

Spore diversity trends in the Middle Devonian of the Chaco-Salteño Plain, northwestern Argentina



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ABSTRACT

Devonian deposits in northwestern Argentina were historically studied with stratigraphical purposes, since these layers conform the source rocks of the producing basins of the region. A fairly well preserved palynomorph assemblage, from the Tonono Formation, provides an opportunity to perform the first quantitative analysis to study the evolution of diversity in the succession. Two associations are here defined by both, stratigraphic distribution of species and cluster analysis, ranging from the lower Eifelian to the lower Givetian. Rarefaction analysis reveals the existence of a relatively rich miospore population. Species richness increases while there is a drop in diversity and evenness towards the top of the column. The increment of the marine components towards the latter section indicates shifts in the shoreline. The influx of warmer water into higher latitudes, as highlighted by the arrival of the brachiopod *Tropidoleptus*, could have favored the inception of new spore species in the settled community. These results add to evidence that some groups build up the number of species in disturbed settings, and evenness is reduced with each new species introduced.

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1. Introduction

The Devonian Period, is one of the most important for the history of plants. It was during this interval when plants, having conquered the terrestrial environment, underwent a major radiation from seemingly insignificant monospecific communities to the development of nearly all major divisions of vascular plants. A long-term sea-level rise began in the Middle Devonian (Ronov, 1994; Haq and Schutter, 2008), resulting in the best known source rocks from the producing basins of Bolivia and northwestern Argentina (Illich et al., 1981).

During the Silurian–Devonian, the Tarija Basin reached the northwest of Argentina, defining the southernmost margin of a greater sedimentary area, whose substantial development was in the center and South of Bolivia and the northwest of Paraguay. In northwestern Argentina, Devonian deposits crop out in the eastern part of the Eastern Cordillera, and extend in the subsurface of both the Sierras Subandinas and the Chaco-Salteño Plain (Starck et al., 1993). Paleontological records suggest interconnections between neighboring basins like the Arizaro, in the North of Chile and the Argentinean Puna, the Madre de Dios, in northern Bolivia and southern Peru, and additional basins of the West of Brazil (Fig. 1.A).

For several years, the Tarija basin was geophysically surveyed for oil exploration. This program included palynological studies, mainly

unpublished, from which several palynostratigraphic schemes were defined. These proposals consist of lists of species with a few or non-illustrated specimens included by zone (e.g., Suárez Soruco and Lobo Boneta, 1983; Suárez Soruco, 1989; Limachi et al., 1996).

There are numerous published palynological systematic works, especially in northwestern Argentina e.g. Ottone (1996), Antonelli and Ottone (2006), Noetinger, (2010), Noetinger and di Pasquo (2010, 2011, 2013). Some of these focus on particular groups, such as chitinozoans (Volkheimer et al., 1983, 1986; Grahn and Gutiérrez, 2001; Grahn, 2003) or acritarchs (Barreda, 1986). From the latter, a few contain very well preserved palynomorphs of continental origin that are worth being studied. The combination of information from both marine and terrestrial microfossil assemblages could draw a better picture of the paleoenvironment and refine previous stratigraphical propositions (Albariño et al., 2002; Alvarez et al., 2003).

This study presents the first quantitative diversity analysis of a palynological assemblage from the Tonono Formation (Noetinger, 2010), recovered from the Santa Victoria x-1 well in northwestern Argentina (Fig. 1.B). The stratigraphical distribution of palynomorph species is analyzed and compared with their global ranges for age determination. To describe the spore community several multivariate statistical analyses are performed. Diversity is estimated by abundance distribution, rarefaction and diversity and evenness indices; while the similarity among samples is tested by cluster analysis. The diversification patterns are correlated to previous determined paleoenvironmental events (e.g. Isaacson and Sablock, 1990; Fernández-Seveso et al., 1999; di Pasquo et al., 2009).

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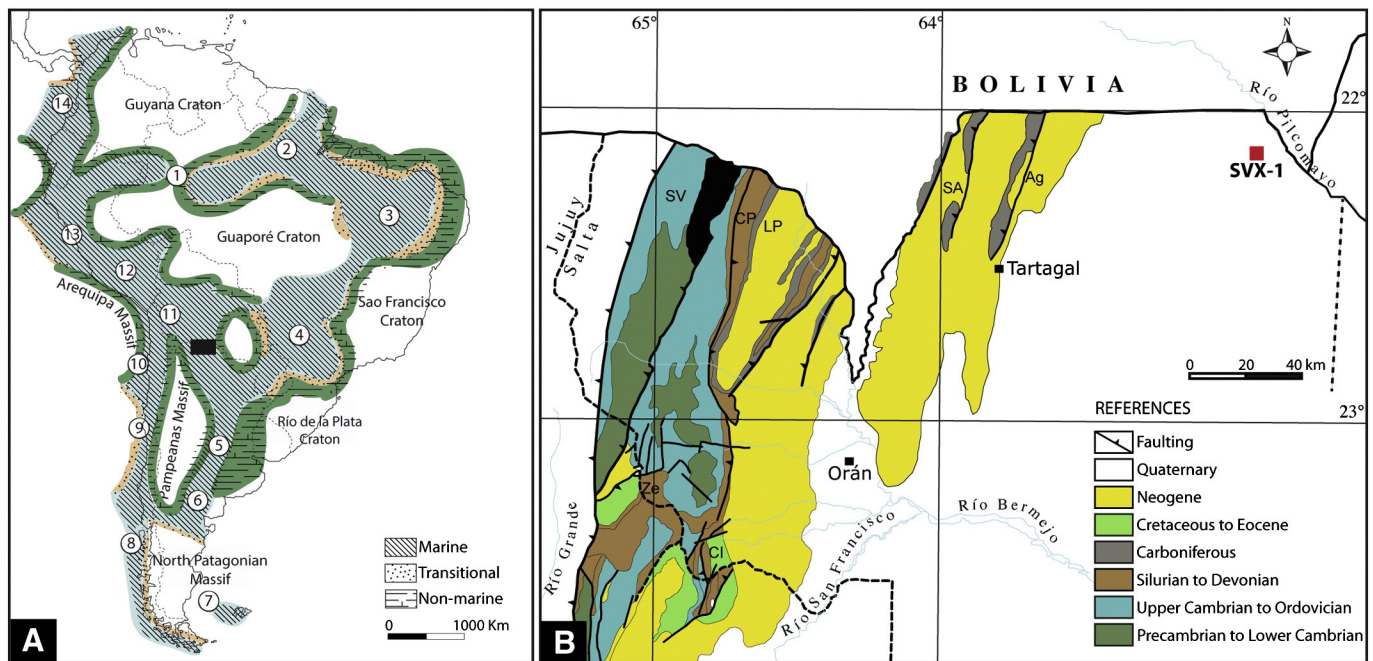


Fig. 1. (A) South America, paleogeographical reconstruction, after Di Pasquo et al. (2009). Rectangle points out the studied area. Basins: 1. Solimões; 2. Amazon; 3. Parnaíba; 4. Paraná; 5. Chaco-Paraná; 6. Sierras Australes; 7. Malvinas (Falklands) Islands; 8. South Patagonian; 9. Cuyana or Precordillerana; 10. Arizaro; 11. Tarija; 12. Madre de Dios; 13. Acre; 14. Llanos Orientales. (B) Location map of the studied area and setting of the studied well (SVX-1). Ranges: Santa Victoria (SV), Zenta (Ze), Cinco Picachos (CP), Las Pavas (LP), Calilegua (Cl), San Antonio (SA) and Aguara Güe (Ag).

2. Material and methods

The Santa Victoria x-1 borehole (ca. S 22° 10', W 62° 50') is located next to the town of Santa Victoria, Salta Province, in the eastern portion of the Chaco-Salteño Plain (Fig. 1.A). Barreda (1986) analyzed the paleomicroplankton content of 24 cuttings between the interval of 1860–2300 meters below ground surface (mbgs), in comparison to this palynological study comprised of 37 cutting samples selected from the 1840–2881 mbgs interval (Fig. 2).

Standard palynological methods (Playford, 1977) were performed, to obtain organic residues from the samples. The residues were sieved through 25 and 107 µm meshes and then mounted on standard microscope slides with glycerine jelly. The identification and illustration of palynomorphs was undertaken at the Laboratory of Paleopalynology (Paleontology Section, Museo de Ciencias Naturales “Bernardino Rivadavia”) using both transmitted light and scanning electron microscopes. Some of the measurements were carried out through the software “AnalyzingDigitalImages v. 11”. The position of illustrated specimens in the respective slides quoted with the BA Pal ex CIRGEO acronym (Repository), are based on England–Finder coordinates. The thermal alteration index (TAI) of the organic material was stipulated following Utting et al. (1989) in Utting and Wielens (1992).

The relative percentage of different groups of palynomorphs, such as miospores, acritarchs (including prasinophytes and chlorophytes) and chitinozoans, was calculated. Between 166 and 326 miospore specimens were counted, one slide per level to keep a constant sample effort, to determine the relative abundance of the species. Statistical analyses, using R version 3.0.1 (R development Core Team, 2013), was carried out to identify and support differences in the composition of the assemblage within the studied section.

To standardize the counting of morphospecies in a given sample (see Jaramillo, 2008 and references therein), rarefaction analysis was performed. Additional measures such as similarity and diversity, were also calculated, using the packages vegan 2.0-8 (Oksanen, 2013). Diversity indices provide more information than richness index since

measure both, the number of species and their relative abundance (Margalef, 1968; Washington, 1984).

The abundance matrix was transformed as in Jaramillo (2008), by taking the square root of each value to minimize the effect of over abundant species. Two similarity indices were calculated, Morisita, for counts, and Horn for frequencies. These indices were used since they are not influenced by species richness nor sample size (Magurran, 2004; Mullins et al., 2004). Hierarchical Cluster analysis was conducted by the R base package testing three different algorithms (UPMGA, Complete Linkage and Ward's) and package pvclust 1.2-2 which includes clusters with *p*-values (Ward's algorithm and Euclidean distance measures). The package rioja 0.8-5 (Juggins, 2012) was used to perform a constrained cluster analysis (CONISS algorithm, Horn dissimilarity index). The arrays were tested with different abundance distribution models. Ranking species from the most abundant to the least, provides another useful way to visualize community data.

3. Results

3.1. Composition, age and correlation

The analyzed association comprises a variety of miospores, acritarchs, chlorophycean algae and chitinozoans. The general preservation of the group of miospores recovered, varies from excellent (TAI 2) to moderate (TAI 3). The assemblage is composed of 75 spore and cryptospore species, some of which are left in open nomenclature. The stratigraphic distribution and global ranges of several key species, support the definition of two assemblages and their associated ages (Fig. 2). Since all the studied samples are from ditch cuttings, the first down-hole occurrence (FDO) was used to define the associations, in order to minimize the effect introduced by caving.

3.1.1. SV1 association (1840–2361 mbgs)

A late Eifelian–early Givetian age is likely for this section. *Biharisporites parviornatus* is recognized as a ?late Eifelian–mid-late Givetian taxon in South America (Di Pasquo, 2007). Other global key

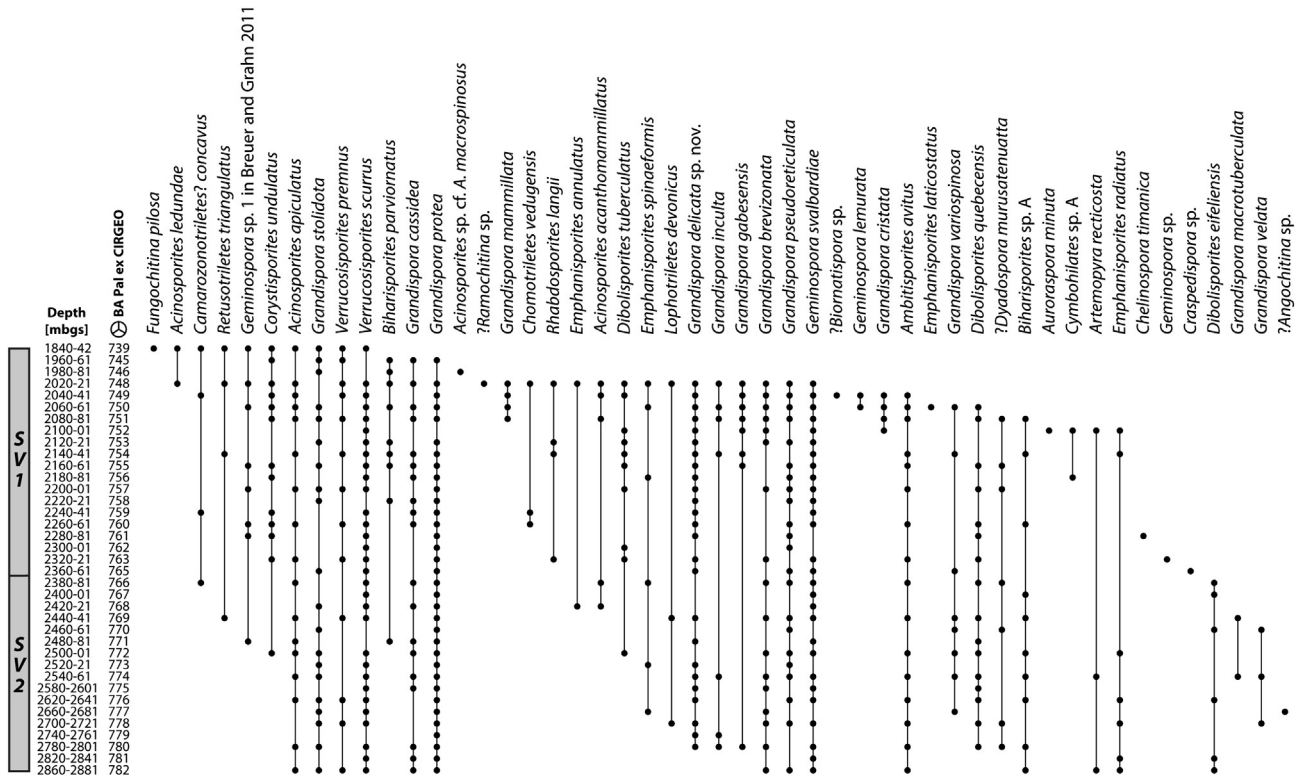


Fig. 2. Stratigraphic distribution of selected species (in last occurrence order) in the analyzed section and the attributed assemblages (SV1, SV2).

species that have their inception in the late Eifelian, include *Grandispora mammillata*, *Chelinospora timanica* and *Geminospira lemurata*. The latter is an important cosmopolitan marker for the late Eifelian–early Givetian, agreeing with the base of the *ensensis obliquimarginatus* conodont zone *sensu* Weddige (1984; see Loboziak and Stree, 1995). These taxa co-occur with *Acinosporites ledundae* which is Givetian in age in southwestern Gondwana (Ottone, 1996; Di Pasquo, 2007; Noetinger, 2010; Noetinger and di Pasquo, 2011) and *Ambitisporites avitus* whose last appearance is in the Eifelian (Breuer, 2007). *Dibolisporites quebecensis* is also known for its last appearance in the early Givetian (Di Pasquo, 2007; Noetinger and di Pasquo, 2011).

Other species in the SV1 assemblage are *Grandispora permulta*, *Emphanisporites annulatus*, *Dibolisporites farraginis*, among others (Fig. 2). Melo and Loboziak (2003) defined the *Grandispora permulta* Interval Zone (*Per*) based on the first occurrence bio-horizon (FOB) of homonymous species, from the Eifelian of north and southwestern Gondwana (Fig. 3), with some other concurring taxa with SV1, such as *Camarozonotriletes? concavus* and *Verrucosporites premmus*. Some species in the association, including *Geminospira lemurata*, *Chelinospora timanica*, *Grandispora mammillata* and *Verrucosporites scurrus* also occur in the succeeding *Lli* Zone (lower Givetian; Melo and Loboziak, 2003). Suárez Soruco et al. in Limachi et al. (1996) established the *Grandispora pseudoreticulata* Zone for Bolivia, of Eifelian age (Fig. 3), based on a series of long-ranging miospores, some of which are also present in this assemblage (e.g. *Dibolisporites bullatus*, *D. echinaceus*, *Grandispora brevizonata*, *G. pseudoreticulata*, *Grandispora* cf. *inculta*). Breuer and Steemans (2013) defined the *Scylaspora rugulata*–*Grandispora libyensis* Assemblage Zone in northwestern Gondwana (Fig. 3), covering the upper Eifelian–lowermost Givetian. Its lower boundary is defined by the lowest occurrence of the species *Camarozonotriletes concavus*, *Chelinospora timanica*, *Grandispora stolidota* and *Verrucosporites premmus*. The latter are also present in SV1, among others. Both assemblages share the main component, *Verrucosporites scurrus* morphon.

In Euramerica, the *Per* Interval Zone is equivalent to the upper part of the *Calyptosporites velatus*–*Rhabdosporites langii* (Fig. 3) and the entire,

middle Eifelian to lower Givetian, *Densosporites devonicus*–*Grandispora naumovii* Assemblage Zone (Richardson and McGregor, 1986). Within the latter there are several species that are present in the SV1 as well e.g. *Grandispora inculta*, *G. mammillata*, *Lophotriletes devonicus*, *Verrucosporites premmus* and *V. scurrus*.

3.1.2. SV2 association (2380–2881 mbgs)

This association is characterized by the FDO of *Dibolisporites eifeliensis*, whose youngest record is in the early Eifelian (Moreau-Benoît, 1989; Al-Ghazi, 2007; Filipiak, 2011). *Geminospira svalbardiae*, *Acinosporites acanthomammillatus*, *Grandispora cassidea*, *G. gabesensis* and *G. velata*, species characteristic of the lower Eifelian, *Geminospira svalbardiae*–*Samarisporites eximius* Assemblage Zone (Fig. 3; Breuer and Steemans, 2013), are also present. Additionally there are *Acinosporites apiculatus*, *Grandispora douglstownensis* and *G. protea*. The latter, first appear in the GS Zone (upper Emsian to the lower Eifelian), and are known to range to the succeeding *Per* and *Lli* zones in Brazil (Fig. 3; Melo and Loboziak, 2003).

3.2. Paleoenvironmental considerations

The palynofacies, particularly the deepest two thirds of the section appear to be homogeneous, with minor variations in the component abundance (Fig. 4). Both marine and continental elements define a marginal marine depositional setting, with presumably minor shoreline shifts.

The shallowest third of the section is characterized by a gradual increment of the marine components, which end up dominating the assemblage at the top of the column. This is in agreement with the model which represents a transgressive and high stand systems tracts of a second order eustatic cycle, as suggested by Fernández-Seveso et al. (1999) for the Middle and Upper Devonian of Bolivia and northwestern Argentina. A coeval maximum flooding surface was also recognized in the neighboring Paraná and Parnaíba basins (Breuer and Grahn, 2011). In Bolivia, Troth et al. (2011) proposed the *Evittia sommerii*

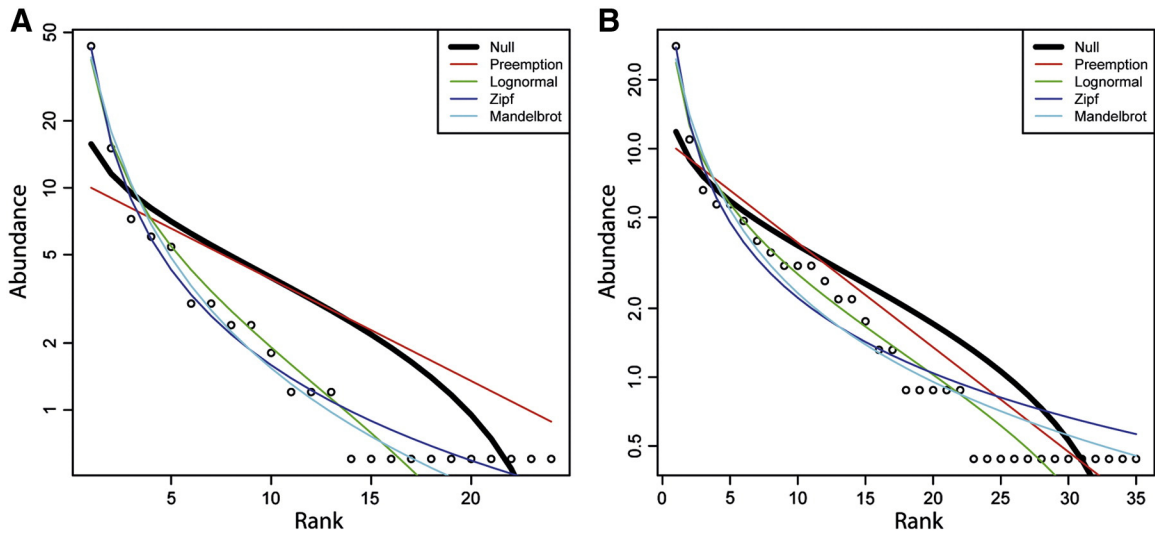


Fig. 6. Species abundance distribution compared to five abundance models. (a) Cluster A has a better fit into Zipf (AIC: 76.4538) and (b) cluster B into Log normal distribution (AIC: 121.951).

This slope fits into a Zipf distribution (AIC: 76,4538) while Cluster B shows a closest fit into a Log normal distribution (AIC: 121,951). However the Zipf (AIC: 122,234) and the Mandelbrot (AIC: 123,774), cannot be discounted. The flatter slope of this graph is an evidence of a more even community.

The rarefaction values (Fig. 7) show a gradual increase of spore species richness towards the top of the well, in coincidence with the continuous rise of the phytoplankton abundance (Fig. 4). Both the Simpson and Shannon–Wiener diversity indices, and the Pielou and Hurlburt's evenness measures (Fig. 8) show a decline in the biodiversity towards the top of the studied section, which also includes the samples assembled in cluster A (Fig. 5).

4. Discussion

The palynomorph association recovered from the Santa Victoria x-1 well, suggests an age span from the early Eifelian to the early Givetian, for the studied interval. Previous studies based on paleomicroplankton (Barreda, 1986) proposed a younger age, such as Givetian–Frasnian for the section. Most of the marine elements encountered by Barreda and later acknowledged by this study have long stratigraphic ranges. Although some of the species were suggested to be exclusively from the Upper Devonian in her work, such as *Cymatiosphaera labyrinthica* and *C. velicarina*, these taxa have scarce occurrences and cannot provide a

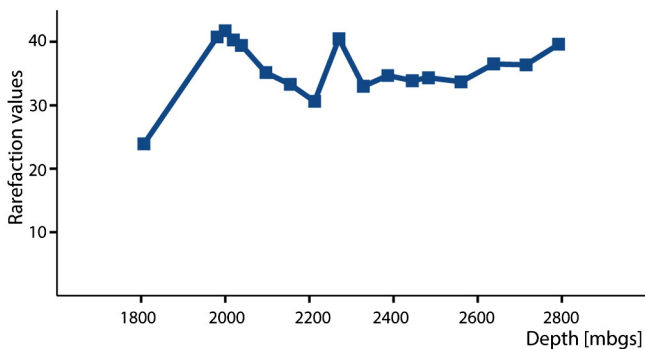


Fig. 7. Species richness standardized through rarefaction. It is noticeable the increment along the younger samples and the drop in the top of the section, in coincidence with the change of the rate of the continental and marine palynomorphs.

reliable biochron. The latter have been quoted also from the Silurian Espejos Formation in Argentina (Rubinstein and García Muro, 2011). Another species in the Santa Victoria x-1 well is *Crassianguina tessellata*, a species known to occur in the Strunian, the Silurian (Le Hérisse et al., 2001), and was recently found in sediments assigned to the Hirnantian (Ghavidel-syooki et al., 2011). Finally, *Umbellaspheeridium deflandrei*, which occurs from the Emsian (see Noetinger and di Pasquo, 2011 and references therein) and *Lunulidia micropunctata*, found in stressed environments from the Paraná Basin after the latest Emsian (Bosetti et al., 2010).

The previous records of coeval Eifelian–Givetian assemblages, from northwestern Argentina (Noetinger, 2010; Noetinger and di Pasquo, 2011) are dominated by continental elements and do not show an increment of the phytoplankton until the late Givetian–early Frasnian. It consequently appears that eastern and western occurrences are diachronous throughout northwestern Argentina due to a transgression coming from the East. This transgression corresponds to the Taghnic onlap of North America (Johnson, 1970), representing a second order transgression as part of the Kaskaskia sequence. It also reflects the tectonic Gamma cycle of Soares et al. (1978). The latter, together with the Delta cycle, comprise the most complete stratigraphic record in Brazil. The marine transgression is represented in both the Parnaíba and Paraná basins by the Pimenteira (Soares et al., 1978) and the shales of the top of the São Domingos formations, respectively (Grahm et al., 2013). Therefore, marine systems reach the western localities (e.g. Noetinger, 2010; Noetinger and di Pasquo, 2010, 2011) later than the eastern ones (see Breuer and Grahm, 2011 and references therein), which have a longer record of marine deposition in the Emsian–Eifelian time frame. These conditions provide a scenario of a stressed environment, during the late Eifelian–early Givetian, that would have led to the change in flora composition. Besides the conventional wisdom that species-rich communities evolved over long periods of physical stability (Fischer, 1960), there is evidence that some groups build up the number of species in disturbed settings (see Abele and Walters, 1979 and references therein). It has been hypothesized that richness fundamentally regulates the variation in the evenness and diversity statistics, where the three should be positively correlated (Hill, 1973). Whether richness or evenness has a larger influence on diversity may relate to the structure and controls that occur in the community. Wilsey and Stirling, (2007) showed a negative correlation between richness and evenness in plant populations. They state that “in situations where communities are regulated by dispersal and migration, evenness should be reduced with each new species detected as long as it remains rare” (Wilsey and Stirling, 2007, p. 260).

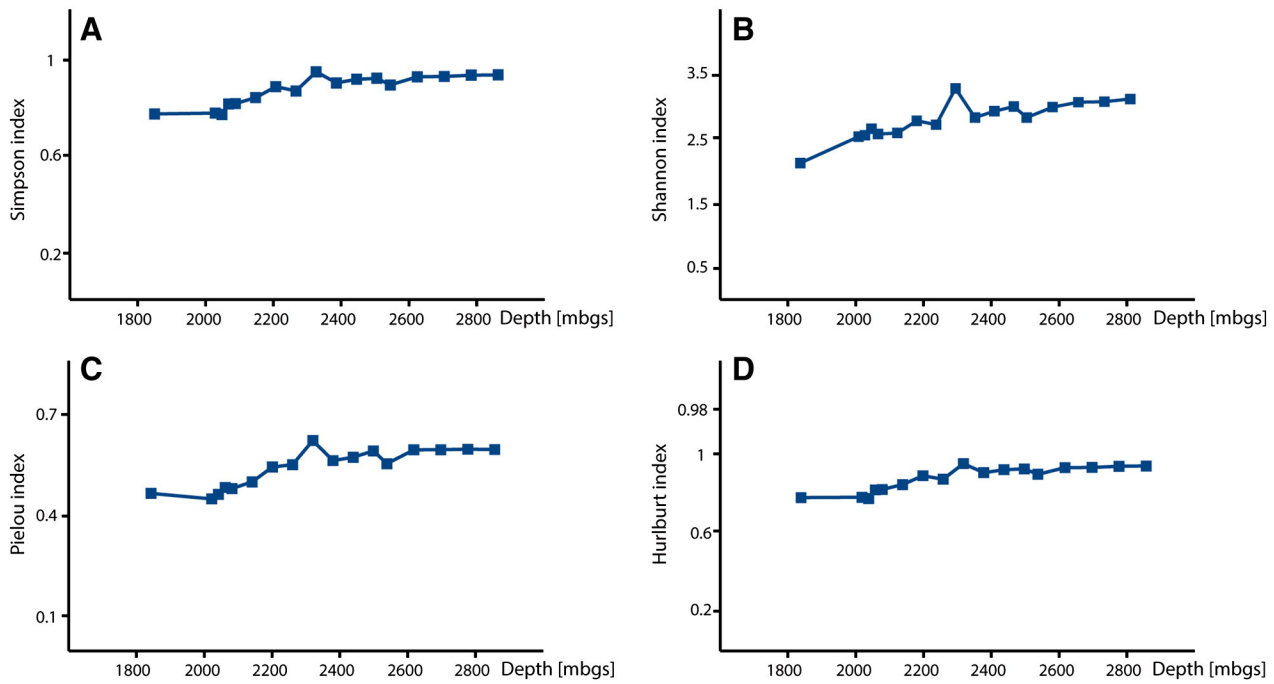


Fig. 8. Diversity and evenness curves. (A) Simpson, (B) Shannon, (C) Pielou, (D) Hurlburt. These measures display a clear tendency to decrease after sample BA Pal ex CIRGEO 754 up to the top of the studied section. The samples involved are also grouped in cluster A.

The rank abundance curves fit into two dominance/diversity models based on statistical theory. Whether or not there is sufficient or consistent information regarding the ecological interpretation of these models (see Barangé and Campos, 1991 and references therein) they explain structures in diverse biological communities (e.g. Pearson, 1975; Magurran, 2004; Spatharis and Tsirtsis, 2013). Some authors assume that undisturbed, equilibrated communities would fit into a Log Normal distribution. This pattern illustrates the result of many environmental factors and cohabitants acting simultaneously on the species whereas the Zipf–Mandelbrot model can be seen as many factors acting sequentially (Bastow, 1991). In the latter, the presence of species are dependent on previous physical conditions and previous species presences. The theory behind the Zipf–Mandelbrot’s model predicts a “reduction in the number of alternatives supported by the environment” (Barangé and Campos, 1991, p. 296). Pioneer species require few prior conditions while late successional species need a more organized ecosystem before they can invade, so they will be rare (Frontier, 1985). Pearson (1975), analyzing the development of a soft-bottom benthic community recorded a reduction in the diversity of the system after a change in the environment. The community was colonized by more opportunistic, less demanding species.

Cluster A contains the FOD of species such as *Acinosporites ledundae*, *Auroraspora minuta*, *Convolutispora subtilis*, *Emphanisporites laticostatus*, *Geminospora lemurata*, *Grandispora mammillata*, *G. cristata*, *G. gabesensis* and *Granulatisporites muninensis* (Fig. 2). Upon the distribution analysis of these new species (Fig. 9), the peak around 2040 mbgs (BA Pl ex CIRGEO 749) coincides with a rise in abundance of the phytoplankton and drop of the relative percentage of the total spores (Fig. 4). Within the time frame, there is evidence, in neighboring basins, of the collapse of the Malvinokaffric shelly fauna (Isaacson, 2007; Bosetti et al., 2010). One cause that has been historically hypothesized, is the influx of warmer water during the Middle Devonian as testified by the inception of the extra-Malvinokaffric articulate brachiopod *Tropidoleptus* (Isaacson, 2007; Di Pasquo et al., 2009; Troth et al., 2011). These new conditions could have resulted in the environmental scenario that would have allowed the establishment of new immigrant species, such as the

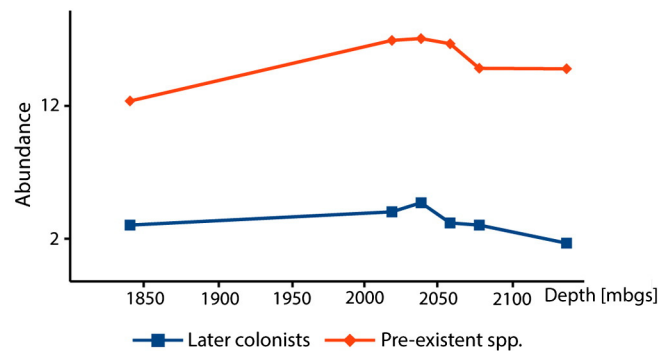


Fig. 9. Abundance (absolute counts squared root transformed) distribution of pioneer species and pre-existent species between 1840–2141 mbgs (cluster A samples).

globally known *Geminospora lemurata*, with recognized affinity with archaeopteridalean progymnosperms, in the existing flora.

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Appendix A

A.1. Systematic paleontology

The recognized taxa are listed alphabetically within each group. Species that merit particular comment or are in open nomenclature are described below. Species marked with an asterisk are first records in Argentina.

Chitinozoans

?*Angochitina* sp.

Fig. 10.1

Description. Vesicle with ovoid shape, cylindrical neck and aperture slightly flaring towards the apertural pole. The vesicle surface is darkened but there are structures near the apex and by the aperture that resemble the base of broken processes.

Dimensions. Total length: 178 μm , maximum width: 94 μm , neck length: 39 μm , aperture: 45 μm . 1 specimen measured.

?*Ramochitina* sp.

Fig. 10.2

Description. Vesicle with a cylindrical-conical shape, cylindrical neck and rounded base. Shoulder absent, flexure slightly discernible. Vesicle surface covered with simple spines that range from 4–14 μm long.

Dimensions. Total length: 134 μm , maximum width: 73 μm , neck length: 32 μm , aperture: 38 μm . 1 specimen measured.

Remarks. The specimen is assigned doubtfully to the genus *Ramochitina* since its diagnostics crests (Paris et al., 1999) are not observable. It resembles *Belonechitina holfeltzii* Ottone but the latter has distally branched spines projections and are remarkably bigger.

Fungochitina pilosa Collinson and Scott 1958 (Fig. 10.3)

Chlorophytes

Chomotriletes vedugensis Naumova 1953 (Fig. 10.4)

Cryptosporites

**Artemopyra recticosta* Breuer, Al-Ghazi, Al-Ruwaili, Higgs, Steemans and Wellman 2007 (Fig. 10.5)

Cymbohilates sp. A

Fig. 10.6

Description. Monad hilated proximally. Circular amb, the curvaturae define an hilum which is laevigated. Wall sculptured sub equatorial and distally homogeneously with strong acuminate spines 2–4 μm high and 1–1.6 μm wide at the base.

Dimensions. 64–78 μm . 2 specimens measured.

Remarks. *Cymbohilates comptulus* Breuer et al. is smaller and has bacula, coni and spinae. The few elements encountered prevent a formal designation.

?*Dyadospora murusattenuata* Morphon Strother and Traverse *sensu* Steemans Le Hérisse and Bozdogan 1996 (Fig. 10.7)

Remarks: The specimens studied herein are assigned apprehensively to the morphon since *Gneudnaspora divellomedia* var. *minor* are the detached components of *Dyadospora murusdensa*–*murusattenuata* Morphon, which can also be encountered as loosely attached dyads (Steemans et al., 2012). This study considers both genera taking in consideration that along the section there are numerous specimens of both *Gneudnaspora* spp. and these dyads.

Gneudnaspora divellomedia (Tchibrkova) Balme 1988

Spores

Acinosporites acanthomammillatus Richardson 1965 (Fig. 10.8)

Acinosporites apiculatus (Streel) Streel 1967

Acinosporites ledundae Ottone, 1996 (Fig. 10.9)

Acinosporites lindlarensis Riegel 1968

Acinosporites lindlarensis Riegel var. *minor* McGregor and Camfield 1976

Acinosporites macrospinosus Richardson 1965

Acinosporites mcgregorii Di Pasquo and Noetinger 2008

Acinosporites sp. cf. *A. macrospinosus* Richardson 1965 (Fig. 10.10)

Remarks. It is not observable the apical prominence of the trilete mark. *Ambitisporites avitus* (Hoffmeister) Steemans, Le Hérisse and Bozdogan 1996 (Fig. 10.11)

Apiculiretusispora densiconata Tiwari and Schaarschmidt 1975

Apiculiretusispora plicata (Allen) Streel 1967

**Auroraspora minuta* Richardson 1965 (Fig. 10.12)

Biharisporites parviornatus Richardson 1965 (Fig. 10.13)

Biharisporites sp. A

Fig. 10.14

Description. Megaspore, amb circular to oval presenting compressional folds. Laesura accompanied by labra 10 μm wide. Curvaturae not easily recognizable, contact areas smooth to slightly scabrated. Equatorial and distal face ornamented with grana and coni 2–4 μm wide at base and 3–4 μm high.

Dimensions. 69–166 μm . 9 specimens measured.

Remarks. *Biharisporites* sp. A resembles *Biharisporites simplex* Mortimer and Chaloner, but these specimens are remarkably smaller and the trilete mark is accompanied by lips.

?*Biornatispora* sp.

Fig. 10.15

Description. Trilete spore, sub circular amb. Distal and equatorial exospore ornamented with coni with rounded and pointed apices, 4.4 μm wide at base and 3–4.3 μm high. The elements are interconnected by ridges 1–1.3 μm high.

Dimensions. 50 μm . 1 specimen measured.

**Camarozonotriletes? concavus* Loboziak and Streel, 1989 (Fig. 11.1)

**Chelinospora timanica* (Naumova) Loboziak and Streel, 1989 (Fig. 11.2)

Convolutispora subtilis Owens 1971

Corystisporites multispinosus Richardson var. *spinulosus* McGregor and Camfield 1982

**Corystisporites undulatus* Turnau 1996 (Fig. 11.3)

Craspedispora sp.

Fig. 11.4

Description. Trilete spore, sub circular amb. Laesurae straight accompanied by lips 4 μm wide. Exospore infra granulated, which extends into a zona 3–5 μm wide covered by 1–2 μm of height spines. Curvatural folds present.

Dimensions. 59 μm . 1 specimen measured.

Remarks. The specimen resembles *Craspedispora crapeda* Allen but the latter is smaller and the zona is laevigated to infra granulated. *Craspedispora ghadamesensis* Loboziak and Streel is bigger.

Cymbosporites catillus Allen 1965

Cymbosporites cyathus Allen 1965

Dibolisporites echinaceus (Eisenack) Richardson 1965

Dibolisporites eifeliensis (Lanninger) McGregor 1973 (Fig. 11.5)

Dibolisporites farraginis McGregor and Camfield 1982

Dibolisporites gaspiensis (McGregor) Breuer and Steemans, 2013

Dibolisporites quebecensis McGregor 1973 (Fig. 11.6)

**Dibolisporites tuberculatus* Breuer and Steemans, 2013 (Fig. 11.7)

Dibolisporites uncatus (Naumova) McGregor and Camfield 1982

Emphanisporites annulatus McGregor 1961 (Fig. 11.8)

Emphanisporites epicautus Richardson and Lister 1969

**Emphanisporites laticostatus* Breuer and Steemans, 2013 (Fig. 11.9)

**Emphanisporites radiatus* Schultz 1968 (Fig. 11.10)

Emphanisporites rotatus McGregor 1973

**Emphanisporites spinaeformis* Schultz 1968 (Fig. 11.11)

Geminispora lemurata Playford 1983 (Fig. 11.12)

**Geminispora punctata* Owens 1971 (Fig. 11.13)

Geminispora sp. (Fig. 11.14)

Description. Camerate spore with subcircular amb. Laesurae straight that reach the equator. Exospore 2 μm thick presenting folds. Proximo-equatorial and distal regions bearing biform elements 1.5–3 μm wide at base and 1.5–2.5 μm high. Some of the elements are surmounted by hair like process. Contact faces with scattered subcircular verrucae up to 3 μm wide at base.

Dimensions. 62 μm . 1 specimen measured.

Remarks. The specimen resembles *Geminispora libyensis* Moreau-Benoît but the sculpture elements are not as dense as in the latter. *G. svalbardiae* has coni, spina and bacula.

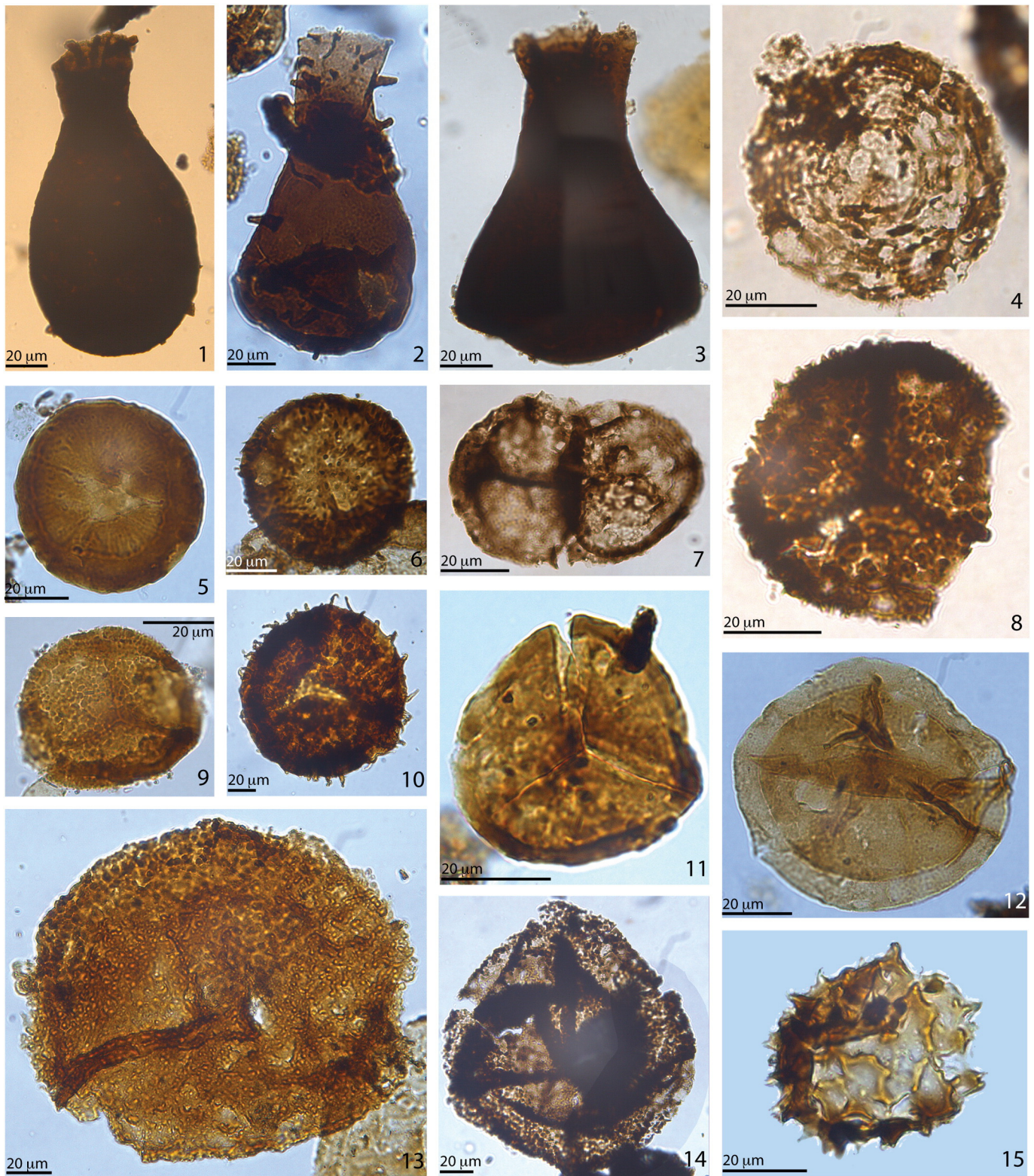


Fig. 10. Selected taxa from the studied borehole. For each illustration, sample and England Finder coordinates are specified. 1. *?Angochitina* sp., BA Pal ex CIRGEO 777, S29; 2. *?Ramochitina* sp., BA Pal ex CIRGEO 748, O35; 3. *Fungochitina pilosa*, BA Pal ex CIRGEO 739, D37/2; 4. *Chomotriletes vedugensis*, BA Pal ex CIRGEO 760, U30/3; 5. *Artemopyra recticosta*, BA Pal ex CIRGEO 752, V37/4; 6. *Cymbohilates* sp. A, BA Pal ex CIRGEO 752, H40; 7. *?Dyadospora murusatenuata*, BA Pal ex CIRGEO 766, F52/4; 8. *Acinosporites acanthomammillatus*, BA Pal ex CIRGEO 766, D41/2; 9. *Acinosporites ledundae*, BA Pal ex CIRGEO 739, R45/3; 10. *Acinosporites* sp. cf. *A. macrospinosus*, BA Pal ex CIRGEO 746, R35/1; 11. *Ambitisporites avitus*, BA Pal ex CIRGEO 749, G48; 12. *Auroraspora minuta*, BA Pal ex CIRGEO 752, U51/3; 13. *Biharisporites parviornatus*, BA Pal ex CIRGEO 745, U39/3; 14. *Biharisporites* sp. A, BA Pal ex CIRGEO 782, N36/4; 15. *?Biomnatispora* sp., BA Pal ex CIRGEO 749, 56/3.

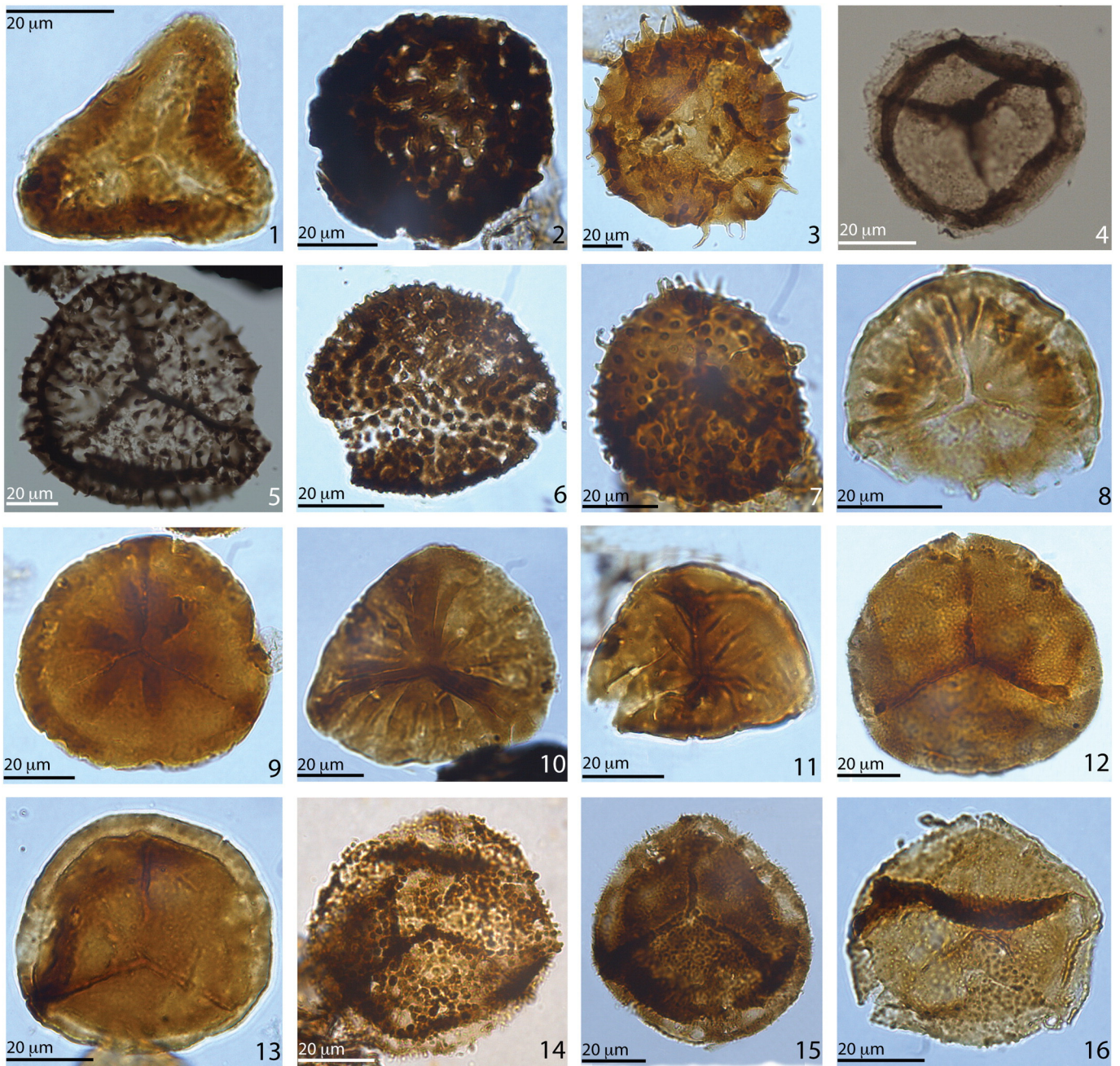


Fig. 11. Selected taxa from the studied borehole. For each illustration, sample and England Finder coordinates are specified. 1. *Camarozonotrites? concavus*, BA Pal ex CIRGEO 749, U30/3; 2. *Chelinospora timanica*, BA Pal ex CIRGEO 761, E50/2; 3. *Corystisporites undulatus*, BA Pal ex CIRGEO 751, V32/1; 4. *Craspedispora* sp., BA Pal ex CIRGEO 765, Q37/3; 5. *Dibolisporites eifeliensis*, BA Pal ex CIRGEO 766, W28; 6. *Dibolisporites quebecensis*, BA Pal ex CIRGEO 771, T25/1; 7. *Dibolisporites tuberculatus*, BA Pal ex CIRGEO 752, F40; 8. *Emphanisporites annulatus*, BA Pal ex CIRGEO 748, Q38/2; 9. *Emphanisporites laticostatus*, BA Pal ex CIRGEO 750, E41; 10. *Emphanisporites radiatus*, BA Pal ex CIRGEO 778, T31/3; 11. *Emphanisporites spinaeformis*, BA Pal ex CIRGEO 748, S35/2; 12. *Geminospora lemurata*, BA Pal ex CIRGEO 750 MEB, V37/2; 13. *Geminospora punctata*, BA Pal ex CIRGEO 749, Q38/3; 14. *Geminospora* sp., BA Pal ex CIRGEO 763, H28; 15. *Geminospora* sp. 1 in Breuer and Grahn, 2011, BA Pal ex CIRGEO 757, X52/1.; 16. *Geminospora svalbardiae*, BA Pal ex CIRGEO 748, F33.

**Geminospora* sp. 1 in Breuer and Grahn, 2011 (Fig. 11.15)

**Geminospora svalbardiae* (Vigran) Allen 1965 (Fig. 11.16)

Grandispora brevizonata (Menéndez and Pöthe de Baldis) Di Pasquo, 2005 (Fig. 12.1)

**Grandispora cassidea* (Owens) Massa and Moreau-Benoît 1976 (Fig. 12.2)

**Grandispora cristata* (Menéndez and Pöthe de Baldis) nov. comb. Basionym. *Hymenozonotrites cristatus* Menéndez and Pöthe de Baldis, 1967, p. 168, pl. I, fig. J. (Fig. 12.3)

Genus *Grandispora* McGregor, 1973

Type species: *Grandispora spinosa* Hoffmeister Staplin and Malloy, 1955
Grandispora delicata sp. nov.

Fig. 13.1–2a,b

Holotype: Fig. 13. 1. Sample BA Pal ex CIRGEO 750 (2060–2061 mbgs). England Finder: U29/3.

Paratype: Fig. 13.2a,b. Sample BA Pal ex CIRGEO 750 MEB-1 (2060–2061 mbgs). England Finder: U39/3.

Derivation of the name: the nature of the endospore which is delicate. Diagnosis: Camerate radial spore, trilete. Subcircular to subtriangular amb. Laesurae straight to slightly sinuous accompanied with labra between 1.5–6 µm wide. Inner body to overall equatorial diameter ratio 3/5. Exospore thin, generally laevigate proximally, some specimens can present a slightly infragranulated one. The proximo-equatorial region display scattered spines, while the distal polar zone is sculptured

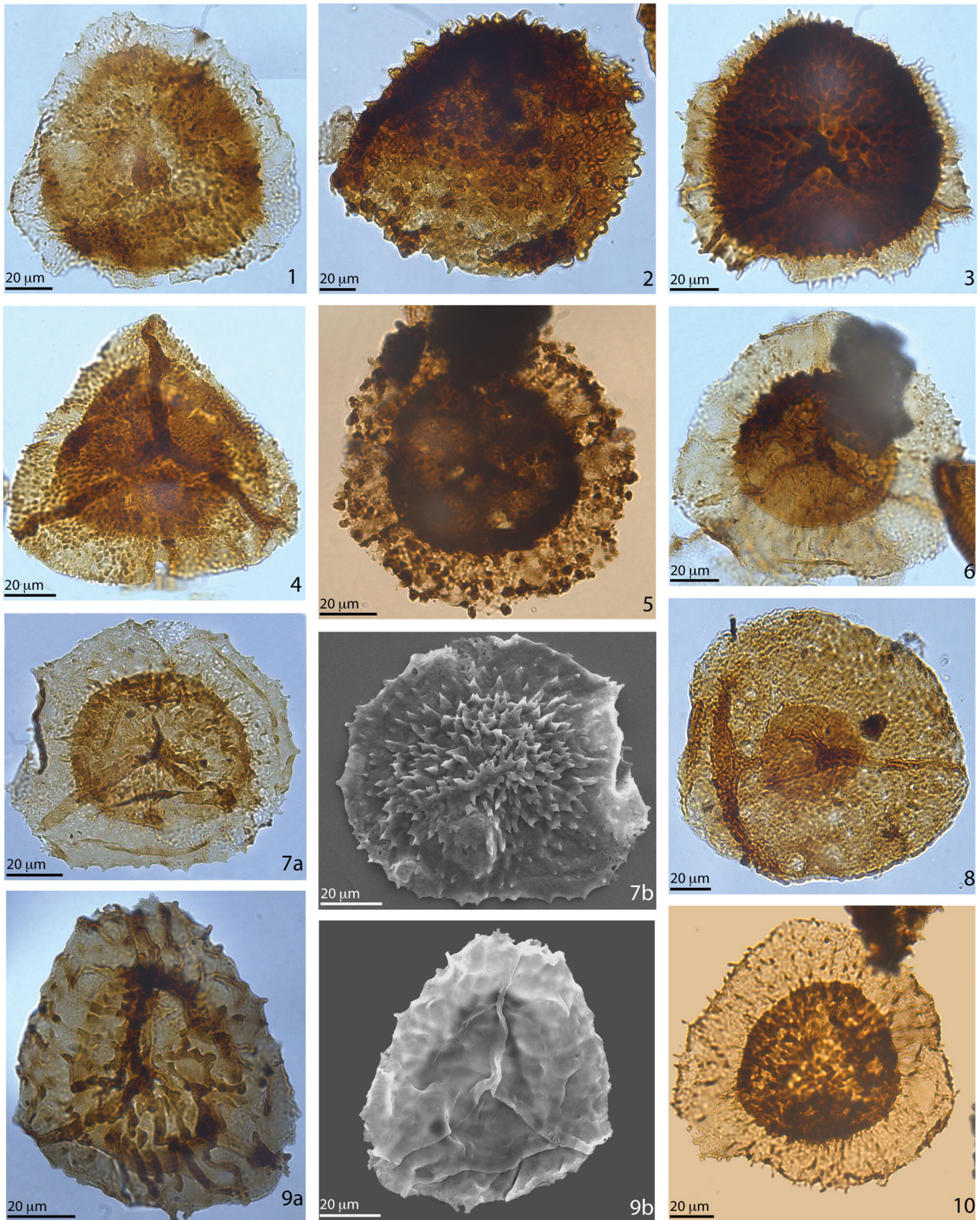


Fig. 12. Selected taxa from the studied borehole. For each illustration, sample and England Finder coordinates are specified. 1. *Grandispora brevizonata*, BA Pal ex CIRGEO 750, G27; 2. *Grandispora cassidea*, BA Pal ex CIRGEO 745, Q31/1; 3. *Grandispora cristata* nov. comb, BA Pal ex CIRGEO 750, Y47/2; 4. *Grandispora gabesensis*, BA Pal ex CIRGEO 749, D48/3; 5. *Grandispora macrotuberculata*, BA Pal ex CIRGEO 769, V29/3; 6. *Grandispora mammillata*, BA Pal ex CIRGEO 749, R45/2; 7a. *Grandispora pseudoreticulata*, BA Pal ex CIRGEO 751 MEB, Q55/1; 7b. *Grandispora pseudoreticulata* SEM; 8. *Grandispora stolidota*, BA Pal ex CIRGEO 745, L25; 9a. *Grandispora variospinosa*, BA Pal ex CIRGEO 750 MEB-2, L36/4; 9b. *Grandispora variospinosa* SEM; 10. *Grandispora velata*, BA Pal ex CIRGEO 770, G47/4.

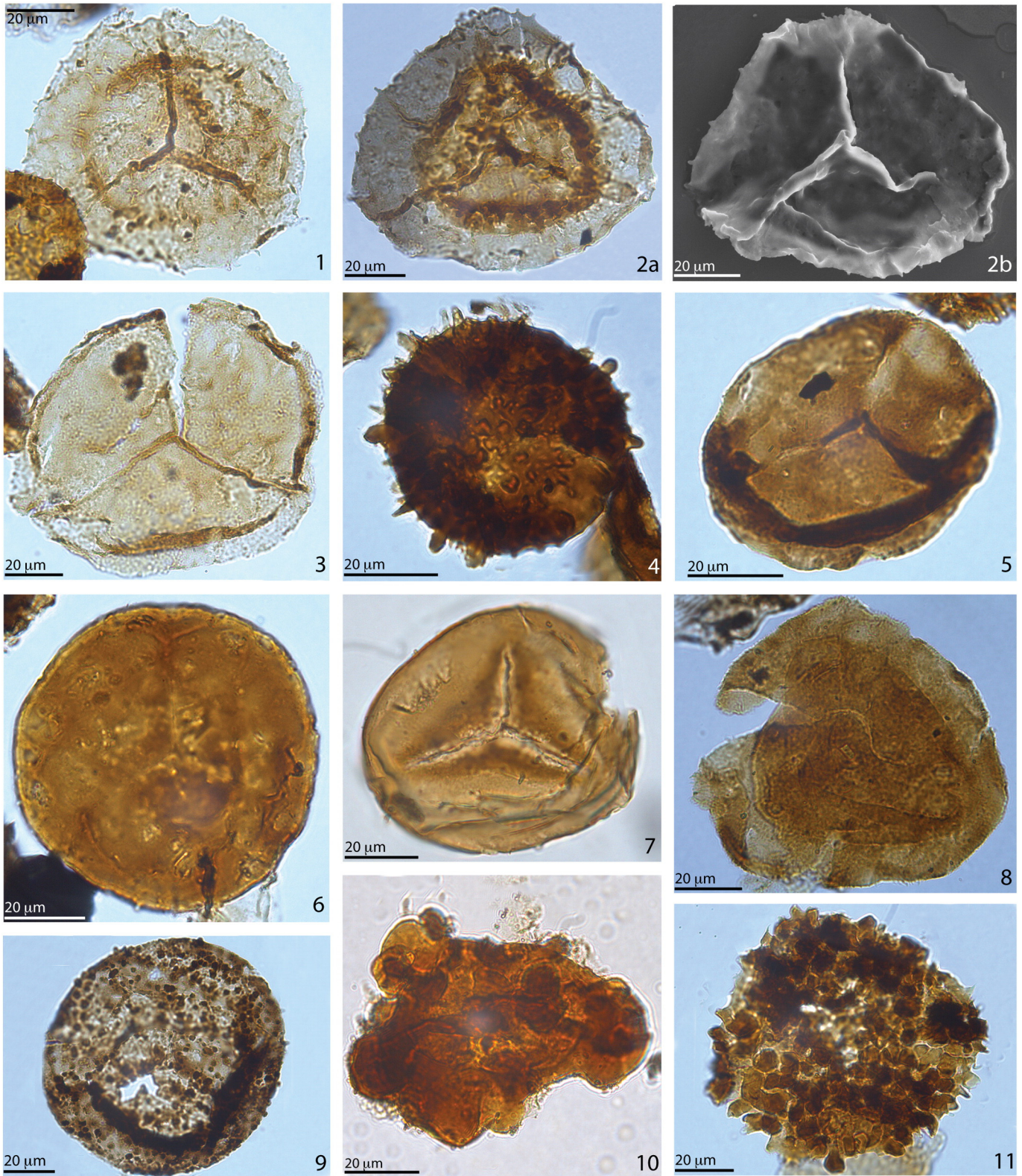


Fig. 13. Selected taxa from the studied borehole. For each illustration, sample and England Finder coordinates are specified. 1. *Grandispora delicata* sp. nov. holotype, BA Pal ex CIRGEO 750, U29/3; 2a. *Grandispora delicata* sp. nov. paratype, BA Pal ex CIRGEO 750 MEB-1, U39/3; 2b. *Grandispora delicata* SEM paratype; 3. *Leiotriletes balapucensis*, BA Pal ex CIRGEO 749, F46/2; 4. *Raistrickia aratra*, BA Pal ex CIRGEO 749, F30; 5. *Retusotriletes albarinii*, BA Pal ex CIRGEO 751, F40; 6. *Retusotriletes ottonei*, BA Pal ex CIRGEO 749, K52/4; 7. *Retusotriletes triangulatus*, BA Pal ex CIRGEO 739, T40/2; 8. *Rhabdosporites langii*, BA Pal ex CIRGEO 753, J32; 9. *Verruciretusispora ornata*, BA Pal ex CIRGEO 771, G34/3; 10. *Verrucosporites premnus*, BA Pal ex CIRGEO 739, F54; 11. *Verrucosporites scurrus*, BA Pal ex CIRGEO 749, Y32/1.

with spines and biform elements, more densely distributed in the equatorial area of the inner body. The endospore, clearly thin, has a thickening in the equatorial perimeter. Ornamentation include both, spines, with blunt and pointed recurved apices, and biform elements with bulbous bases or expanded apices, 1–5 µm wide at base, 1–16 µm high. Dimensions: 82 (97,2) 120 µm (mode: 100 µm; 27 specimens measured) Description of holotype: Trilete camerate spore, subcircular amb. Laesurae straight, accompanied with labra 3 µm wide. Inner body to overall equatorial diameter ratio 7/10. Proximal region laevigate, equatorial and distal exospore sculptured with scattered spines with blunt and pointed apices and biform elements with bulbous bases 3–6.4 µm high and 1.3–3.5 µm wide at base.

Dimensions: Overall equatorial diameter, 82 µm; inner body equatorial diameter 55 µm.

Comparison: *Grandispora pseudoreticulata* (Menéndez and Pöthe de Baldis) Ottone has sculptured elements which are fused on the base and form ridges. *Grandispora protea* (Naumova) Moreau-Benoît 1980 can be bigger and has rounded conical or biform spines as ornamentation. *Grandispora velata* (Richardson) McGregor is bigger and has spines with acute apices and conical as ornamentation.

Grandispora douglastownensis Loboziak, Streeel and Burjack 1989

Grandispora gabesensis Loboziak and Streeel 1989 (Fig. 12.4)

Grandispora inculata Allen 1965

**Grandispora macrotuberculata* (Arkhangelskaya) McGregor 1973 (Fig. 12.5)

Grandispora mammillata Owens 1971 (Fig. 12.6)

Grandispora permulta (Daemon) Loboziak, Streeel and Melo 1999

Grandispora protea (Naumova) Moreau-Benoît, 1980

Grandispora pseudoreticulata (Menéndez and Pöthe de Baldis) Ottone, 1996 (Fig. 12.7a,b)

**Grandispora stolidota* (Balme) Breuer and Steemans, 2013 (Fig. 12.8)

**Grandispora variospinosa* McGregor and Camfield 1982 (Fig. 12.9a,b)

**Grandispora velata* (Richardson) McGregor 1973 (Fig. 12.10)

Granulatisporites muninensis Allen 1965

Leiotriletes balapucensis Di Pasquo, 2007 (Fig. 13.3)

Leiotriletes pagius Allen 1965

Lophotriletes devonicus (Naumova ex Chivrikova) McGregor and Camfield 1982

Punctatisporites spp.

Raistrickia aratra Allen 1965 (Fig. 13.4)

Retusotriletes albarinii Di Pasquo and Noetinger 2008 (Fig. 13.5)

Retusotriletes ottonei Noetinger and di Pasquo, 2011 (Fig. 13.6)

Retusotriletes simplex Naumova 1953

**Retusotriletes triangulatus* (Streeel) Streeel 1967 (Fig. 13.7)

**Rhabdosporites langii* (Eisenack) Richardson 1960 (Fig. 13.8)

Verruciretusispora ornata (Menéndez and Pöthe de Baldis) Pasquo 2005 (Fig. 13.9)

Verrucosporites premnus Richardson 1965 (Fig. 13.10)

Verrucosporites scurrus (Naumova) McGregor and Camfield 1982 (Fig. 13.11)

Verrucosporites tumultentus Clayton and Graham 1974

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.palaeo.2014.10.027>.

References

- Abele, L.G., Walters, K., 1979. The stability-time hypothesis: reevaluation of the data. *Am. Nat.* 559–568.
- Albariño, L., Dalenz-Farjat, A., Alvarez, L.A., Hernández, R.M., Pérez Leyton, M., 2002. Las secuencias sedimentarias del Devónico en el Subandino Sur y el Chaco. Bolivia y Argentina. Presented at the 5 Congreso de Exploración y Desarrollo de Hidrocarburos, Mar del Plata.
- Al-Ghazi, A., 2007. New evidence for the Early Devonian age of the Jauf Formation in northern Saudi Arabia. *Rev. Micropaleontol.* 50, 59–72.
- Allen, K.C., 1965. Lower and Middle Devonian spores of North and Central Vestspitsbergen. *Palaeontology* 8, 687–748.
- Alvarez, L.A., Dalenz-Farjat, A., Hernández, R.M., Albariño, L.M., 2003. Integración de facies y biofacies en un análisis secuencial en plataformas clásticas devónicas del Sur de Bolivia y Noroeste Argentino. *AAS Rev.* 10, 103–121.
- Antonelli, J., Ottone, E.G., 2006. Palinología de coronas del Devónico y Carbonífero Superior del Pozo YPF.SE.ECX-1, El Caburé, provincia de Santiago del Estero, Argentina. *Rev. Museo Argent. Cienc. Nat.* 8, 111–117.
- Avchimovitch, V.I., Byvsheva, T.V., Higgs, K., Streeel, M., Umnova, V.T., 1988. Miospore systematics and stratigraphic correlation of Devonian–Carboniferous boundary deposits in the European part of the USSR and Western Europe. *Cour. Forschungsinstitut Senckenberg.* 100, 169–191.
- Avchimovitch, V.I., Tchibrikova, E.V., Obukhovskaya, T., Nazarenko, A.M., Umnova, V.T., Raskatova, L.G., Mantsurova, V.N., Loboziak, S., Streeel, M., 1993. Middle and Upper Devonian miospore zonation of Eastern Europe. *Bull. Centres Rech. Explor. Prod. Elf-Aquitaine* 17, 79–147.
- Balme, B.E., 1988. Miospores from Late Devonian (Early Frasnian) strata, Carnarvon Basin, Western Australia. *Palaeontographica Abteilung B Palaophytologie* 209, 109–166.
- Barangé, M., Campos, B., 1991. Models of species abundance: a critique of and an alternative to dynamics model. *Mar. Ecol. Prog. Ser.* 69, 293–298.
- Barreda, V., 1986. Acritarcos Givetiano-Frasnianos de la Cuenca del Noroeste. Provincia de Salta, Argentina. *Rev. Esp. Micropaleontol.* 18, 229–245.
- Bastow, W.J., 1991. Methods for fitting dominance/diversity curves. *J. Veg. Sci.* 2, 35–46.
- Bosetti, E.P., Grahn, Y., Horodyski, R.S., Mendlowicz Mauller, P., Breuer, P., Zabini, C., 2010. An earliest Givetian “Lilliput Effect” in the Paraná Basin, and the collapse of the Malvinokaffric shelly fauna. *Palaeontol. Z.* 85, 49–65.
- Breuer, P., 2007. Devonian miospore palynology in Western Gondwana: an application to oil exploration. Unpublished PhD Thesis, Université de Liège, Liège, Belgium.
- Breuer, P., Al-Ghazi, A., Al-Ruwaili, M., Higgs, K.T., Steemans, P., Wellman, C.H., 2007. Early to middle Devonian miospores from northern Saudi Arabia. *Rev. Micropaleontol.* 50, 27–57.
- Breuer, P., Grahn, Y., 2011. Middle Devonian spore stratigraphy in the eastern outcrop belt of the Parnaíba Basin, northeastern Brazil. *Rev. Esp. Micropaleontol.* 43, 19–38.
- Breuer, P., Steemans, P., 2013. Devonian spore assemblages from northwestern Gondwana: taxonomy and biostratigraphy. *Spec. Pap. Palaeontol.* 89, 1–163.
- Byvsheva, T.V., 1997. Spores from the Early Carboniferous of the Russian Platform and interregional correlation. *Pr. Panstw. Inst. Geol.* 157, 53–61.
- Clayton, G., Graham, J.R., 1974. Miospore assemblages from the Devonian Sherkin Formation of south-west County Cork, Republic of Ireland. *Pollen et Spores* 16, 565–588.
- Collinson, C., Scott, A.J., 1958. Chitinozoan faunule of the Devonian Cedar Valley Formation. Illinois State Geological Survey, Circular 247, 1–34.
- Development Core Team, R., 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Di Pasquo, M., 2005. Resultados palinológicos preliminares de estratos del Devónico y Carbonífero en el perfil de Balapuca, Sur de Bolivia. Presented at the XVI Congreso Geológico Argentino, La Plata pp. 293–298.
- Di Pasquo, M., Noetinger, S., 2008. First record of Early Devonian (Lochkovian) flora from the Santa Rosa Formation–Alarache. Southern Bolivia. *Geol. Acta* 6, 191–210.
- Di Pasquo, M., Amenábar, C.R., Noetinger, S., 2009. Middle Devonian microfloras and megaflores from western Argentina and southern Bolivia: their importance in the palaeobiogeographical and palaeoclimatic evolution of western Gondwana. *Geol. Soc. Lond., Spec. Publ.* 314, 193–213. <http://dx.doi.org/10.1144/SP314.11>.
- Fernández-Seveso, F., Vistalli, M.C., Viñes, R.F., 1999. The Silurian–Devonian Chaco Basin: a review for reservoir correlation in Argentina and Bolivia. Presented at the INGPET.
- Filipiak, P., 2011. Palynology of the Lower and Middle Devonian deposits in southern and central Poland. *Rev. Palaeobot. Palynol.* 166, 213–252.
- Fischer, A.G., 1960. Latitudinal variations in organic diversity. *Evolution* 14, 64–81.
- Frontier, S., 1985. Diversity and structure in aquatic ecosystems. *Oceanography and Marine Biology: An Annual Review*. Aberdeen University Press, Aberdeen, UK, pp. 253–312.
- Ghavidel-syooki, M., Álvaro, J.J., Popov, L., Pour, M.G., Ehsani, M.H., Suyarkova, A., 2011. Stratigraphic evidence for the Hirnantian (latest Ordovician) glaciation in the Zagros Mountains, Iran. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 307, 1–16.
- Grahn, Y., 2003. Silurian and Devonian chitinozoan assemblages from the Chaco-Paraná Basin, northeastern Argentina and central Uruguay. *Rev. Esp. Micropaleontol.* 35, 1–8.
- Grahn, Y., Gutiérrez, P.R., 2001. Silurian and Middle Devonian chitinozoa from the Zapla and Santa Bárbara ranges, Tarija Basin, northwestern Argentina. *Ameghiniana* 38, 35–50.
- Grahn, Y., Mauller, P.M., Bergamaschi, S., Bosetti, E.P., 2013. Palynology and sequence stratigraphy of three Devonian rock units in the Apucarana Sub-basin (Paraná Basin, south Brazil): additional data and correlation. *Rev. Palaeobot. Palynol.* 198, 27–44. <http://dx.doi.org/10.1016/j.revpalbo.2011.10.006>.
- Haq, B.U., Schutter, S.R., 2008. A chronology of Paleozoic sea-level changes. *Science* 322, 64–68. <http://dx.doi.org/10.1126/science.1161648>.
- Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54, 427–432.
- Hoffmeister, W.S., Staplin, F.L., Malloy, R.E., 1955. Mississippian Plant Spores from the Hardinsburg Formation of Illinois and Kentucky. *J. Paleontol.* 29, 372–399.
- Illich, H., Haney, F., Mendoza, M., 1981. Geochemistry of oil from Santa Cruz Basin, Bolivia. *Am. Assoc. Pet. Geol. Bull.* 65, 2388–2402.
- Isaacson, P.E., 2007. Mid-Paleozoic biogeography of the central Andes: endemic faunas, immigrants, and paleogeography. In: Díaz-Martínez, E., Rábano, I. (Eds.), 4th European Meeting on the Palaeontology and Stratigraphy of Latin America: Cuadernos Del Museo Geominero, pp. 213–218.
- Isaacson, P., Sablock, P., 1990. Devonian palaeogeography and palaeobiogeography of the central Andes. *Geol. Soc. Lond. Mem.* 12, 431–435.
- Jaramillo, C.A., 2008. Five useful techniques for analysing palynological data. *Palaeobotanist* 57, 529–537.
- Johnson, J.G., 1970. Taphanic onlap and the end of North American provinciality. *Geol. Soc. Am. Bull.* 81, 2077–2106.
- Juggins, S., 2012. rioja: Analysis of Quaternary Science Data, R package.

- Le Hérisse, A., Melo, J.H.G., Quadros, L.P., Grahn, Y., Steemans, P., 2001. Palynological characterization and dating of the Tianguá Formation, Serra Grande Group, northern Brazil. *Correlação de Sequências Paleozóicas Sul-Americanas* 20.
- Limachi, R., Goitia, V.H., Sarmiento, D., Arispe, O., Montecinos, R., Díaz Martínez, E., Dalenz-Farjat, A., Liachenco, N., Pérez Leyton, M., Aguilera, E., 1996. Estratigrafía, geoquímica, correlaciones, ambientes sedimentarios y bioestratigrafía del Silúrico-Devónico de Bolivia. *Memorias. Presented at the XII Congreso Geológico de Bolivia, Tarija, Bolivia*, pp. 183–197.
- Loboziak, S., Streeel, M., 1989. Middle-upper devonian miospores from the Ghadamis Basin (Tunisia-Libya): Systematics and stratigraphy. *Rev. Palaeobot. Palynol* 58, 173–196. [http://dx.doi.org/10.1016/0034-6667\(89\)90084-5](http://dx.doi.org/10.1016/0034-6667(89)90084-5).
- Loboziak, S., Streeel, M., De Almeida-Burjack, M.L., 1989. Déductions paléoclimatiques d'une comparaison entre les assemblages de miospores du Dévonien moyen et supérieur de Libye et du Brésil. *Geobios* 22, 247–251. [http://dx.doi.org/10.1016/S0016-6995\(89\)80130-5](http://dx.doi.org/10.1016/S0016-6995(89)80130-5).
- Loboziak, S., Streeel, M., Melo, J.H.G., 1999. *Grandispora* (al. *Contagisporites*) permulta Loboziak, Streeel et Melo, comb. nov., a senior synonym of *Grandispora riegelii* Loboziak et Streeel, 1989—nomenclature and stratigraphic distribution. *Rev. Palaeobot. Palynol* 106, 97–102.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell Publishing, Malden, Massachusetts (256 pp.).
- Margalef, R., 1968. *Perspectives in Ecological Theory (Biology Series)*. University of Chicago Press, Chicago (111 pp.).
- McGregor, D.C., 1961. Spores with proximal radial pattern from the Devonian of Canada. *Geological Survey of Canada Bulletin* 76, 1–11.
- McGregor, D.C., 1973. Lower and Middle Devonian spores of eastern Gaspé, Canada. *Palaeontographica Abteilung B* 142, 1–77.
- McGregor, D.C., Camfield, M., 1976. Upper Silurian? to Middle Devonian spores of the Moose River Basin, Ontario. *Geological Survey of Canada Bulletin* 263, 1–63.
- McGregor, D.C., Camfield, M., 1982. Middle Devonian miospores from the Cape de Bray, Weatherall, and Hecla Bay formations of northeastern Melville Island, Canadian Arctic. *Geological Survey of Canada* 348, 1–105.
- Massa, D., Moreau-Benoît, A., 1976. Essai de synthèse stratigraphique et palynologique du Système Dévonien en Libye occidentale. *Revue de l'Institut Français du Pétrole* 41, 287–333.
- Melo, J.H.G., Loboziak, S., 2003. Devonian–Early Carboniferous miopore biostratigraphy of the Amazon Basin, Northern Brazil. *Rev. Palaeobot. Palynol* 124, 131–202.
- Menéndez, C.A., Pöthe de Baldi, E.D., 1967. Devonian spores from Paraguay. *Rev. Palaeobot. Palynol* 1, 161–172. [http://dx.doi.org/10.1016/0034-6667\(67\)90118-2](http://dx.doi.org/10.1016/0034-6667(67)90118-2).
- Moreau-Benoît, A., 1980. Les spores du Dévonien de Libye - Deuxième Partie. *Cahiers de Micropaléontologie* 1, 1–53.
- Mullins, G.L., Aldridge, R.J., Siveter, D.J., 2004. Microplankton associations, biofacies and palaeoenvironment of the type lower Ludlow Series, Silurian. *Rev. Palaeobot. Palynol* 130, 163–194.
- Naumova, S.N., 1953. Spore-pollen complexes of the Upper Devonian of the Russian Platform and their stratigraphical value. *Akademi Nauk SSSR, Geologicheskii Institut, Geologicheskii seriya* 60, 1–204.
- Noetinger, S., 2010. Middle-Upper Devonian palynoflora from the Tonono x-1 borehole, Salta Province, northwestern Argentina. *Ameghiniana* 47, 165–184.
- Noetinger, S., di Pasquo, M., 2010. Palynomorphs from Abra Límite, Zenta Range, Eastern Cordillera, Northwestern Argentina. *Rev. Bras. Paleontol.* 13, 13–20.
- Noetinger, S., di Pasquo, M., 2011. Devonian palynological assemblages from the San Antonio x-1 borehole, Tarija Basin, northwestern Argentina. *Geol. Acta* 9, 199–216.
- Noetinger, S., Di Pasquo, M., 2013. New palynological information from the subsurface Copo, Caburé and Rincón formations (upper Lochkovian–Emsian), Salta Province, Argentina. *Mem. Assoc. Australas. Palaeontol.* 44, 107–121.
- Oksanen, J., 2013. Vegan: ecological diversity 1–11.
- Ottone, E.G., 1996. Devonian palynomorphs from the los monos formation, Tarija Basin, Argentina. *Palynology* 20, 105–155.
- Owens, B., 1971. Miospores from the Middle and Early Upper Devonian rocks of the Western Queen Elizabeth Islands, Arctic Archipelago. *Geological Survey of Canada Paper* 70–38, 1–157.
- Paris, F., Grahn, Y., Nestor, V., Lakova, I., 1999. A revised chitinozoan classification. *J. Paleontol.* 73, 549–570.
- Pearson, T.H., 1975. The benthic ecology of Loch Linnhe and Loch Eil, a sea-loch system on the west coast of Scotland. IV. Changes in the benthic fauna attributable to organic enrichment. *J. Exp. Mar. Biol. Ecol.* 20, 1–41.
- Playford, G., 1977. Lower to Middle Devonian acritarchs of the Moose River Basin, Ontario. *Geol. Surv. Can.* 279, 1–87.
- Playford, G., 1983. The Devonian miopore genus *Geminispora* Balme 1962: a reappraisal based upon topotypic *G. lemurata* (type species). *Memoirs of the Association of Australasian Palaeontologists* 1, 311–325.
- Playford, G., 1985. Palynology of the Australian Lower Carboniferous: a review. *Comptes Rendus. Presented at the 10th International Congress Carboniferous Stratigraphy and Geology, Madrid, Spain*, pp. 247–265.
- Playford, G., 1991. Australian Lower Carboniferous miospores relevant to extra-Gondwanic correlations: an evaluation. *Cour. Forschungsinstitut Senckenberg* 130, 85–125.
- Richardson, J.B., 1960. Spores from the Middle old red sandstone of Cromarty, Scotland. *Palaeontology* 3, 45–63.
- Richardson, J.B., 1965. Middle Old Red Sandstone spore assemblages from the Orcadian Basin North-East Scotland. *Palaeontology* 7, 559–605.
- Richardson, J.B., Lister, T.R., 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology* 12, 201–252.
- Richardson, J.B., McGregor, D.C., 1986. Silurian and Devonian spore zones of the Old Red Sandstone continent and adjacent regions. *Geol. Surv. Can.* 364, 1–79.
- Riegel, W., 1968. Die Mitteldevon-Flora von Lindlar (Rheinland). 2. *Sporae dispersae*. *Palaeontographica. Abteilung B* 123, 76–96.
- Ronov, A.B., 1994. Phanerozoic transgressions and regressions on the continents; a quantitative approach based on areas flooded by the sea and areas of marine and continental deposition. *Am. J. Sci.* 294, 777–801.
- Rubinstein, C.V., García Muro, V.J., 2011. Fitoplancton marino de pared orgánica y miosporas síuricos de la Formación Los Espejos, en el perfil del Río de las Chacritas, Precordillera de San Juan, Argentina. *Ameghiniana* 48, 618–641.
- Schultz, G., 1968. Eine unterdevonische mikroflora aus den Kerfer Schichten der Eifel (Rheinisches Schiefergebirge). *Palaeontographica. Abteilung B* 123, 4–42.
- Soares, C.P., Barbosa Landim, P.M., Fulfaro, V.J., 1978. Tectonic cycles and sedimentary sequences in the Brazilian intracratonic basins. *Geol. Soc. Am. Bull.* 89, 181–191.
- Spatharis, S., Tsirtsis, G., 2013. Zipf–Mandelbrot model behavior in marine eutrophication: two way fitting on field and simulated phytoplankton assemblages. *Hydrobiologia* 714, 191–199. <http://dx.doi.org/10.1007/s10750-013-1536-3>.
- Starck, D., Gallardo, E., Schulz, A., 1993. The pre-Carboniferous unconformity in the Argentine portion of the Tarija Basin. *Comptes Rendus XII ICC-P. Presented at the Douzième Congrès International de la Stratigraphie et Géologie du Carbonifère et Permien, Buenos Aires, Argentina*, pp. 373–384.
- Steenmans, P., Le Hérisse, A., Bozdoğan, N., 1996. Ordovician and Silurian cryptospores and miospores from southeastern Turkey. *Rev. Palaeobot. Palynol.* 93, 35–76.
- Steenmans, P., Petus, E., Breuer, P., Mauller, P.M., Gerrienne, P., 2012. Palaeozoic innovations in the micro and megafossil plant record: from the earliest plant spores to the earliest seeds. In: Talent, J.A. (Ed.), *Earth and Life. Springer, International Year of Planet Earth*, pp. 437–477.
- Streeel, M., 1967. Associations de spores du Dévonien inférieur belge et leur signification stratigraphique. *Annales de la Société Géologique de Belgique* 90, 11–54.
- Streeel, M., Higgs, K., Loboziak, S., Riegel, W., Steemans, P., 1987. Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenne–Rhenish regions. *Rev. Palaeobot. Palynol.* 50, 211–229.
- Suárez Soruco, R., 1989. El ciclo Cordillerano (Siúrico–Carbonífero inferior) en Bolivia y su relación con países limítrofes. *Rev. Téc. YPF* 10, 233–243.
- Suárez Soruco, R., Lobo Boneta, J., 1983. La fase compresiva Eohercínica en el sector oriental de la Cuenca Cordillerana de Bolivia. *Rev. Téc. YPF* 9, 189–202.
- Tiwari, R.S., Schaarschmidt, F., 1975. Palynological studies in the Lower and Middle Devonian of Prüm Syncline, Eifel (Germany). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 534, 1–129.
- Troth, I., Marshall, J.E.A., Racey, A., Becker, R.T., 2011. Devonian sea-level change in Bolivia: a high palaeolatitude biostratigraphical calibration of the global sea-level curve. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 304, 3–20.
- Turnau, E., 1996. Miopore stratigraphy of Middle Devonian deposits from western Pomerania. *Rev. Palaeobot. Palynol.* 93, 107–125. [http://dx.doi.org/10.1016/0034-6667\(95\)00122-0](http://dx.doi.org/10.1016/0034-6667(95)00122-0).
- Utting, J., Goodarzi, F., Dougherty, B.J., Henderson, C.M., 1989. Thermal maturity of Carboniferous and Permian rocks of the Sverdrup Basin, Canadian Arctic Archipelago. *Geol. Surv. Can. Pap.* 89–19, 1–20.
- Utting, J., Wielens, H., 1992. Organic petrology, thermal maturity, geology and petroleum source rock potential of Lower Permian Coal, Karoo Supersystem, Zambia. *Energy Sources* 14, 337–354.
- Volkheimer, W., Melendi, D.L., Salas, A., 1983. Quitinozoarios silúricos y devónicos del noroeste argentino—su importancia estratigráfica. *Rev. Téc. YPF* 9, 171–183.
- Volkheimer, W., Mendoza, D., Salas, A., 1986. Devonian chitinozoans from northwestern Argentina. *Palaeontogr. Abt. B* 173, 229–251.
- Washington, H.G., 1984. Diversity, biotic and similarity indices. A review with special relevance to aquatic ecosystems. *Water Res.* 18, 653–694.
- Wilsey, B., Stirling, G., 2007. Species richness and evenness respond in a different manner to propagule density in developing prairie microcosm communities. *Plant Ecol.* 190, 259–273.
- Young, G.C., 1996. Devonian. In: Young, G.C., Laurie, J.R. (Eds.), *An Australian Phanerozoic Timescale*. Oxford University Press, Melbourne, Australia, pp. 96–109.