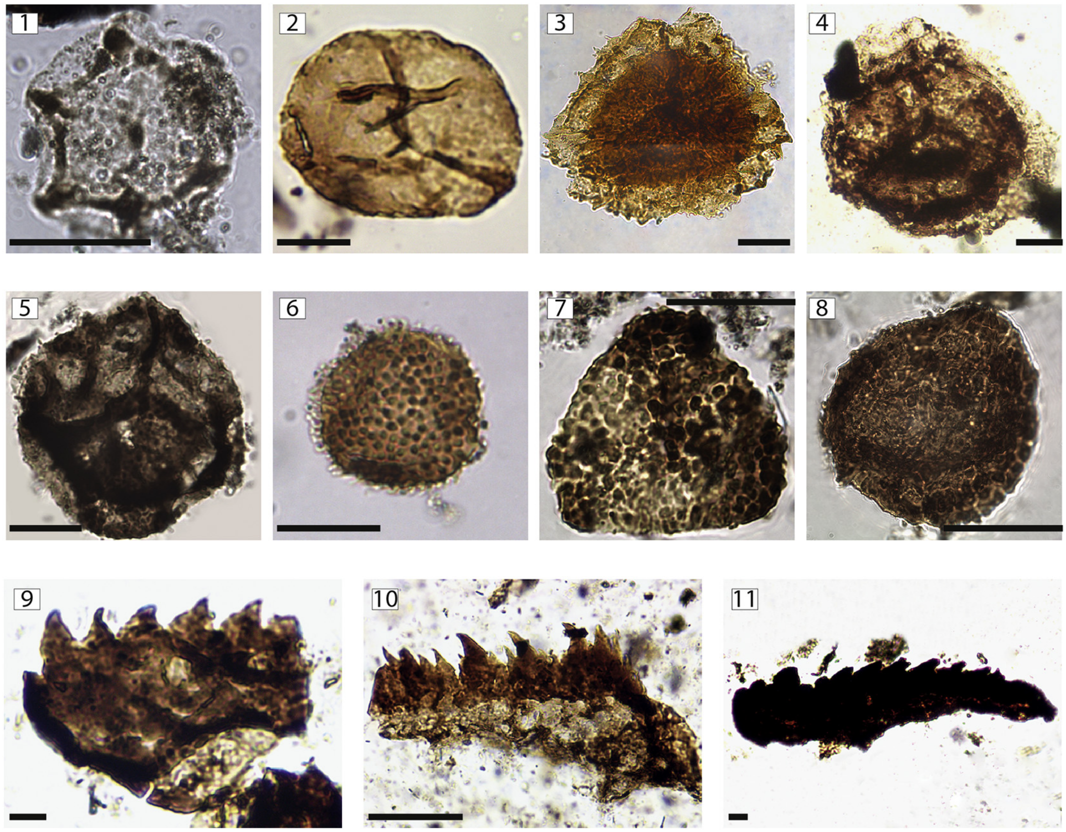


**Plate IV.** Selection of taxa from the studied sections. Each illustration has the sample number and England Finder coordinates specified. Scale = 20 μm. 1. *Perotrilites heterocorpus* in Steemans, 1995. CICyTTP-Pl 440(1), L58/3. 2. *Punctatisporites picuibaensis*. CICyTTP-Pl 1239(1), M48/2. 3. *Samarisporites angulatus*. CICyTTP-Pl 450(1), A36/2. 4. *Samarisporites praetervisus*. CICyTTP-Pl 1242(1), H27. 5. *Verruciretusispora* sp. 1. CICyTTP-Pl 443(1), E41. 6. *Verrucosisporites onustus*. CICyTTP-Pl 454(1), C29/1. 7. *Verrucosisporites* sp. 1 in Breuer and Steemans, 2013. CICyTTP-Pl 443(1), U56/4. 8. *Verrucosisporites tumulentus*. CICyTTP-Pl 456(1), O37. 9–11. Undetermined scolecodonts. (I) CICYTTP-Pl 1243(2), N15. (J) CICYTTP-Pl 306 (1), T34/4. (K) CICYTTP-Pl 1318(3), Y28/2.

*Dimensions (3 specimens)*: Overall: 55–66 μm. Eilyma thickness: 0.7–1.2 μm; vesicle diameter: 40.7–47.9 μm; process length: 2.8–15.3 μm.

*Occurence*: Angosto del Pescado

*Comparisons*: *Elektoriskos* sp.1 resembles *E. tenuis* Playford in Playford and Dring 1981 but the latter is smaller overall (22–32 μm). *Elektoriskos araiothriches* Loeblich and Wicander 1976 has a smaller vesicle (25 μm) and shorter processes (2–6 μm); *E. intonsus* Loeblich and Wicander 1976 has a more dense distribution of processes and its vesicle is also smaller (31–37 μm); *E. dolos* Wicander and Loeblich 1977 has wider processes at base and the vesicle is smaller (18–21 μm) and *E. villosa* Playford 1981 is smaller overall (21–35 μm) and the eilyma is thicker (1.6–2.6 μm).

*Estiastra* sp. cf. *E. culcita* Wicander, 1974.

Plate I, 7

*Dimensions (one specimen)*: Overall: 53.6 μm; process length: 17.1–17.7 μm; process base width: 8–14.8 μm.

*Occurence*: Angosto del Pescado.

*Remarks*: The poor preservation prevents to asses the presence of grana in the eylima.

*Estiastra* sp. cf. *E. rhytidoa* Wicander and Wood, 1981.

Plate I, 8

*Description*: Vesicle triangular in shape with straight to slightly concave sides. Eilyma laevigate to granulated. There is one process in each of the vertices of the vesicle. The latter are short homomorphic and are apparently a thickening of the eilyma.

*Dimensions (3 specimens)*: Overall: 76.3–103.2 μm. Eilyma thickness: 1.8 μm; vesicle sides: 65.8–72.5-76.3 μm; process length: 6.1–21.3 μm; process base width: 5.9–8.9 μm.

*Occurence*: Angosto del Pescado.

*Remarks*: The poor preservation prevents to asses the presence of grana in the eylima.

*Evittia* sp. cf. *E. sommeri* Brito, 1967.

Plate I, 9

*Description*: Vesicle quadrangular with scabrated eilyma. Short processes at each corner of the vesicle, with barely discernible ramifications.

*Dimensions (one specimen)*: Overall: 44 μm. Process length: 4.4–6.6 μm; Wall thickness: 1.2 μm.

*Occurence*: Angosto del Pescado.

*Remarks*: The poor preservation of the specimen which prevents the clear observation of the bifurcations in the processes and the smaller size avoid the inclusion of the specimen in the species.

Genus: ***Gorgonisphaeridium*** Staplin, Jansonius and Pocock, 1965.

*Type species*: *Gorgonisphaeridium winslowii* Staplin, Jansonius and Pocock, 1965.

*Gorgonisphaeridium impexus* sp. nov.

Plate I, 11-13

*Holotype*: Plate I, 11. Sample CICYTTP-Pl 682, K50/2.

*Paratype*: Plate I, 12. Sample CICYTTP-Pl 682, D43.

*Derivation of the name*: The “uncombed” appearance of the processes.

*Diagnosis*: Vesicle boldly spherical. Wall laevigate under light transmission microscope. Numerous homomorphic processes not less than 15, generally over 30, with rounded bases that end in acuminated recurved tips.

*Description of holotype*: Vesicle originally spherical 17.2 μm in diameter. Eilyma laevigated, 0.7.μm thick. Numerous homomorphic processes (>20), with rounded bases 1.3–2.1 μm wide, extending 20.8–25.4 μm to end in acuminated recurved tips.

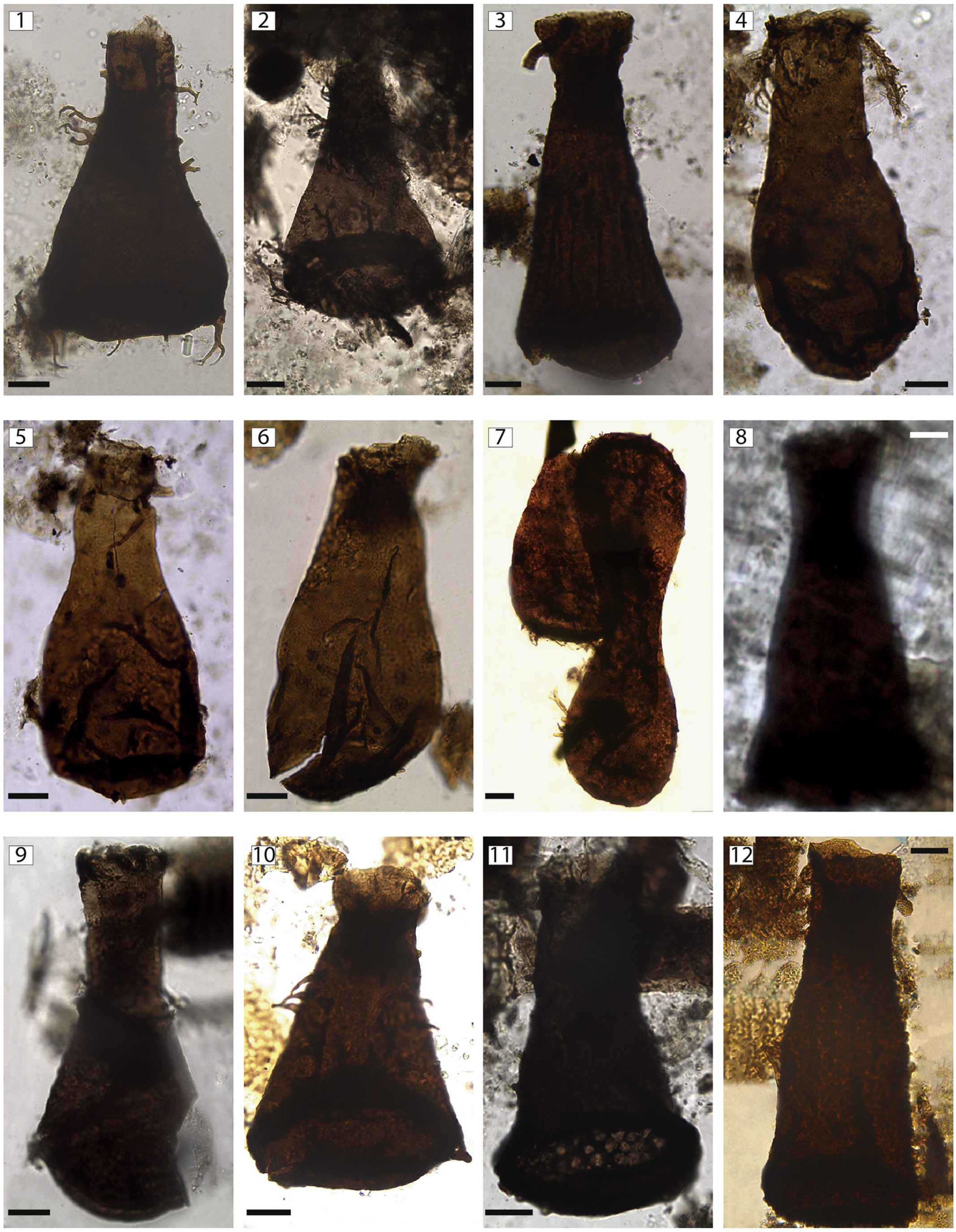


**Plate V.** Selection of taxa from the studied sections. Each illustration has the sample number and England Finder coordinates specified. Scale = 20 μm. 1–2. *Ancyrochitina morzadeci*. (1) CICYTTP-Pl 311(1), X22/2; (2) CICYTTP-Pl 311(4), N48. 3. *Ancyrochitina* sp. 1. CICyTTP-Pl 451(1), F43. 4–6. *Angochitina plicata* sp. nov. (4) Holotype. CICyTTP-Pl 308(2), L43/1; (5) Paratype. CICyTTP-Pl 310(2), S39; (6) CICyTTP-Pl 310(2), M29/3. 7. *Angochitina* sp. 1, CICyTTP-Pl 1314(1), K46/4. 8. *Cyathochitina*? sp. 1 CICyTTP-Pl 452(1), Y30/1. 9. *Lagenochitina* sp. cf. *L. praeavelinoi*. CICyTTP-Pl 309(3), D52/1. 10. *Ramochitina autasmirimense*. CICyTTP-Pl 311(1), Q21/4. 11. *Sagenachitina* sp. 1 CICyTTP-Pl 311(4), M46. 12. *Spinachitina* aff. *S. biconstricta*. CICyTTP-Pl 450(1), E53/4.

*Dimensions (8 specimens)*: Overall: 32.6–48.5 μm. Eilyma thickness: 0.6–0.7 μm; vesicle diameter: 12–19.5 μm; process basal width: 0.8–2.3 μm; process length: 8.4–25.4 μm.

*Occurence*: Angosto de San Ignacio.

*Comparisons*: *Gorgonisphaeridium absitum* Wicander 1974 has a bigger vesicle (53–66 μm), as well as *G. elongatum* Wicander 1974, which has a bigger vesicle (48 μm average) and an average of longer processes (21 μm). *Gorgonisphaeridium furcillatum* Wicander and Playford 1985 has bi- and trifurcated processes as well as *Gorgonisphaeridium* sp. in Ottone (1996). *Gorgonisphaeridium ohioense* (Winslow) Wicander 1974 has stiffer processes while this specimens bear more flexible and recurved ones. *Gorgonisphaeridium savertonense* Wicander and Playford 2013 has a wider range for the processes length (10–22 μm).

*Gorgonisphaeridium* sp. cf. *G. absitum* Wicander, 1974.

Plate I, 14

*Description*: Vesicle originally spherical deformed by pyrite precipitation covered by numerous, slightly slender, short processes, rounded at base with simple sharp tips.

*Dimensions (one specimen)*: Vesicle diameter: 28 μm; processes length: 2.7–4 μm; processes basal width: 0.8–1.7 μm.

*Occurence*: Angosto de San Ignacio.

*Remarks*: *Gorgonisphaeridium absitum* is bigger overall (53–66 μm).

*Gorgonisphaeridium* sp. 1
Plate I, 15
*Description*: Vesicle boldly spherical. Wall apparently laevigate under transmission microscope. Numerous homomorphic processes (>30) with rounded bases that end in acuminated recurved tips that are furcated at the tip.
*Dimensions (2 specimens)*: Overall: 25.6–30 μm. Vesicle diameter: 18.7–20.3 μm; process basal width: 1.7 μm; process length: 3.6–4.6 μm.
*Occurence*: Angosto del Pescado.
*Comparisons*: This specimen resembles *Gorgonisphaeridium* sp. 3 in Barreda (1986) and *Gorgonisphaeridium* sp. in Ottone (1996) but those species are considerable bigger than this one (53 and 61 μm respectively).
*Gorgonisphaeridium* sp. 2.
Plate I, 16
*Description*: Vesicle originally spherical. Eilyma laevigated. Numerous homomorphic processes (>20), with rounded bases, extending shortly to end in acuminated recurved tips.
*Dimensions (5 specimens)*: Overall: 32.7–46.70 μm. Vesicle diameter: 20.3–32.7 μm; process basal width: 1.3–2.4 μm; process length: 4.6–12.3 μm.
*Occurence*: Angosto del Pescado, Arasayal.
*Comparisons*: *Gorgonisphaeridium* sp. 2 resembles *Gorgonisphaeridium* sp. in Ottone (1996) but the latter has bi- or trifurcate extremities as well as *G. furcillatum.* Wicander and Playford 1985. *Gorgonisphaeridium ohioense* (Winslow) Wicander 1974 has stiffer process that may be flexible from the midpoint to the tip, whilst *Gorgonisphaeridium* sp. 2 has more flexible ones.
*Umbellasphaeridium* sp. cf. *U. deflandrei (*Moreau-Benoît) Jardiné, Combaz, Magloire, Peniguel and Vachey, 1972.
Plate II, 1
*Description*: Vesicle sub spherical covered by numerous long processes, rounded at base with simple expanded tips in the shape of funnels.
*Dimensions (one specimen)*: Overall: 64 μm. Vesicle diameter: 34 μm; processes length: 15–18 μm; processes basal width: 1.9–2.6 μm.
*Occurence*: Balapuca.
*Remarks*: *Umbellasphaeridium deflandrei* has shorter processes.
Chlorophycean algae
*Genus*: ***Cymatiosphaera*** Wetzel, *ex* Deflandre, 1954.
*Type species*: *Cymatiosphaera radiata* Wetzel, 1933.
*Cymatiosphaera robusta* sp. nov.
Plate II, 5, 6
*Holotype*: Plate II, 5. Sample CICYTTP-Pl 443, S46/2.
*Paratype*: Plate II, 6. Sample CICYTTP-Pl 444, E47.
*Derivation of the name*: The nature of solid muri.
*Diagnosis*: Vesicle circular to subcircular with its surface divided into several hexagonal to polygonal fields, which diagonal varies from 6.8 to 19.4 μm long, defined by mostly laevigated muri 1.2–4.7 μm wide and up to 3.2 μm high that in some cases are surmounted by crests. Some specimens show a larger lacunae up to 24.5 μm wide. Field surfaces often granulated.
*Description of holotype*: Vesicle circular to subcircular with its surface divided into several hexagonal fields, which diagonal varies from 9.4 to 13.1 μm long. Muri 2.1–3 μm wide. Field surfaces laevigated. Overall equatorial diameter, 50 μm.
*Dimensions (10 specimens)*: Overall: 40–65 μm (mode: 52 μm).
*Occurence*: Angosto del Pescado, Arasayal, Balapuca.
*Comparisons*: *Cymatiosphaera apiaria* Ottone 1996 has pentagonal areas and very thin muri. *Cymatiosphaera parvicarina* Wicander 1974 has a prominent a reticulocristate surface. *Cymatiosphaera ambotrocha* Wicander and Loeblich 1977 has a granulated surface.
*Deflandrastrum*? sp. 1
Plate II, 4
*Description*: Colony? composed of 4 units. The latter have pyramidal shape with triangular bases. A long and slender process emerge from each vertex of the base, connecting the units between each other.
*Dimensions (one specimen)*: Diagonal -between to the vertices of two units-: 108 μm. Length of unit: 43.7–45 μm; base of unit: 15.1 μm; process length: 18.5 μm.
*Occurence*: Angosto del Pescado.
*Comparisons*: *Deflandrastrum millepiedi* Combaz 1962 and *Deflandrastrum* sp. A in Richardson and Ioannides (1973) has a direct contact between the units or through a basal expansion and not by a process. *Deflandrastrum leonardi* Combaz 1962 is similar but the processes that conect the units are wider and shorter.
Genus: ***Pterospermella***Eisenack, 1972.
*Type species*: *Pterospermella aureolata* (Cookson and Eisenack) Eisenack, 1972.
*Pterospermella simplex* sp. nov.
Plate II, 9, 10
*Holotype*: Plate II, 9. Sample CICYTTP-Pl 684, X47.
*Paratype*: Plate II, 10. Sample CICYTTP-Pl 684, O29/1.
*Derivation of the name*: The simple nature of the specimens.
*Diagnosis*: Central vesicle and overall amb spherical. Central body laevigated, surrounded by an also laevigated thin equatorial flange, that may fold equatorially resembling a crassitud. The flange does not present radial folds.
*Description of holotype*: Vesicle circular. Central body circular, laevigated by an also laevigated thin equatorial flange without radial folds. Dimensions. Overall: 41.2 μm; central body: 19.1 μm; flange: 9.4–10.2 μm.
*Dimensions (12 specimens)*: Overall: 23–57.5 μm (mode: 41 μm); central body diameter: 12.3–19.1 μm; flange width: 4.5–13 μm. Ratio vesicle – flange: 3.8–1.3 (mode: 1.7).
*Occurence*: Angosto del Pescado, Arasayal, Angosto de San Ignacio.
*Comparisons*: *Pterospermella simplex* sp. nov. resembles *Helios umbelliferum* Pöthe de Baldis 1977, nonetheless as well explained by the author the “lamellae” is supported by regular distributed processes not observed in any of the specimens studied herein. *Pterospermella hermosita* (Cramer) Eisenack et al., 1973 has an ornamented central body; *P. tenellula* Playford 1981 has an ornamented central body and radial folds in the flange. *Pterospermella capitana* Wicander 1974 is bigger (central vesicle 43–62 μm) with a scabrated central body while *P. latibalteus* Wicander 1974 has also a scabrated vesicle and a wider flange (18–26 μm wide) with radial folds.
*Remarks*: This species dominates the level CICYTTP 684.
*Pterospermella* sp. 1
Plate II, 11
*Description*: Central vesicle and overall amb spherical. Central vesicle laevigated, surrounded by an also laevigated thin equatorial flange with numerous radial folds.
*Dimensions (one specimen)*: Overall: 57 μm. Vesicle diameter: 17 μm; flange width: 21 μm.
*Occurence*: Angosto del Pescado.
*Comparisons*: *Pterospermella* sp. 1 resembles *P. latibalteus* Wicander 1974 nonetheless the central vesicle of the former seems to be laevigate. *Pterospermella simplex* sp. nov. is smaller (see above) and it does not present radial folds.
Cryptospores
*Cymbohilates* sp. 1
Plate II, 12
*Description*: Cryptospore hilate proximally. Circular to subcircular amb. Distal and subequatorial exospore sculptured with scattered spines, coni and bacula. Elements 1–2.8 μm high and 1.1–2.6 μm wide at base, separated a distance equivalent to one to two base diameters. .
*Dimensions (3 specimens)*: Overall: 45.2–50.4 μm.
*Occurence*: Angosto del Pescado.
*Comparisons*: *Cymbohilates* sp. A in Wellman et al., 2000 has only spines as ornamentation. *Cymbohilates* sp. A in Noetinger (2015) has higher elements (2–4 μm high). *Cymbohilates comptulus* Breuer et al., 2007 has smaller elements. (0.5–1.5 μm high) *Cymbohilates* sp. A in

Mehlqvist et al. (2012) resembles *Cymbohilates* sp. 1 but the latter has a denser ornamentation.

*Cymbohilates* sp. 2

Plate II, 14

*Description*: Cryptospore hilate proximally. Circular to subcircular amb. Hilum laevigated defined by a subequatorial crassitud. Distal and subequatorial exospore sculptured with scattered slender spines with bulbous bases. Elements 3.6–6.1 μm high and 1.1–2.1 μm wide at base.

*Dimensions (2 specimens)*: Overall: 59.2–66.7 μm.

*Occurence*: Angosto del Pescado.

*Comparisons*: *Cymbohilates* sp. 2 resembles *Cymbohilates* sp. A in Wellman et al. (2000) but the latter has a microgranulated hilum and is smaller overall (35–46 μm). *Cymbohilates* sp. A in Noetinger (2015) has shorter elements (2–4 μm high).

Spores

*Genus*: ***Apiculatasporites*** (Ibrahim) *emend.* Smith and Butterworth, 1967.

*Type species*: *Apiculatasporites spinulistratus* (Loose) Ibrahim, 1933.

*Apiculatasporites ruptus* sp. nov.

Plate II, 17,18.

*Holotype*: Plate II, 17. Sample CICYTTP-Pl 454, D42.

*Paratype*: Plate II, 18. Sample CICYTTP-Pl 311, X34/1.

*Derivation of the name*: The common preservation state of the specimens.

*Diagnosis*: Trilete spore. Amb subtriangular to subcircular. Laesurae straight, slightly discernible or covered by lips, extended to the equator. Exine thin laevigated proximally. Distally ornamented with cones 1.2–1.8 μm wide at base and 0.8–1.1 μm high.

*Description of holotype*: Trilete spore. Amb subcircular, deformed. Laesurae straight, covered by lips 1.4 μm. Exine thin laevigated proximally. Distally ornamented with cones 1.2–1.6 μm wide at base and 1.1 μm high. Overall diameter: 60.4 μm.

*Dimensions (16 specimens)*: 34.4–75 μm.

*Occurence*: Angosto de San Ignacio, Angosto del Pescado, Balapuca.

*Comparisons*: These specimens resemble *Apiculatasporites brevidenticulatus* McGregor and Camfield 1982 but the latter bears more variable ornamentation (grana, coni, spinae). *Apiculatisporis* sp. A in Amenábar et al. (2006) bears higher coni (2–2.3 μm). *Apiculatasporites caperatus* Menéndez and Azcuy 1969 has smaller coni (1 μm high) and grana.

*Remarks*: The specimens are always plicated and broken, exhibiting the delicate nature of the wall.

*Archaeozonotriletes* sp. 1

Plate II, 19

*Description*: Patinated spore, trilete. Amb subtriangular with broad rounded corners to subcircular. Laesurae straight to slightly sinuous extended to the equator, accompanied by labra 1.2–2.2 μm wide. Exine thin proximally, crumpled conforming a concentric fold along the equator. The exine distally is psilate to punctate.

*Dimensions (9 specimens)*: 29–58.6 μm.

*Occurence*: Angosto de San Ignacio, Angosto del Pescado, Balapuca.

*Comparisons*: *Archaeozonotriletes chulus* (Cramer) Richardson and Lister 1969 has a laevigated exine; *A. variabilis* (Naumova) Allen 1965 has a wide patina that could reach the 30% of the total diameter.

*Biornatispora* sp. cf. *B. dubia* (McGregor) Steemans, 1989.

Plate III, 1

*Dimensions (one specimen)*: Overall: 69.3 μm. Ornamentation: 1.6–2.4 μm wide at base. Ridges 0.8–1.3 μm wide.

*Occurence*: Angosto del Pescado.

*Remarks*: The specimen is bigger overall in comparison with the size range proposed for the species (21–33 μm), and the ornamentation is barely larger.

*Dibolisporites* sp. cf. *D. uncatus* (Naumova) McGregor and Camfield, 1982.

Plate III, 9

Dimensions (one specimen). Overall: 53.3 μm. Ornamentation: 1.5–1.7 μm wide at base; 1.6–2.3 μm high.

Occurence. Angosto del Pescado.

Remarks. The ornamentation is smaller that the size range proposed for the species (3–5 μm at basal width and up to 10 μm long) .

*Dibolisporites* sp. 1

Plate III, 10

*Description*: Spore, trilete. Amb subcircular. Exine laevigated proximally. Equatorial and distal exine ornamented with varied elements mostly biform, bacula, coni and spines densely distributed. The elements are 1.7–2.8 μm in height and 1.5–2.2 μm wide at base.

*Dimensions (3 specimens)*: Overall: 43.8–65.2 μm.

*Occurence*: Angosto del Pescado.

*Comparisons*: *Dibolisporites bullatus* (Allen) Riegel 1973 is much bigger overall (average 137 μm). The sculpture on *Dibolisporites farraginis* McGregor and Camfield, 1982 can show a wide range in distribution (from densely to 8 μm apart) and the ornamentation is more variable in comparison with *Dibolisporites* sp. 1.

*Geminospora* sp. 1

Plate III, 18

*Description*: Camerate spore, trilete. Amb subcircular to subtriangular. Laesurae straight extended to the margin of the intexine, accompanied by labra 2.2–3.5 μm wide. Exoexine 3–6 μm thick. *Intexine faintly granular*: Ornamentation distributed closed-packed on the equator and distal face consisting of coni, spines and bacula 1.4–3 μm high, 0.9–2.7 μm wide at base.

*Dimensions (5 specimens)*: 71.6–118 μm.

*Occurence*: Angosto del Pescado.

*Comparisons*: *Geminospora lemurata* Balme 1962 is smaller overall and even though Marshall (1996) proposes a wider size range for this species with specimens up to 110 μm, the ornamentation of *Geminospora* sp. 1 is bigger. *Geminospora antaxios* (Chibrikova) Owens 1971 has grana and microverrucae up to 1 μm high. *Geminospora micropaxila* (Owens) McGregor and Camfield 1982 has shorter elements. (usually less than 0.5 μm high). *Geminospora* sp. 1 resembles *Rhabdosporites langii* (Eisenack) Richardson 1965, but the latter has baculi up to 1.5 to 2 μm high.

*Verruciretusispora* sp. 1

Plate IV, 5

*Description*: Spore, trilete. Amb subcircular. Laesurae straight extended two quarters of the distance to the equatorial margin, accompanied by labra 3.7–4 μm wide. The equatorial margin is darkened due to the density of ornamentation, which define a curvaturae perfectae. Contact face laevigated to faintly granulated. Ornamentation distributed on the distal face consists of verrucae that can anastomose forming rugulae and coni.

*Dimensions (2 specimens)*: Overall: 66–79 μm. Ornamentation: 1.6–3.9 μm wide at base.

*Occurence*: Angosto del Pescado.

*Comparisons*: *Verruciretusispora dubia* (Eisenack) Richardson and Rasul 1978 has wider verrucae (1.5–10 μm wide at base); *V. ornata* (Menéndez and Pöthe de Baldis) Pérez Leyton *ex* Di Pasquo, 2005 has cilindrical processes of various sizes (1.1–4.4 μm high). These specimens resemble *Verruciretusispora pallida* Owens 1971, but the latter has elements that are surmounted by a small cone.

*4.2.1.2. Chitinozoans. Ancyrochitina* sp. 1

Plate V, 3

*Description*: Vesicle with a cylindric-conical shape and very short neck that widens towards the aperture. Shoulder absent, flexure discernible. Vesicle laevigated with longitudinal structures. It is observable the development of a process around the aperture being 7.8 μm wide and around the margin.

*Dimensions (one specimen)*: Total length: 203.7 μm, maximum chamber width: 61.5 μm, neck length: 11 μm, neck width: 35.8 μm, aperture: 54.1 μm, flexure angle: 140°.

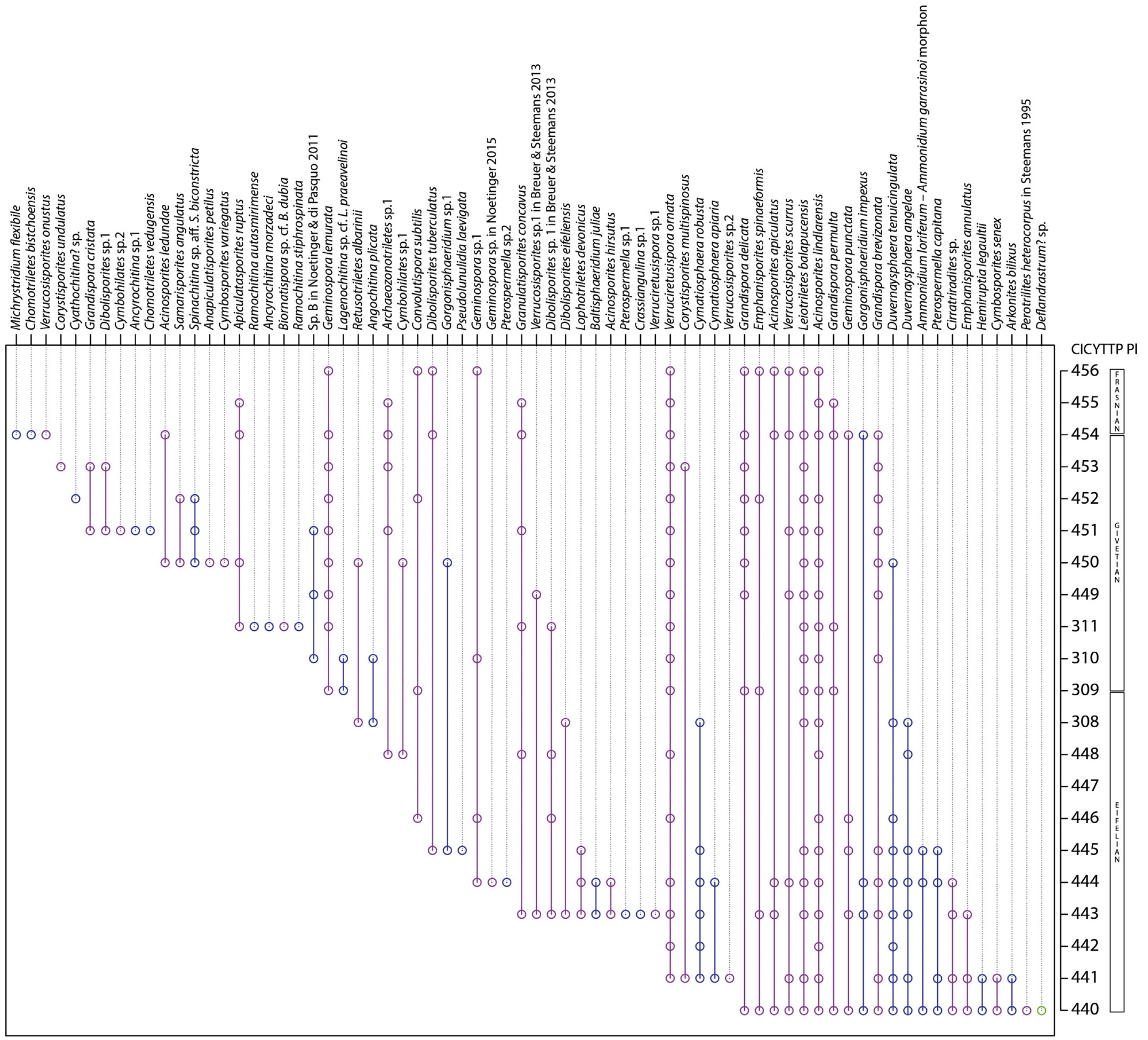


**Fig. 4.** Stratigraphic distribution of selected species in the Angosto del Pescado section. Marine components (acritarchs, chitinozoans and prasinophytes) are coloured in blue, spores are portrayed in pink and chlorophytes in green.

*Occurence*: Angosto del Pescado, Balapuca.

*Comparisons*: The specimen resembles *Ancyrochitina* sp. A in De Amorim Gaugris and Grahn, (2006) but in the latter the aperture does not evidently expands like in this specimen.

*Genus*: ***Angochitina***Eisenack, 1931.

*Type species*: *Angochitina echinata* Eisenack, 1931; neotype: *Angochitina echinata* Eisenack, 1964.

*Angochitina plicata* sp. nov.

Plate V, 4-6

*Holotype*: Plate V, 4. Sample CICYTTP-Pl 310, L43/1.

*Paratype*: Plate V, 5. Sample CICYTTP-Pl 308, S39.

*Derivation of the name*: The nature of the folded vesicle.

*Diagnosis*: Vesicle with a cylindric-conical shape, cylindrical neck and rounded base. Shoulder absent, flexure discernible. Vesicle profusely folded mainly laevigated bearing simple and branched spines scattered in the chamber, 6.5–46.8 µm long, 3.7–4.6 µm wide at base and, branched spines around the aperture severely longer 10.6–46.8 µm.

*Description of holotype*: Vesicle with a cylindric-conical shape, cylindrical neck and rounded base. Shoulder absent, flexure discernible. Vesicle profusely folded mainly laevigated. The aperture is crowned by branched spines 44.5 µm long and 6 µm wide at base. Dimensions: Total length: 170.1 µm, maximum width: 74.8 µm, neck length: 68.5 µm, neck width: 42.5 µm, aperture: 48 µm, flexure angle: 150°.

*Dimensions (10 specimens)*: Total length: 167.8–186.7 µm, maximum width: 72.5–83.5 µm, neck length: 27.5–68.5 µm, neck width: 33.2–42.5 µm, aperture: 30.3–48 µm, flexure angle: 146–154°.

*Occurence*: Angosto del Pescado, Balapuca.

*Comparisons*: *Alpenachitina eisenackii* Dunn and Miller 1964 has neat rows of multi branched processes along the margin, the base of the shoulder and the aperture. This species resembles *Ramochitina boliviensis* Grahn 2002 but the latter bears spongy spines scattered in six rows. The spines surrounding the aperture resemble those of *Alpenachitina crameri* Hutter, 1979, in some of the specimens occurring herein.

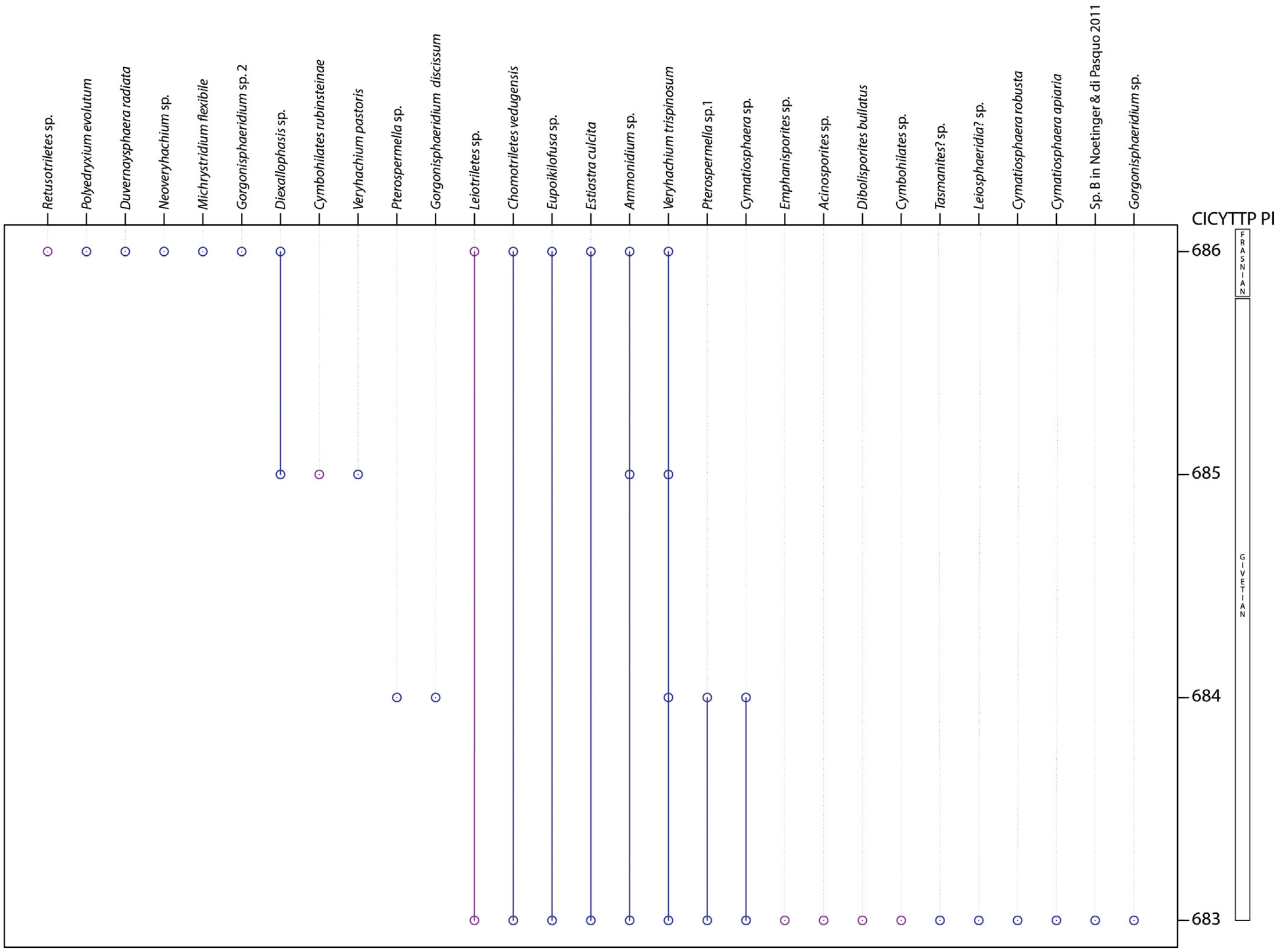


**Fig. 5.** Stratigraphic distribution of selected species in the Arasayal section. Marine components (acritarchs, chitinozoans and prasinophytes) are coloured in blue, spores are portrayed in pink and chlorophytes in green.

*Angochitina* sp. 1

Plate V, 7

*Description*: Vesicle with a cylindric-conical shape, cylindrical neck and rounded base. Shoulder absent, flexure discernible. Vesicle mainly laevigated but with scattered short spines 9–13 µm long, mainly in the margin and stout bifurcated processes in the chamber. The aperture is faintly detected in one of the specimens.

*Dimensions (2 specimens)*: Total length: 187–193.6 µm, maximum width: 77–79.7 µm, neck length: 62.7 µm, neck width: 38.7 µm, aperture: 41.5 µm, flexure angle: 167.6°. Processes: 6.9–19.1 µm long; 3.6 µm wide with rounded bases 1.8–2.8 µm diameter.

*Occurence*: Balapuca.

*Comparisons*: *Angochitina* sp. 1 resembles *A. filosa* Eisenack 1955 but the latter does not have processes. *Angochitina gurupiense* Grahn, Melo & Steemans, 2005 has a neck that widens into a collarette and hair like spines. *Angochitina devonica* Eisenack 1955 has further processes.

*Cyathochitina*? sp. 1

Plate V, 8

*Description*: Vesicle with a conical shape, cylindrical neck and rounded base. Flexure discernible.

*Dimensions (2 specimens)*: Overall length: 160–194 µm, chamber maximum width: 73–73.1 µm, margin: 94–102.7 µm, neck length: 28.2–40 µm, neck width: 39–45 µm, aperture: 51.9.1 µm.

*Occurence*: Angosto del Pescado, Balapuca.

*Remarks*: The specimen is assigned to the genus doubtfully due to dubious presence of the carina.

*Lagenochitina* sp. cf. *L. praeavelinoi* Grahn and de Melo, 2004.

Plate V, 9

*Dimensions (2 specimens)*: Total length: 167.3–178 µm, maximum width: 75–83.6 µm, neck length: 37.3–69 µm, neck width: 31.8–35.2 µm, aperture: 35.9–43.2 µm.

*Occurence*: Angosto del Pescado.

*Remarks*: The specimens encountered herein are smaller than the size range proposed for the species (204–360 µm) and the neck slightly widens towards the aperture.

*Sagenachitina* sp.

Plate V, 11

*Description*: Vesicle with a conical shape, cylindrical neck and rounded base. Flexure discernible. Basal margin bearing a perforated carina with lumina in between 3.5 and 4.8 µm diagonal length.

*Dimensions (one specimen)*: Overall length: 149 µm, chamber maximum width: 60.3 µm, neck length: 55.9 µm, neck width: 33.1 µm, aperture: 44.1 µm.

*Occurence*: Angosto del Pescado.

*Comparison*: *Sagenachitna* sp. A in Grahn (2005a) of the Amazonas Basin is considerably bigger (439 µm).

### *4.3. Age and correlation*

The inception and disappearance of several global and South American marker species allowed for a well-constrained age assignment.

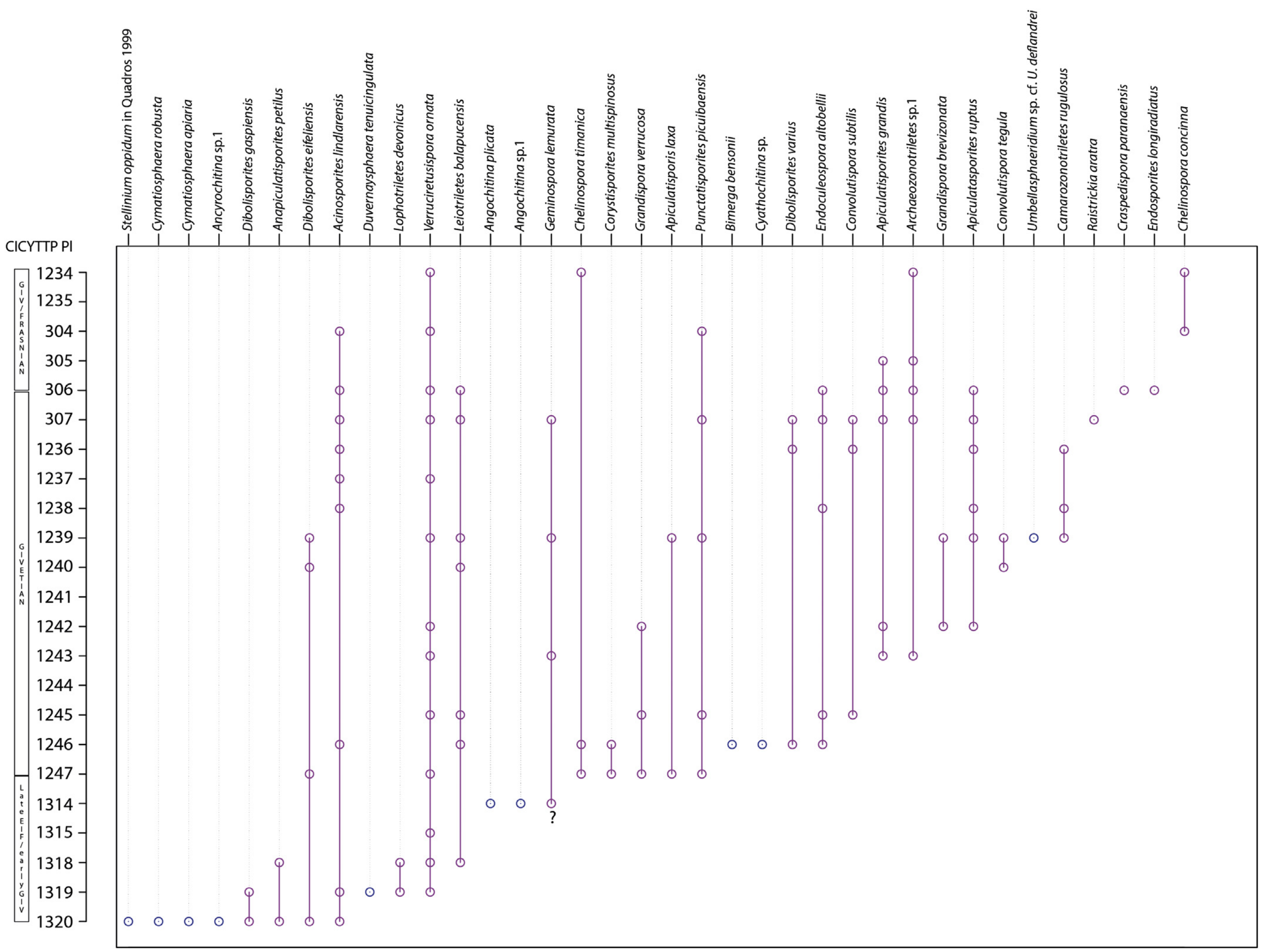


**Fig. 6.** Stratigraphic distribution of selected species in the Balapuca section. Question mark mean doubtful occurrence. Marine components (acritarchs, chitinozoans and prasinophytes) are coloured in blue, spores are portrayed in pink and chlorophytes in green.

#### 4.3.1. Angosto de San Ignacio

The assemblage recovered from this locality has a very high proportion of marine elements with the input of very few spores (5 species). From the latter *Cymbosporites catillus*, *Dibolisporites turriculatus* and *Retusotriletes simplex* are the only species that have been recorded before. *Cymbosporites catillus* is the only species that is rather more restricted in age than the other two. In southwestern Gondwana, the oldest record of *C. catillus* come from the association SA1 from Argentina, dated late Emsian–mid Eifelian (Noetinger and Di Pasquo, 2011). Also, this species first appears in the highest levels of the Lli and Trg interval zones of the Amazon Basin, of early Givetian age (Melo and Loboziak, 2003) continuing in younger strata. In northwestern Gondwana, in Turkey, *C. catillus* has been quoted as far back in time as the Silurian (Steemans et al., 1996) and it also defines, together with *Samarisporites triangulatus*, the homonymous assemblage zone of middle-upper Givetian age (Breuer and Steemans, 2013). Species from the phytoplankton such as *Cymatiosphaera apiaria*, described from Givetian-Frasnian levels in northwestern Argentina (Ottone, 1996), *C. turbinata* known from the Late Devonian of USA and Iran (Wicander and Loeblich, 1977, Ghavidel-Syooki, 1995) and the Givetian of Poland (Turnau and Racki, 1999) and *Gorgonisphaeridium furcillatum* from the Late Devonian of South America and Euramerica (e.g. Wicander and Playford, 1985; Vavrdová et al., 1996; Gonzalez et al., 2005, Marynowski et al., 2008, Di Pasquo et al., 2015) allow to bound a Givetian – Frasnian age range for the sample CICYTTP Pl 682.

#### 4.3.2. Angosto del Pescado

The presence of South American index species (Fig. 4) such as *Leiotriletes balapucensis*, *Grandispora delicata* known to range from the Eifelian (Di Pasquo et al., 2009; Noetinger, 2015) together with, *Acinosporites apiculatus*, *Dibolisporites eifeliensis*, *Grandispora permulta*, *Verrucosisporites scurrus* and, some species of *Geminospora*, suggest an Eifelian age for the lower part of the section (CICYTTP Pl 440–309). Microplankton species such as *Arkonites bilixus* and *Duvernaysphaera angelae* support such assignment (see appendix in Di Pasquo et al., 2009; Grahn et al., 2013 and references therein). The inception of *Geminospora lemurata* in the level CICYTTP Pl 309 (Fig. 3) marks the end of the Eifelian and beginning of the Givetian (see Loboziak and Streel, 1995). The disappearance of the chitinozoans *Ancyrochitina morzadeci* and *Spinachitina* aff. *S. biconstricta* denotes the top of the late early Givetian interval of the Trg Zone recognized in the Amazonas and Parnaíba basins (Melo and Loboziak, 2003; Grahn et al., 2006). Finally, the occurrence of *Chomotriletes bistchoensis* and *Michrystridium flexibile* in the level CICYTTP Pl 454 allow for the appraisal of a Frasnian age for the top of the section. Both species are known from the Frasnian of Euramerica and the former also from Australia and northwestern

**Table 1**
PMI values, from left to right the localities are organized in north–south direction. Samples are distributed in accordance with the age column on the left, but their separation within each locality are not proportional. Arrow represent the inception of *Geminospora lemurata* (late Eifelian – early Givetian) in both, Balapuca and Angosto del Pescado, localities.

| Age | Balapuca Samples | PMI | Angosto del Pescado Samples | PMI | Angosto de San Ignacio Samples | PMI | Arasayal Samples | PMI |
|---|---|---|---|---|---|---|---|---|
| Frasnian | | | CICYTTP-Pl 456 | 14 | | | | |
| | | | CICYTTP-Pl 455 | 7 | | | | |
| | | | CICYTTP-Pl 454 | 16 | | | CICYTTP-Pl 686 | 367 |
| la Givetian – ea Frasnian? | CICYTTP-Pl 1234 | 4 | | | CICYTTP-Pl 682 | 314 | CICYTTP-Pl 685 | 200 |
| | CICYTTP-Pl 1235 | 0 | | | | | CICYTTP-Pl 684 | 500 |
| | CICYTTP-Pl 304 | 0 | | | | | CICYTTP-Pl 683 | 217 |
| | CICYTTP-Pl 305 | 0 | | | | | | |
| Givetian | CICYTTP-Pl 306 | 6 | | | | | | |
| | CICYTTP-Pl 307 | 0 | | | | | | |
| | CICYTTP-Pl 1236 | 6 | | | | | | |
| | CICYTTP-Pl 1237 | 0 | | | | | | |
| | CICYTTP-Pl 1238 | 11 | | | | | | |
| | CICYTTP-Pl 1239 | 21 | | | | | | |
| | CICYTTP-Pl 1240 | 0 | | | | | | |
| | CICYTTP-Pl 1241 | 0 | CICYTTP-Pl 453 | 10 | | | | |
| | CICYTTP-Pl 1242 | 0 | CICYTTP-Pl 452 | 15 | | | | |
| | CICYTTP-Pl 1243 | 0 | CICYTTP-Pl 451 | 33 | | | | |
| | CICYTTP-Pl 1244 | 18 | CICYTTP-Pl 450 | 32 | | | | |
| | CICYTTP-Pl 1245 | 0 | CICYTTP-Pl 449 | 20 | | | | |
| | CICYTTP-Pl 1246 | 8 | CICYTTP-Pl 311 | 40 | | | | |
| | CICYTTP-Pl 1247 | 18 | CICYTTP-Pl 310 | 41 | | | | |
| Eifelian | CICYTTP-Pl 1314 | 50 | CICYTTP-Pl 309 | 50 ← | | | | |
| | CICYTTP-Pl 1315 | 30 | CICYTTP-Pl 308 | 92 | | | | |
| | CICYTTP-Pl 1318 | 63 | CICYTTP-Pl 448 | 47 | | | | |
| | CICYTTP-Pl 1319 | 54 | CICYTTP-Pl 446 | 44 | | | | |
| | CICYTTP-Pl 1320 | 76 | CICYTTP-Pl 445 | 160 | | | | |
| | | | CICYTTP-Pl 444 | 96 | | | | |
| | | | CICYTTP-Pl 443 | 70 | | | | |
| | | | CICYTTP-Pl 442 | 136 | | | | |
| | | | CICYTTP-Pl 441 | 100 | | | | |
| | | | CICYTTP-Pl 440 | 122 | | | | |

Gondwana (Wicander, 1974; Wicander and Playford, 1985; Ghavidel-Syooki, 1995).

*4.3.3. Arasayal*

The lower section is characterized by the presence of scarce but important Givetian species (Fig. 5) such as *Chomotriletes vedugensis* and *Cymatiosphaera apiaria*. *Dibolisporites bullatus* is recorded in the *Grandispora pseudoreticulata* Zone of Eifelian-?early Givetian age in southwestern Gondwana (Suárez Soruco and Lobo Boneta, 1983; Limachi et al., 1996), in northwestern Gondwana occurs in the *Latosporites ovalis-Dictyotriletes biornatus* Assemblage Zone Breuer and Steemans 2013 while in Euramerica is recorded earlier, in the Givetian-Frasnian boundary (Loboziak and Streel, 1980). The co-ocurrence of the species mentioned above place the samples (CICYTTP Pl 683–685) in the Givetian. The rest of the species in the assemblage are badly preserved elements left in open nomenclature and species with broad age ranges. The top of the section represented by level CICYTTP Pl 686 includes the occurrence of *Michrystridium flexibile* recognized in the Frasnian of Euramerica (see above).

*4.3.4. Balapuca*

*Dibolisporites eifeliensis, D. echinaceus, Acinosporites lindlarensis, Apiculiretusispora brandtii* and *A. plicata,* in between other species characterize the *Emphanisporites annulatus-Camarozonotriletes sextantii* Assemblage Zone of early and early late Emsian age in the Old Red Sandstones (Richardson and McGregor, 1986). In this case these species co-occur with other ones (Fig. 6) that have more modern inceptions worldwide such as *Leiotriletes balapucensis* (see above), *Chelinospora timanica* and *Geminospora lemurata,* which are included in the *Geminospora lemurata-Chelinospora* ex gr. *ligurata* Interval Zone (Lli) in the Amazonas Basin (see appendix in Di Pasquo et al., 2009). *Leiotriletes balapucensis* is also cited in the *Scylaspora rugulata-Grandispora libyensis* Assemblage Zone in northwestern Gondwana, *G. lemurata* appears further high (*Geminospora lemurata* Interval Zone). *Grandispora verrucosa* is known from the Eifelian of southwestern Gondwana (Menéndez and Pöthe de Baldis, 1967; Di Pasquo, 2007). All of the latter suggests a late Eifelian- early Givetian age for the lower part of the section (CICYTTP Pl 1320-1247, Fig. 3). The inception of *Endoculeospora altobellii*, known from the middle Givetian (Di Pasquo, 2007) allows to infer a Givetian *s.l.* age for the section comprised in between the samples CICYTTP Pl 1246- 307. A Givetian-Frasnian age for the uppermost of the section (CICYTTP Pl 306–1234, Fig. 3) is supported by the presence of *Craspedispora paranaensis* that ranges from the upper Eifelian to Givetian in southwestern Gondwana to Frasnian in northwestern Gondwana (Breuer and Steemans, 2013 and references therein), *Endosporites longiradiatus* quoted for the Givetian-Frasnian of Argentina, Bolivia and Paraguay (Menéndez and Pöthe de Baldis, 1967; Ottone, 1996; Di Pasquo, 2007; Di Pasquo et al., 2009), and *Chelinospora concinna,* which its first occurrence defines the *Ancyrospora langii-Chelinospora concinna* Assemblage Zone in northwestern Gondwana (Breuer and Steemans, 2013).

*4.4. Palynological marine index*

We calculated the Palynological Marine Index (PMI) in order to analyse the evolution of the depositional environments (Table 1). The progress of the index is better seen in the localities with more samples (i.e. Angosto del Pescado, Balapuca).From north to south, Balapuca seems to have been deposited in mostly a nearshore environment, whilst Angosto del Pescado, farther south and west, transition from a seaward environment, during the Eifelian, to nearshore in the Givetian- Frasnian (Table 1). As described above, both the Las Pavas

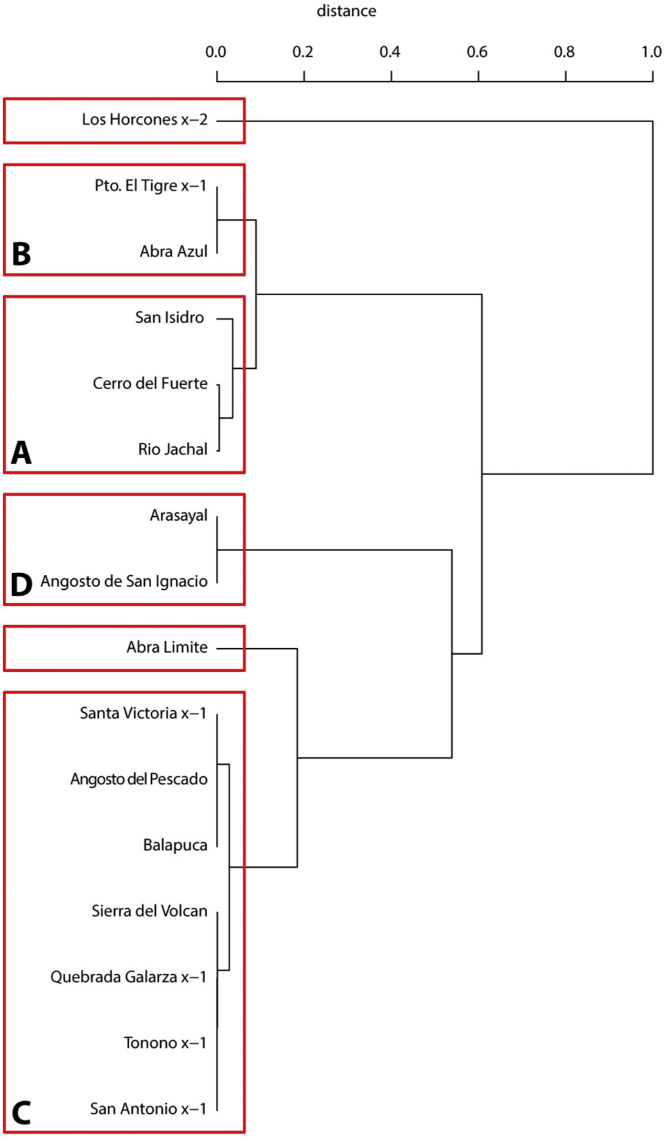


**Fig. 7.** Dendrogram plot derived from the Raup dissimilarity index using UPGMA algorithm. Group A comprises localities dated as Early Devonian, group B range from late Lochkovian to the Emsian and group C encloses localities assigned to the Middle–Upper Devonian. Group D also dated as Middle–Upper Devonian. References: Los Horcones x-2 Grahn and Gutierrez (2001), Puesto El Tigre x-1 (Volkheimer et al., 1986; Noetinger and di Pasquo, 2013), Abra Azul (Noetinger et al., 2016), San Isidro (Rubinstein and Steemans, 2007), Cerro del Fuerte (Le Hérissé et al., 1996), Río Jáchal (García Muro et al., 2014), Arasayal (this paper), Angosto de San Ignacio (this paper), Abra Límite (Noetinger and di Pasquo, 2010), Santa Victoria x-1 (Barreda, 1986; Noetinger, 2015), Angosto del Pescado (this paper), Balapuca (this paper), Sierra del Volcán (Amenábar et al., 2006, 2007), Quebrada Galarza (Ottone, 1996), Tonono x-1 (Noetinger, 2010) and San Antonio x-1 (Noetinger and di Pasquo, 2011).

and Aguararagüe supersequences, (Figs. 2, 3), are upward – coarsening sequences, a shelf that shallows. Coincidently, is in these deposits where the chitinozoans were more numerous (Fig. 3). Chitinozoans are known to occur from near-shore to deep oceanic environments. Paris (2006) also links the shallowing of the shelf with the increase of the abundance of this faunule. The latter seems to be the case in the localities studied here (Angosto del Pescado, Balapuca). The disappearance of some particular species (i.e. *Ancyrochitina morzadeci* and *Spinachitina* aff. *S. biconstricta*) could imply the turnover of this fauna, as stated in Grahn (2005b); poor preservation of the organic material due to the deposition of more coarser sediments or both facts combined. Unfortunately the regional Carboniferous erosion (Starck et al., 1993), prevents the recovery of Upper Devonian material. Towards the south and west, the localities Angosto de San Ignacio and Arasayal, even with their small number of samples, show a very different depositional environment, with PMI values in the order of hundreds (Table 1), implying an offshore depositional environment.

### *4.5. Hierarchical cluster analysis*

This method serves as data visualization better than a statistical analysis per se (Hammer and Harper, 2006) and its application, in this instance, was to explore the existence of any pattern of correlation between the localities and/ or basins, during a particular time range. Cluster analysis performed with the two different algorithms and indices (Fig. 7, S. Fig. 1) coincide roughly in the composition of the groups. The following analysis was based in the dendrogram reached with Raup dissimilarity index and UPMGA (Fig. 7) because it is the one that best reflects our observations. The differences between the dendrograms might be in the intrinsic characteristics of each algorithm and/ or index (i.e. Complete Linkage is biased towards producing clusters of equal diameter, and is also very sensitive to outliers - Milligan 1980, SAS Institute Inc. 1999).

Group A comprises most of the localities from Precordillera (San Isidro, Cerro del Fuerte, Río Jáchal) dated as Early Devonian. Group B includes two localities, one from the Chaco-Salteña plain (Puesto El Tigre x-1) and one from the Subandean (Abra Azul) that range from late Lochkovian to the Emsian. Group C encloses localities assigned to the Middle-Upper Devonian and group D is constituted by the localities Arasayal and Angosto de San Ignacio studied herein, which are also dated as Middle-Upper Devonian. The latter dissociation might be due to differential environmental conditions and richness of the samples. Cluster C has very rich localities while Arasayal and Angosto de San Ignacio are conformed by a lower proportion of species and a higher proportion of marine and brackish elements (Table 1). Los Horcones x-2 and Abra Límite, are isolated probably because the low count of species.

## 5. Discussion

Few biostratigraphical schemes have been attempted for the southwestern Gondwanan region (e.g. Suárez Soruco and Lobo Boneta, 1983; Limachi et al., 1996; Melo and Loboziak, 2003; Grahn, 2005b) as well for Euramerica and northwestern Gondwana (e.g. Richardson and McGregor, 1986; Streel et al., 1987; Breuer and Steemans, 2013) (Fig. 8). Some are more rigorous than others, including not only illustrations but systematic descriptions. The Argentinian palynological assemblages despite its poor preservation, present a considerable number of global recognized species (see appendix in Di Pasquo et al., 2009) that have served to characterize the stages within the different biozonations (e.g. Noetinger, 2010, 2015; Noetinger et al., 2016; Aráoz et al., 2016 and references therein); but on the other hand, there are several key species used to define those zones that are absent in northern Argentina. There is also a diachronism in the first and last occurrences and acme events of species, i.e. characteristic species from the Givetian *Geminospora lemurata-Rhabdosporites langii* Assemblage Zone (Breuer and Steemans, 2013) such as *Rhabdosporites langii*, *Geminospora lemurata*, *Corystisporites undulatus* and *Dibolisporites turriculatus* co-occur with known younger species in the top of the succession studied here. From the latter, *Chomotriletes bistchoensis*, known from the Upper Devonian of Euramerica (Staplin, 1961; Wicander and Playford, 1985) and northwestern Gondwana (Ghavidel-Syooki, 1995), also reworked in the Upper Carboniferous of the Tarija Basin (Di Pasquo, 2002), and *Michrystridium flexibile* from the Upper Devonian – Lower Mississippian of Euramerica (Wicander, 1974). There are, also, species with younger records that occur earlier in this assemblage. *Cymatiosphaera apiaria,* described from Givetian-Frasnian strata in the Tarija Basin (Ottone, 1996); *Estiastra culcita,* from the Upper Devonian of Euramerica

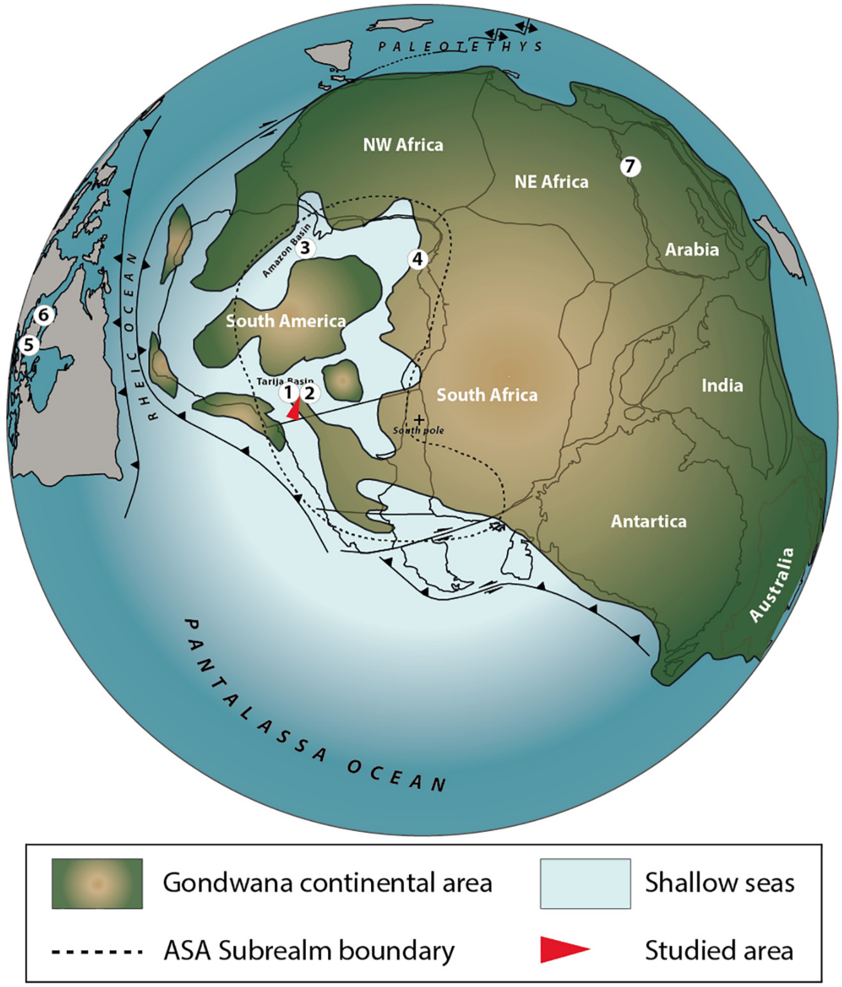


**Fig. 8.** Palaeogeographical map featuring the Gondwana continent during the Middle Devonian (after Uriz et al., 2016 and references therein) showing the locations where biostratigraphical schemes, cited in text, were proposed. Southwestern Gondwana. (1) Suárez Soruco and Lobo Boneta (1983). (2) Limachi et al. (1996). (3) Melo and Loboziak (2003). (4) Grahn (2005). Euramérica. (5) Richardson and McGregor (1986). (6) Streel et al. (1987). Northwestern Gondwana. (7) Breuer and Steemans (2013). Dashed line encircles the Afrosouthamerican Subrealm (ASA) (after di Pasquo et al., 2009, 2015).

(Wicander, 1974; Wicander and Playford, 2013), and *Pterospermella capitana* from the Upper Devonian of Euramerica (Wicander, 1974; Martin, 1984; Filipiak, 2005) and the Givetian – Frasnian of the Tarija Basin (Ottone, 1996; Noetinger, 2010). Furthermore, Kemp et al. (1977) suggest to use biozones cautiously for correlation, since the palynoassemblages may be affected by local climatic and palaeoecological factors. The geographical position of the continents (Fig. 8) may have also affected the stratigraphical distribution or time of inception of the species in this region and finally, the interaction of all the latter circumstances. The groups conformed by hierarchical clustering recognized two well-differentiated periods of time for Argentina, Early and Middle-Late Devonian (Fig. 7). Nonetheless, a correlation between the different basins of Argentina was rather inconclusive (e.g. Sierra del Volcán – western Argentina – is grouped with northern localities). Several endemic palynological species closely distributed, both terrestrial and marine (e.g. *Acinosporites ledundae*, *Grandispora cristata*, *G. delicata*, *G. pseudoreticulata, Lagenochitina praeavelinoi, Spinachitina* aff. *S. biconstricta*) support the singularity of the regional conditions, which altogether conformed the Afrosouthamerican Subrealm (ASA) (Fig. 8, Di Pasquo et al., 2009, 2015). All of the latter reflects the necessity for a local biostratigraphical proposal, which with the addition of more localities would be a plausible goal to achieve. The palynoassemblage studied in this paper provides an invaluable source of reference to improve former strata correlation in the Tarija and neighbouring basins.

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## Appendix

Complete list of species, in major groups and alphabetical order, from the studied sections with illustration reference if applicable and the occurrence in the corresponding sections. Species marked with asterisks are first records in Argentina.

### *Acritarchs*

*Ammonidium loriferum* (Deunff) Hashemi and Playford, 1998 – *Ammonidium garrasinoi* Ottone, 1996 (morphon) Di Pasquo et al. 2017 (Plate I, 1) Occurrence: Angosto de San Ignacio; Angosto del Pescado.

*Ammonidium* spp. Occurrence: Angosto de San Ignacio, Arasayal, Balapuca.

*Baltisphaeridium juliae* Cramer, 1964 (Plate I, 2). Occurrence: Angosto del Pescado.

*Bimerga bensonii* Wood 1995. Occurrence: Balapuca.

*Chomotriletes bistchoensis* Staplin, 1961 (Plate I, 3). Occurrence: Angosto del Pescado.

*Chomotriletes vedugensis* Naumova, 1953 (Plate I, 4). Occurrence: Angosto del Pescado, Arasayal.

*Crassiangulina* sp. 1 (Plate I, 5). Occurrence: Angosto del Pescado.

*Diexallophasis remota* (Deunff) Playford, 1977. Occurrence: Angosto de San Ignacio, Angosto del Pescado, Balapuca.

*Diexallophasis simplex* Wicander and Wood, 1981. Occurrence: Angosto de San Ignacio, Angosto del Pescado.

*Diexallophasis* spp. Occurrence: Arasayal.

*Elektoriskos* sp. 1 (Plate I, 6). Occurrence: Angosto del Pescado.

*Estiastra culcita* Wicander, 1974. Occurrence: Arasayal.

*Estiastra* sp. cf. *E. culcita* Wicander, 1974 (Plate I, 7). Occurrence: Angosto del Pescado.

*Estiastra* sp. cf. *E. rhytidoa* Wicander and Wood, 1981 (Plate I, 8). Occurrence: Angosto del Pescado.

*Estiastra* spp. Occurrence: Angosto de San Ignacio.

*Eupoikilofusa* spp. Occurrence: Arasayal.

*Evittia* sp. cf. *E. sommeri* Brito 1967 (Plate I, 9). Occurrence: Angosto del Pescado.

*Exochoderma arca* Wicander and Wood, 1981. Occurrence: Angosto de San Ignacio, Angosto del Pescado, Balapuca.

*Exochoderma irregulare* Wicander, 1974. Occurrence: Balapuca.

*Exochoderma triangulata* Wicander and Wood, 1981. Occurrence: Angosto del Pescado, Balapuca.

*Gorgonisphaeridium discissum* Playford in Playford and Dring, 1981. Occurrence: Angosto de San Ignacio, Angosto del Pescado, Arasayal.

*Gorgonisphaeridium furcillatum* Wicander and Playford, 1985 (Plate I, 10). Occurrence: Angosto de San Ignacio.

*Gorgonisphaeridium impexus* sp. nov. (Plate I, 11–13). Occurrence: Angosto de San Ignacio.

*Gorgonisphaeridium* sp. cf. *G. absitum* Wicander, 1974 (Plate I, 14). Occurrence: Angosto de San Ignacio.

*Gorgonisphaeridium* sp. 1 (Plate I, 15) Occurrence: Angosto del Pescado.

*Gorgonisphaeridium* sp. 2 (Plate I, 16) Occurrence: Angosto del Pescado, Arasayal.

*Hemiruptia legaultii* Ottone, 1996. Occurrence: Angosto del Pescado.

*Leiosphaeridia* spp. Occurrence: Balapuca.

*Maranhites mosesii* (Sommer) Brito emend. González, 2009. Occurrence: Angosto del Pescado.

*Michrystridium flexibile* Wicander, 1974 (Plate I, 17). Occurrence: Angosto del Pescado, Arasayal.

*Multiplicisphaeridium ramusculosum* Deflandre emend. Lister, 1970. Occurrence: Angosto de San Ignacio, Angosto del Pescado, Balapuca.

*Multiplicisphaeridium* spp. Occurrence: Angosto del Pescado.

*Navifusa bacilla* (Deunff) Playford, 1977. Occurrence: Angosto del Pescado, Balapuca.

*Neoveryhachium* spp. Occurrence: Arasayal.

*Ozotobrachion furcillatus* (Deunff) Playford, 1977 (Plate I, 18). Occurrence: Angosto del Pescado.

*Palacanthus ledanoisii* Deunff emend. Playford, 1977. Occurrence: Angosto del Pescado.

*Polygonium barredae* Ottone, 1996. Occurrence: Angosto del Pescado.

*Polygonium* spp. Occurrence: Angosto del Pescado.

*Pseudolunulidia laevigata* Brito and Quadros, 1985. Occurrence: Angosto del Pescado.

Sp. B in Noetinger and Di Pasquo, 2011 (Plate I, 19). Occurrence: Angosto del Pescado, Arasayal.

*Stellinium micropolygonale* (Stockmans and Willière) Playford, 1977. Occurrence: Angosto del Pescado.

*Stellinium oppidum* (Deunff) Le Hérissé and Deunff, 1988 in Quadros 1999 (Plate I, 20). Occurrence: Balapuca.

*Stellinium* spp. Occurrence: Angosto del Pescado.

*Triangulina alargada* Cramer, 1964. Occurrence: Angosto de San Ignacio, Angosto del Pescado, Balapuca.

*Tunisphaeridium caudatum* Deunff and Evitt, 1968. Occurrence: Angosto del Pescado.

*Tunisphaeridium tentaculaferum* (Martin) Cramer, 1971. Occurrence: Angosto del Pescado.

*Tunisphaeridium* spp. Occurrence: Angosto del Pescado, Balapuca.

*Umbellasphaeridium* sp. cf. *U. deflandrei (*Moreau-Benoît) Jardiné et al., 1972(Plate II, 1) Occurrence: Balapuca.

*Veryhachium downiei* Stockmans and Williére, 1962. Occurrence: Balapuca.

*Veryhachium europaeum* Stockmans and Williére, 1960 (Plate II, 2). Occurrence: Angosto de San Ignacio.

*Veryhachium lairdii* Group Servais, Vecoli, Li, Molyneux, Raevskaya and Rubinstein, 2007. Occurrence: Angosto del Pescado.

*Veryhachium pastoris* Deunff, 1966 (Plate II, 3). Occurrence: Angosto de San Ignacio, Angosto del Pescado, Arasayal, Balapuca.

*Veryhachium polyaster* Staplin, 1961. Occurrence: Angosto del Pescado, Balapuca.

*Veryhachium trispinosum* Group Servais, Vecoli, Li, Molyneux, Raevskaya and Rubinstein, 2007. Occurrence: Angosto de San Ignacio, Angosto del Pescado, Arasayal, Balapuca.

### Chlorophycean algae

*Arkonites bilixus* Legault, 1973. Occurrence: Angosto del Pescado.

*Cymatiosphaera apiaria* Ottone, 1996. Occurrence: Angosto de San Ignacio, Angosto del Pescado, Arasayal, Balapuca.

*Cymatiosphaera perimembrana* Staplin, 1961. Occurrence: Angosto de San Ignacio.

*Cymatiosphaera robusta* sp. nov. (Plate II, 5–6). Occurrence: Angosto del Pescado, Arasayal, Balapuca.

*Cymatiosphaera turbinata* Wicander and Loeblich, 1977 (Plate II, 7). Occurrence: Angosto de San Ignacio.

*Cymatiosphaera* spp. Occurrence: Arasayal, Balapuca.

*Deflandrastrum? sp. 1* (Plate II, 4) *Occurrence: Angosto del Pescado.*

*Dictyotidium variatum* Playford, 1977. Occurrence: Balapuca.

*Dictyotidium* spp. Occurrence: Angosto de San Ignacio.

*Duvernaysphaera angelae* Deunff, 1964. Occurrence: Angosto del Pescado, Balapuca.

*Duvernaysphaera radiata* Brito, 1967 (Plate II, 8). Occurrence: Arasayal, Angosto de San Ignacio.

*Duvernaysphaera tenuicingulata* Staplin, 1961. Occurrence: Angosto del Pescado, Balapuca.

*Duvernaysphaera* spp. Occurrence: Balapuca.

*Quadrisporites granulatus* (Cramer) Cramer and Diez, 1972. Occurrence: Angosto del Pescado, Balapuca.

*Quadrisporites horridus* Hennelly ex Potonié and Lele, 1961. Occurrence: Balapuca.

*Quadrisporites* spp. Occurrence: Angosto del Pescado.

*Quadrisporites variabilis* (Cramer) Ottone and Rosello, 1996. Occurrence: Angosto del Pescado, Balapuca.

*Leiosphaeridia* spp. Occurrence: Angosto de San Ignacio, Angosto del Pescado, Arasayal, Balapuca.

*Muraticavea munificus* Wicander and Wood, 1981. Occurrence: Angosto del Pescado.

*Polyedryxium ambitum* Wicander and Wood, 1981. Occurrence: Angosto del Pescado.

*Polyedryxium evolutum* Deunff, 1955. Occurrence: Arasayal.

*Polyedryxium fragosulum* Playford, 1977, Occurrence: Angosto del Pescado.

*Polyedryxium* pharaonis (Deunff) Deunff, 1961. Occurrence: Angosto del Pescado, Balapuca.

*Polyedryxium* spp. Occurrence: Angosto del Pescado, Balapuca.

*Pterospermella capitana* Wicander, 1974. Occurrence: Angosto del Pescado.

*Pterospermella pernambucensis* (Brito) Eisenack, Cramer and Diez Rodriguez, 1973. Occurrence: Angosto del Pescado.

*Pterospermella simplex* sp. nov. (Plate II, 9–10). Occurrence: Angosto de San Ignacio, Angosto del Pescado, Arasayal.

*Pterospermella* sp. 1 (Plate II, 11). Occurrence: Angosto del Pescado.

*Pterospermella* spp. Occurrence: Balapuca.

*Tasmanites* spp. Occurrence: Angosto del Pescado.

## Cryptospores

*Artemopyra recticosta* Breuer et al., 2007. Occurrence: Angosto del Pescado.

*Cymbohilates rubinsteinae* Noetinger et al., 2016(Plate II, 13). Occurrence: Angosto de San Ignacio, Arasayal.

*Cymbohilates* sp. 1 (Plate II, 12). Occurrence: Angosto del Pescado.

*Cymbohilates* sp. 2 (Plate II, 14) Occurrence: Angosto del Pescado.

*Dyadospora murusattenuata* morphon Strother and Traverse sensu Steemans Le Hérissé and Bozdogan, 1996. Occurrence: Angosto del Pescado.

*Gneudaspora divellomedia* (Tchibrikova) Balme, 1988. Occurrence: Angosto del Pescado.

**Rimosotetras problematica* Burgess, 1991 (Plate II, 15). Occurrence: Angosto del Pescado.

*Tetrahedraletes medinensis* Ströther and Traverse, 1979. Occurrence: Balapuca.

## Spores

*Acinosporites acanthomammillatus* Richardson, 1965. Occurrence: Angosto del Pescado, Balapuca.

*Acinosporites apiculatus* (Streel) Streel, 1967. Occurrence: Angosto del Pescado, Balapuca.

*Acinosporites hirsutus* McGregor and Camfield, 1982. Occurrence: Angosto del Pescado.

*Acinosporites ledundae* Ottone, 1996. Occurrence: Angosto del Pescado.

*Acinosporites lindlarensis* Riegel, 1968. Occurrence: Angosto del Pescado, Balapuca.

*Acinosporites macrospinosus* Richardson, 1965. Occurrence: Angosto del Pescado, Balapuca.

*Acinosporites* spp. Occurrence: Arasayal.

*Ambitisporites avitus* Hoffmeister, 1959. Occurrence: Angosto del Pescado, Balapuca.

**Anapiculatisporites petilus* Richardson emend. McGregor and Camfield, 1982 (Plate II, 16). Occurrence: Angosto del Pescado, Balapuca.

*Apiculatasporites microconus* (Richardson) McGregor and Camfield, 1982. Occurrence: Balapuca.

*Apiculatasporites ruptus* sp. nov. (Plate II, 17–18). Occurrence: Angosto del Pescado, Balapuca, Angosto de San Ignacio.

*Apiculatisporites grandis* Menéndez and Pöthe de Baldis, 1967. Occurrence: Balapuca.

*Apiculiretusispora brandtii* Streel, 1964. Occurrence: Angosto del Pescado, Balapuca.

*Apiculiretusispora densiconata* Tiwari and Schaarschmidt, 1975. Occurrence: Balapuca.

*Apiculiretusispora laxa* Amenábar, di Pasquo, Carrizo and Azcuy, 2006. Occurrence: Balapuca.

*Apiculiretusispora plicata* (Allen) Streel, 1967. Occurrence: Angosto del Pescado, Balapuca.

*Archaeozonotriletes chulus* (Cramer) Richardson and Lister, 1969. Occurrence: Angosto del Pescado, Balapuca.

*Archaeozonotriletes* sp. 1 (Plate II, 19). Occurrence: Angosto de San Ignacio, Angosto del Pescado, Balapuca.

*Archaeozonotriletes* spp. Occurrence: Balapuca.

*Aulicosporites* spp. Occurrence: Balapuca.

*Auroraspora minuta* Richardson, 1965. Occurrence: Angosto del Pescado.

*Biharisporites parviornatus* Richardson, 1965. Occurrence: Angosto del Pescado, Balapuca.

*Biornatispora* sp. cf. *B. dubia* (McGregor) Steemans, 1989 (Plate III, 1). Occurrence: Angosto del Pescado.

*Camarozonotriletes*? *concavus* Loboziak and Streel, 1989. Occurrence: Angosto del Pescado, Balapuca.

**Camarozonotriletes rugulosus* Breuer, Al-Ghazi, Al-Ruwaili, Higgs, Steemans and Wellman, 2007 (Plate III, 2). Occurrence: Balapuca.

**Chelinospora concinna* Allen, 1965 (Plate III, 3). Occurrence: Balapuca.

**Chelinospora ligurata* Allen, 1965 (Plate III, 4). Occurrence: Balapuca.

*Chelinospora timanica* (Naumova) Loboziak and Streel, 1989. Occurrence: Balapuca.

*Chelinospora* spp. Occurrence: Angosto de San Ignacio, Balapuca.

*Convolutispora subtilis* Owens, 1971. Occurrence: Angosto del Pescado, Balapuca.

**Convolutispora tegula* Allen, 1965 (Plate III, 5). Occurrence: Balapuca.

*Convolutispora* spp. Occurrence: Balapuca.

*Corystisporites multispinosus* Richardson, 1965. Occurrence: Angosto del Pescado, Balapuca.

**Corystisporites* sp. cf. *Acanthotriletes horridus* in McGregor and Camfield, 1982 (Plate III, 6). Occurrence: Balapuca.

*Corystisporites undulatus* Turnau, 1996. Occurrence: Angosto del Pescado.

**Craspedispora paranaensis* Loboziak, Streel and Burjack, 1988 (Plate III, 7). Occurrence: Balapuca.

*Craspedispora* spp. Occurrence: Balapuca.

*Cymbosporites catillus* Allen, 1965. Occurrence: Angosto de San Ignacio, Angosto del Pescado, Balapuca.

**Cymbosporites variegatus* Breuer and Steemans, 2013 (Plate III, 8). Occurrence: Angosto del Pescado.

*Cymbosporites* spp. Occurrence: Balapuca.

*Densosporites devonicus* Richardson, 1960. Occurrence: Angosto del Pescado.

*Densosporites* spp. Occurrence: Balapuca.

*Dibolisporites bullatus* (Allen) Riegel, 1973. Occurrence: Angosto del Pescado, Arasayal.

*Dibolisporites echinaceus* (Eisenack) Richardson, 1965. Occurrence: Angosto del Pescado, Balapuca.

*Dibolisporites eifeliensis* (Lanninger) McGregor, 1973. Occurrence: Angosto del Pescado, Balapuca.

*Dibolisporites farraginis* McGregor and Camfield, 1982. Occurrence: Angosto del Pescado, Balapuca.

*Dibolisporites gaspiensis* (McGregor) Breuer and Steemans, 2013. Occurrence: Angosto del Pescado, Balapuca.

*Dibolisporites quebecensis* McGregor, 1973. Occurrence: Angosto del Pescado, Balapuca.

*Dibolisporites* sp. cf. *D. uncatus* (Naumova) McGregor and Camfield, 1982 (Plate III, 9). Occurrence: Angosto del Pescado.

*Dibolisporites* sp. 1 (Plate III, 10). Occurrence: Angosto del Pescado.

**Dibolisporites* sp. 1 in Breuer and Steemans, 2013 (Plate III, 11). Occurrence: Angosto del Pescado.

**Dibolisporites tuberculatus* Breuer and Steemans, 2013 (Plate III, 12). Occurrence: Angosto del Pescado.

**Dibolisporites turriculatus* Balme, 1988 (Plate III, 13). Occurrence: Angosto de San Ignacio, Angosto del Pescado.

*Dibolisporites uncatus* (Naumova) McGregor and Camfield, 1982. Occurrence: Angosto del Pescado, Balapuca.

*Dibolisporites varius* Tiwari and Schaardschmidt, 1975. Occurrence: Balapuca.

*Dibolisporites* spp. Occurrence: Angosto del Pescado, Balapuca.

*Emphanisporites annulatus* McGregor, 1961. Occurrence: Angosto del Pescado, Balapuca.

*Emphanisporites epicautus* Richardson and Lister, 1969. Occurrence: Angosto del Pescado, Balapuca.

**Emphanisporites robustus* McGregor, 1961 (Plate III, 14). Occurrence: Angosto del Pescado.

*Emphanisporites rotatus* McGregor emend. McGregor, 1973. Occurrence: Angosto del Pescado, Balapuca.

*Emphanisporites* spp. Occurrence: Arasayal.

*Emphanisporites spinaeformis* Schultz, 1968. Occurrence: Angosto del Pescado.

**Endoculeospora altobellii* di Pasquo, 2007 [(Plate III, 15) Occurrence: Balapuca.

**Endosporites longiradiatus* Menéndez and Pöthe de Baldis, 1967 (Plate III, 16) Occurrence: Balapuca.

**Geminospora antaxios* (Chibrikova) Owens, 1971 (Plate III, 17). Occurrence: Angosto del Pescado.

*Geminospora lemurata* (Balme) emend. Playford, 1983. Occurrence: Angosto del Pescado, Balapuca.

*Geminospora punctata* Owens 1971. Occurrence: Angosto del Pescado.

*Geminospora* sp. in Noetinger, 2015. Occurrence: Angosto del Pescado.

*Geminospora* sp. 1 (Plate III, 18) Occurrence: Angosto del Pescado.

*Geminospora svalbardiae* (Vigran) Allen, 1965. Occurrence: Angosto del Pescado.

*Grandispora brevizonata* (Menéndez and Pöthe de Baldis) di Pasquo, 2005. Occurrence: Angosto del Pescado, Balapuca.

*Grandispora cristata* (Menéndez and Pöthe de Baldis) Noetinger, 2015. Occurrence: Angosto del Pescado.

*Grandispora delicata* Noetinger, 2015. Occurrence: Angosto del Pescado.

*Grandispora douglastownensis* Loboziak, Streel and Burjack,1989. Occurrence: Angosto del Pescado.

*Grandispora inculta* Allen, 1965. Occurrence: Angosto del Pescado, Balapuca.

*Grandispora mammillata* Owens, 1971. Occurrence: Balapuca.

**Grandispora megaformis* (Richardson) McGregor, 1973 (Plate III, 19). Occurrence: Balapuca.

*Grandispora permulta* (Daemon) Loboziak, Streel and Melo, 1999. Occurrence: Angosto del Pescado.

*Grandispora protea* (Naumova) Moreau-Benoît, 1980. Occurrence: Angosto del Pescado, Balapuca.

*Grandispora pseudoreticulata* (Menéndez and Pöthe de Baldis) Ottone, 1996. Occurrence: Angosto del Pescado, Balapuca.

*Grandispora velata* (Richardson) McGregor, 1973. Occurrence: Balapuca.

*Grandispora* spp. Occurrence: Balapuca.

*Granulatisporites muninensis* Allen, 1965. Occurrence: Balapuca.

**Granulatisporites concavus* Breuer and Steemans, 2013 (Plate III, 20). Occurrence: Angosto del Pescado.

*Leiotriletes balapucencis* di Pasquo, 2007. Occurrence: Angosto del Pescado, Balapuca.

*Leiotriletes pagius* Allen, 1965. Occurrence: Angosto del Pescado, Balapuca.

*Leiotriletes* spp. Occurrence: Angosto del Pescado, Arasayal.

*Lophotriletes devonicus* (Naumova ex Chivrikova) McGregor and Camfield, 1982. Occurrence: Angosto del Pescado, Balapuca.

**Perotrilites heterocorpus* Steemans 1989 in Steemans, 1995 (Plate IV, 1). Occurrence: Angosto del Pescado.

**Punctatisporites picuibaensis* Menéndez and Pöthe de Baldis, 1967 (Plate IV, 2). Occurrence: Balapuca.

*Punctatisporites* spp. Occurrence: Angosto del Pescado.

*Retusotriletes albarinii* di Pasquo and Noetinger, 2008. Occurrence: Angosto del Pescado.

*Retusotriletes maculatus* McGregor and Camfield, 1976. Occurrence: Angosto del Pescado.

*Retusotriletes ottonei* Noetinger and di Pasquo, 2011. Occurrence: Angosto del Pescado, Balapuca.

*Retusotriletes paraguayensis* Menéndez and Pöthe de Baldis, 1967. Occurrence: Angosto del Pescado, Balapuca.

*Retusotriletes simplex* Naumova, 1953. Occurrence: Angosto de San Ignacio, Angosto del Pescado.

*Retusotriletes* spp. Occurrence: Angosto de San Ignacio, Angosto del Pescado, Balapuca.

*Rhabdosporites langii* (Eisenack) Richardson, 1960. Occurrence: Angosto del Pescado.

**Samarisporites angulatus* (Tiwari and Schaarschmidt) Loboziak and Streel, 1989 (Plate IV, 3). Occurrence: Angosto del Pescado.

**Samarisporites praetervisus* (Naumova) Allen, 1965 (Plate IV, 4). Occurrence: Balapuca.

*Samarisporites* spp. Occurrence: Angosto del Pescado, Balapuca.

*Verruciretusispora dubia* (Eisenack) Richardson and Rasul, 1978. Occurrence: Angosto del Pescado.

*Verruciretusispora ornata* (Menéndez and Pöthe de Baldis) Pérez Leyton *ex* di Pasquo, 2005. Occurrence: Angosto del Pescado, Balapuca.

*Verruciretusispora* sp. 1 (Plate IV, 5) Occurrence: Angosto del Pescado.

**Verrucosisporites onustus* Breuer and Steemans, 2013 (Plate IV, 6). Occurrence: Angosto del Pescado.

*Verrucosisporites scurrus* (Naumova) McGregor and Camfield, 1982. Occurrence: Angosto del Pescado, Balapuca.

**Verrucosisporites* sp. 1 in Breuer and Steemans, 2013 (Plate IV, 7) Occurrence: Angosto del Pescado.

*Verrucosisporites* spp. Occurrence: Angosto del Pescado.

*Verrucosisporites tumulentus* Clayton and Graham, 1974 (Plate IV, 8). Occurrence: Angosto del Pescado.

### *Chitinozoans*

**Ancyrochitina morzadeci* Paris, 1981 (Plate V, 1–2). Occurrence: Angosto del Pescado.

*Ancyrochitina* spp. Occurrence: Angosto del Pescado, Balapuca.

*Ancyrochitina* sp. 1 (Plate V, 3). Occurrence: Angosto del Pescado, Balapuca.

*Angochitina plicata* sp. nov. (Plate V, 4–6). Occurrence: Angosto del Pescado, Balapuca.

*Angochitina* sp. 1 (Plate V, 7). Occurrence: Balapuca.

*Cyathochitina*? sp. 1 (Plate V, 8). Occurrence: Angosto del Pescado, Balapuca.

*Fungochitina* spp. Occurrence: Angosto del Pescado, Balapuca.

**Lagenochitina* sp. cf. *L. praeavelinoi* Grahn and Melo, 2004 (Plate V, 9). Occurrence: Angosto del Pescado.

**Ramochitina autasmirimense* Grahn and Melo, 2004 (Plate V, 10). Occurrence: Angosto del Pescado.

*Ramochitina* spp. Occurrence: Angosto del Pescado.

*Sagenachitina* sp. 1 (Plate V, 11). Occurrence: Angosto del Pescado.

**Spinachitina* aff. *S. biconstricta* (Lange) Grahn and Melo, 2005 (Plate V, 12). Occurrence: Angosto del Pescado.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2018.07.009.

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