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The utility of *Desmidiospora*: a paradigm shift based on Paleogene fungal remains from the Ñirihuau Basin, Argentina

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ABSTRACT

Fungal remains similar to those described as *Desmidiospora willoughbyi* were found in samples from the Río Foyel section (El Foyel Group of Paleogene age), Ñirihuau Basin, Argentina. A full description and illustrations are presented. The names *D. willoughbyi* and *D. marginiconvoluta* as defined are shown to be inadequate. The history of the names and actual affinity of taxa presently assigned to those names are discussed. Arguments against the use of *Desmidiospora* for fungal remains other than the conidia of an entomopathogenic species are presented. Instead, the lobulate fossil remains should be treated as germlings or immature ascomata from epiphyllous fungi of polyphyletic origin.

KEYWORDS

Desmidiospora; epiphyllous fungal remains; Ñirihuau Basin; Paleogene; Argentina

1. Introduction

The frequency of fungal remains in palynological samples is highly variable. In Quaternary sediments they can be abundant and are generally easily recognised, and many can be assigned to extant genera. This move towards application of modern fungal morphological taxonomy and away from form-genera has won more followers, as this method of identification makes it easier to establish a robust palaeoecological signal based upon modern fungal ecological tolerances, rather than assuming that the fungal signal, by proxy, is mirroring that of plant and algal palynomorphs (Kalgutkar 1997; O'Keefe 2017).

The value of fungal palynomorphs for the Holocene is indisputable, as they are recognised and widely used as palaeoenvironmental proxies. However, for pre-Quaternary palynological studies the situation is quite different. Pirozynski (1976) and Kalgutkar and Jansonius (2000) presented a short but detailed review of the history of palaeomycology, which was greatly expanded by Taylor et al. (2015). Interest in the discipline has been cyclical, being very active in the earliest days of palynology (late 1800s), largely forgotten, then reinstated in the 1960s and now revalued and growing, although fungi are still only sporadically cited in deep-time fossil samples, mostly as indeterminate remains or as taxa with open assignations, and they are seldom studied in depth. Throughout the history of palaeomycology, researchers have doubted its usefulness because it is not possible to refer all fossil fungi convincingly to modern analogues (Pirozynski 1976; Kalgutkar and Jansonius 2000; Taylor et al. 2015). For this reason, the value of fungi as palaeoenvironmental indicators could be considered limited, even though their biostratigraphical value is important (Elsik 1980, 1992; Norris 1986; Kalgutkar and Braman 2008), especially in early Cenozoic studies, where their evolution is closely linked to the diversification of the angiosperms (Traverse 2007). The problem increases with the massive introduction of morphogenera (ending in -*ites*), many of which are redundant, and few of which take asexual morphs into account (Pirozynski 1976). This issue was recognised early on (O'Keefe 2017), and now this trend is in reverse (Hawksworth et al. 2016; Nuñez Otaño et al. 2017; Shumilovskikh et al. 2017; Pound et al. 2018), but there are still many fossil taxa to review and discuss. With the introduction of the 'one fungus, one name' concept in fungal nomenclature and the removal of protections for multiple names for dispersed fossil parts of single organisms with the Melbourne Code (Hawksworth 2011), these reviews must be undertaken with care to avoid violations of the International Code of Nomenclature (ICN) (Turland et al. 2018).

The discovery of remains that matched those commonly identified as *Desmidiospora willoughbyi* faced us with the dilemma of using a well-known and accepted but erroneous name or trying to resolve a nomenclatural problem. Here we present a full description along with a thorough discussion of the validity of the name and arguments for avoiding its use in the future.

2. Geological setting

The Ñirihuau Basin is located in the western part of Río Negro and Chubut provinces, Argentina (Figure 1). The general stratigraphical column of the Ñirihuau Basin is

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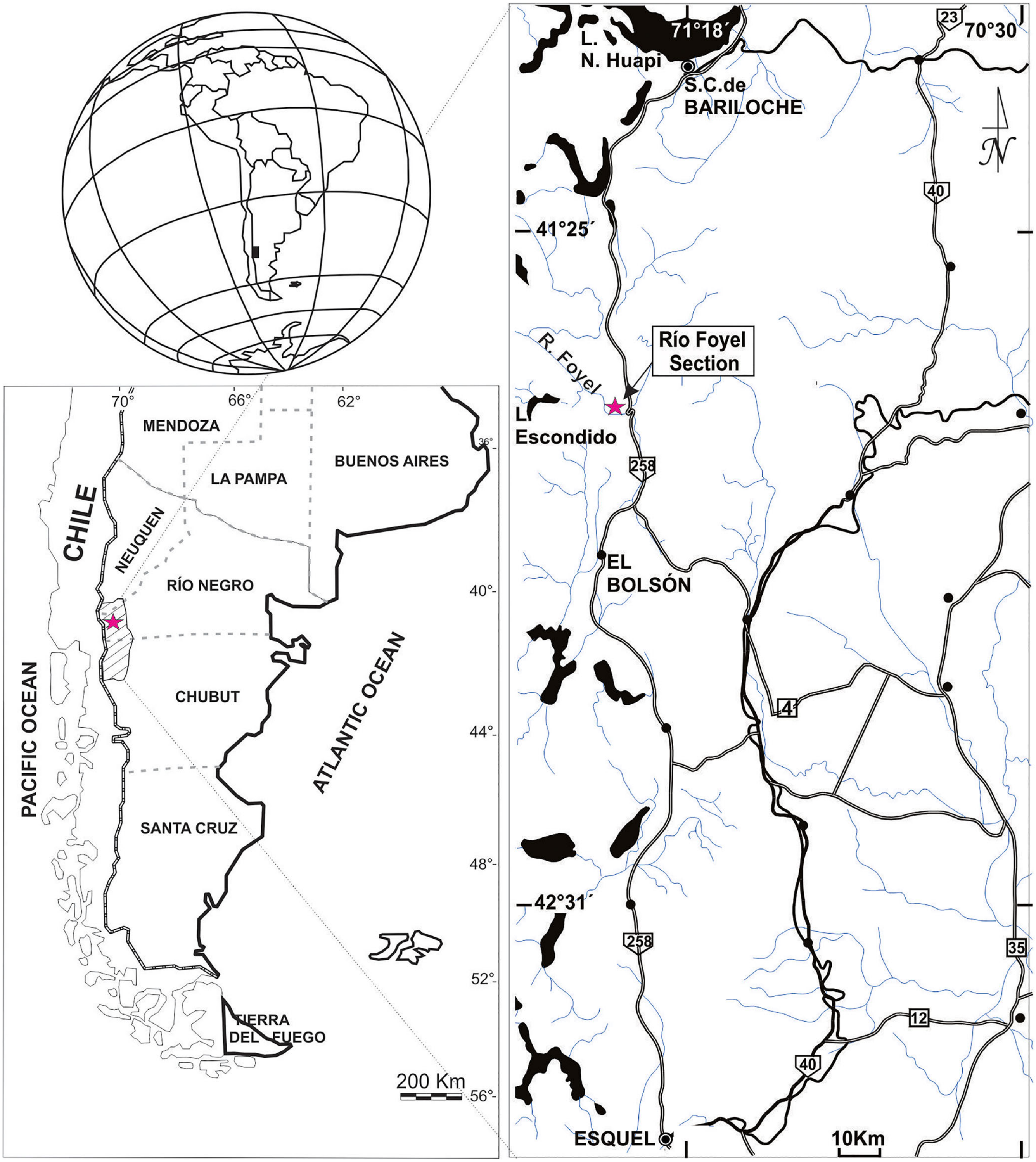

Figure 1. Location map of the Ñirihuau Basin with the position of the Río Foyel section indicated (modified from Cornou et al. 2014).

comprised, from the base to the top, of the Huitrera Formation (Ravazzoli and Sesana 1977) or its lateral equivalent the Cerro Bastión Formation (Diez and Zubia 1981), the El Foyel Group (Asensio et al. 2005), and the Nahuel Huapi Group (González Bonorino 1973; González Bonorino and González Bonorino 1978). The type section of the El Foyel Group (Figure 2), at the Rio Foyel section (41°44′S, 71°30′W), is exposed in the middle valley of the river of the same name, about 80 km south of Lago Nahuel Huapi. This group consists, from the base to top, of the Troncoso (Asensio et al. 2005), Salto del Macho (Asensio et al. 2005), and Río Foyel formations (Pöthe de Baldis 1984). Together, these formations are a 2000 m thick section of volcaniclastics, thick siliciclastics, and minor limestones outcropping along the Foyel River.

The stratigraphical ordering of the formations that make up the El Foyel Group and their age are still controversial. Here we follow the proposal of Asensio et al. (2005) which

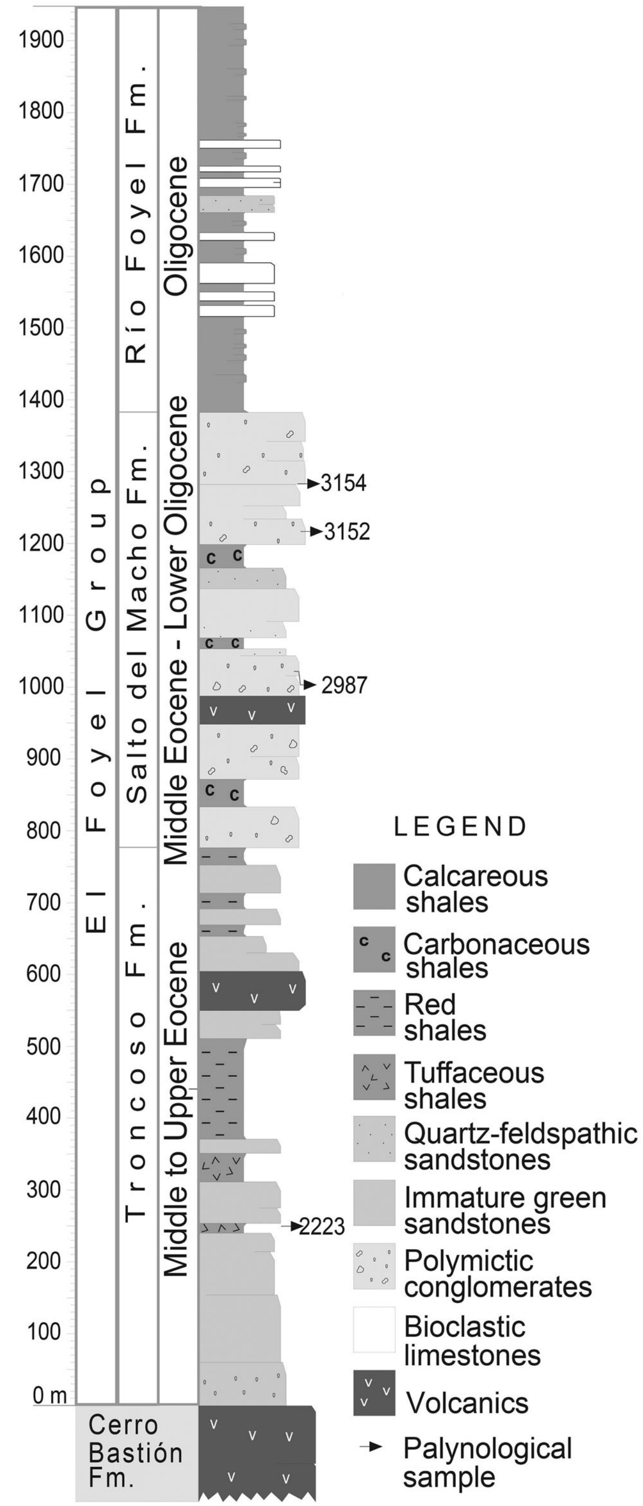

Figure 2. The Rio Foyel section and the distribution of studied samples (adapted from Martínez et al. 2016).

was reinforced by several palynological studies (Cornou 2012; Quattrocchio et al. 2012; Cornou et al. 2014; Martínez et al. 2016). The Río Foyel section overlies volcanics from the Cerro Bastión Formation (Middle Eocene), although this contact is obscured by the dense forest cover characteristic of the area. The basal unit corresponds to the Troncoso Formation (Middle to Upper Eocene), which is about 800 m of immature green sandstones with intercalations of tuffaceous shales and red shales. The Salto del Macho Formation (Middle Eocene–Lower Oligocene) overlies the Troncoso Formation with a sharp erosive contact. This unit is composed of thick beds of polymictic conglomerate with a maximum thickness of 560 m and with thinner layers of sandstone and intercalations of black shales and ignimbrites. The section ends with the lowermost part of the Río Foyel Formation (Oligocene) which is approximately 600 m in thickness, and composed mostly of black shales, with some intercalations of bioclastic limestone and conglomerate.

3. Materials and methods

Four outcrop samples of siltstone and shales from the Troncoso and Salto del Macho Formations in the El Foyel Group at the Rio Foyel section (Figure 2) were found to contain *Desmidiospora*-types and related fungi during the course of a study of fungal spores (Martínez et al. 2016). Fungal remains were extracted from the rocks using mineral-acid palynological techniques involving treatments with hydrochloric and hydrofluoric acids (Volkheimer and Melendi 1976). The slides were examined using a transmitted light microscope (Olympus BX40A) equipped with an Olympus CAMEDIA C-5060 digital camera. Slides are housed in the Universidad Nacional del Sur-Instituto Geológico del Sur, Bahía Blanca, Buenos Aires province, Argentina. They are identified by the abbreviation UNSP (Universidad Nacional del Sur, Palynology) and a catalogue number followed by letters denoting each formation: T (Troncoso), SM (Salto del Macho) or RF (Rio Foyel). Specimen locations on sample slides are noted with England Finder coordinates.

Fungal germlings were classified and described following Lange (1976). Neither the germlings nor the ascomata illustrated here are formally designated, since they will be treated in a future publication, along with other thyriothecia recovered from the El Foyel Group.

4. Results

Hofmann (2010) presented a schematic reconstruction of the life cycle of an *Asterina* species to exemplify those of microthyriaceous-like fungi. Following the diagram presented in Hofmann's thesis (2010), we selected some of the fossil materials recovered from our samples and tried to relate them to the stages of the life cycle (Figure 3). The hypothetical life cycle begins with the germination of ascospores (Figure 3a–b; Plate 1, figures 7, 10 – white arrows), to develop surface hyphae with appresoria (Figure 3c; Plate 1, figures 6, 8 – black arrow and arrowhead). When conditions are favourable, the formation of the reproductive sexual body is initiated; the immature stages of the development of ascoma are also termed germlings (Figure 3d–e; Plate 1, figures 1–4, 8 – arrow). The mature ascoma (Figure 3f), called the thyriothecium, is delta-shaped in lateral view (Plate 1, figure 11) and has a circular outline in surface view. The thick scutellum (upper ascomatal wall) is the structure that is best preserved and most frequently recovered from palynological

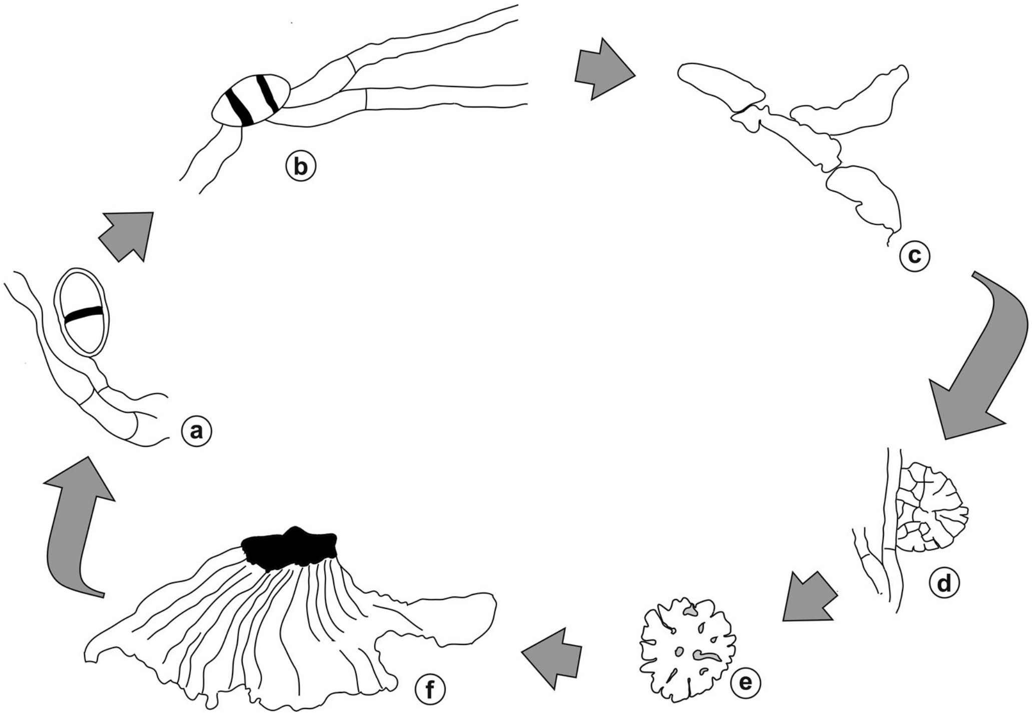

Figure 3. Hypothetical reconstruction of the life cycle of microthyriaceous-like fungi based on the observations of Hofmann (2010), redrawn from fossil specimens recovered from the Paleogene of the Ñirihuau Basin (not to scale). (a–b) Ascospore germinating. (c) Surface hyphae with appresoria. (d–e) Immature stages of the development of ascoma (germlings). (f) Mature ascomata in lateral view.

samples (Plate 1, figures 5, 9). Our materials, consisting of germlings (specimens 1 to 3) and ascomata (specimens 4 to 8), are described and illustrated (Plate 1).

Specimens 1–3

Plate 1, figures 1–3

Three specimens of dispersed germlings were recovered in this study from the Troncoso and Salto del Macho formations.

Material

UNSP-T 2223b: L19/4 (Plate 1, figure 1); UNSP-T 2223f: J24/2 (Plate 1, figure 2); UNSP-SM 3152c: A17/3 (Plate 1, figure 3).

Description

Flattened, circular, elliptical to irregular in outline, scarcely to deeply lobate. Wall smooth, *ca.* 1 μm thick, light to dark brown. The distinctive lobes are separated by invaginations which occur in radial sets of differing lengths.

Dimensions

22 × 28 μm, 20 × 20 μm, 30 × 41 μm. Range of dimensions, width: 20(24)30 μm, length: 20(30)41 μm.

Remarks

Our specimens resemble those described from the Upper Eocene in southern New Zealand by Conran et al. (2016, fig. 2T) and Bannister et al. (2016, fig. 4I); however, ours are much larger than those examples. Each meets the current diagnosis for *Desmidiospora willoughbyi*. They correspond to the 'Grade V germlings' in Lange (1976). In Quaternary palynology these may also be recognised as HDV-13 (van Geel 1978).

Specimen 4

Plate 1, figure 4

Material

UNSP-SM 2987b: Q53.

Description

Ascoma immature, flattened, sub-circular in outline. Wall smooth, *ca.* 1 μm thick, medium brown. Radial and transverse septa produce an imperfect reticulum. A remnant of dark brown, septate hypha of *ca.* 4 μm in width is recognised (Plate 1, figure 4 – black arrow).

Dimensions

24 × 30 μm.

Remarks

This material could be associated with early stages of development of ascomata, like those illustrated in Hofmann and Piepenbring (2006). This specimen resembles immature stages of *Phragmothyrites concentricus* Carlie J. Phipps & Rember (Phipps and Rember 2004, fig. 2). In Quaternary sediments it may also be recognised as HDV-8A-e (van Geel 1978).

Specimen 5

Plate 1, figures 5–8

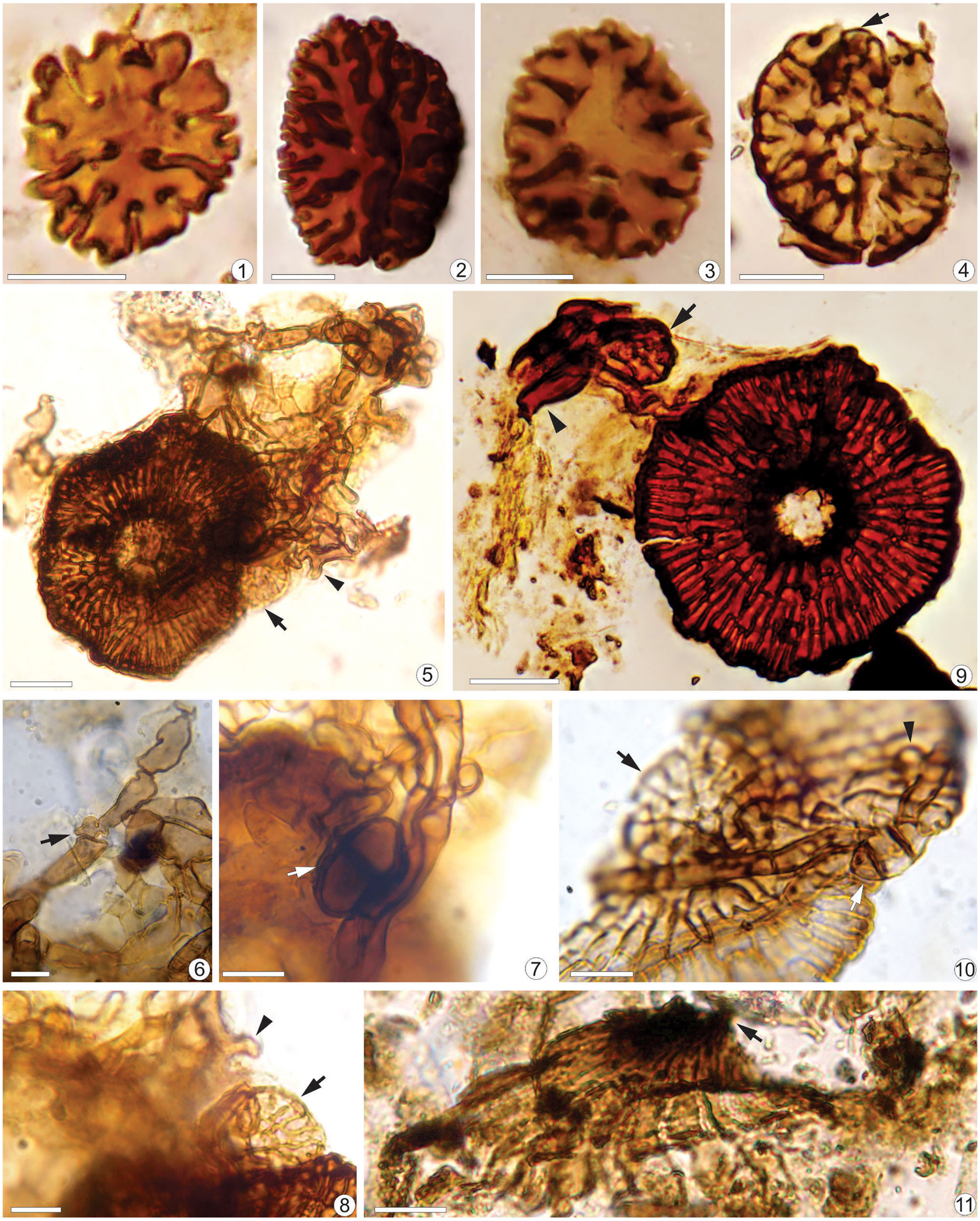

Plate 1. Figures 1–3. Germlings; Figure 1. UNSP-T 2223b: L19/4; Figure 2. UNSP-T 2223f: J24/2; Figure 3. UNSP-SM 3152c: A17/3. Figure 4. Immature ascomata, UNSP-SM 2987b: Q53, dark brown septate hyphae (arrow). Figures 5–8. Specimen 5, in general view (figure 5) and details (figures 6–8) showing mature thyriothecia, young ascoma, spore, mycelium and hyphopodia, UNSP-SM 3154c: V37/3; Figure 6. initial stages of the development of the thyriothecia (arrow), similar to the one illustrated by Hofmann (2010, p. 294, fig. 4.4); Figure 7. detail of mycelium and 1-septate spore (white arrow); Figure 8. detail of young ascoma (arrow) and hyphopodia (arrowhead); Figure 9. Specimen 6, showing mature thyriothecia, young ascoma (arrow) and hyphopodia (arrowhead), UNSP-SM 3154c: C24/1; Figure 10. a young ascoma beneath a fragmented thyriothecium (arrow), 2-septate spore (white arrow), germinating through each of its three cells and a hook-like appressorium (arrowhead), similar to that illustrated in Vishnu et al. (2017); Figure 11. mature thyriothecium in lateral view showing the black neck (arrow), UNSP-T 2223b: N56/2. Scale bars: 1–4, 6–8, 10 = 10 µm; 5, 9, 11 = 20 µm.

Material

UNSP-SM 3154c: V37/3.

Description

Thyriothecia roughly polygonal, margin irregular, ostiolate (Plate 1, figure 5). Ostiole circular, up to 20 µm in diameter, internally surrounded by brown denticulate cells of up to 4 µm in height. Wall comprising four rows of cells, radiating from the centre, more or less quadrangular around the ostiole, and branched in an irregularly dichotomised pattern around the periphery. In close proximity with the mature ascoma, a young one, *ca*. 25 µm diameter (Plate 1, figures 5, 8 – black arrows), one 1-septate spore, 11 × 19 µm (Plate 1, figure 7 – white arrow), some hyphopodia (Plate 1, figures 5, 8 – black arrowheads, figure 6 – black arrow), and abundant mycelium (hyphae 4–11 µm wide) can be recognised.

Dimensions

Diameter: 80 × 87 µm.

Remarks

No thickening zone around the ostiole is observed in this specimen. These materials exemplify a growth continuum for a single taxon that taken individually would be assigned to several taxa. The mature ascoma illustrated in Plate 1, figure 5 would be assigned to *Trichothyrites denticulatus* (Ramanujam & K.P. Rao) Kalgutkar & Janson., and the material illustrated in Plate 1, figures 6–8 could be identified as *Ascodesmisites malayensis* Trivedi, Chaturv. & C.L. Verma.

Specimen 6

Plate 1, figure 9

Material

UNSP-SM 3154c: C24/1.

Description

Thyriothecia subcircular, medium orange-brown. Upper wall comprising up to five rows of more or less rectangular cells, radiating from the centre, and branched at the margin, thickened and strongly crenulate, forming a darkened rim of up to 4 µm wide. Ostiole central, *ca.* 13 µm in diameter, surrounded by a thickened and darkened zone *ca.* 5 µm wide, formed by two rows of darkened cells. Internally to the ostiole, subhyaline cells can be recognised with a radial arrangement, giving the opening a star-shaped outline. Connected with the thyriothecia, several hyphae of medium brown colour, an initial of an ascoma around 20 µm in diameter (Plate 1, figure 9 – black arrow), and two probable dark brown hyphopodia, of 7 × 19 µm and 7 × 11 µm, are recognised (Plate 1, figure 9 – black arrowhead).

Dimensions

Maximum diameter: 74 µm.

Remarks

This specimen would be also assigned to *Trichothyrites denticulatus*.

Specimen 7

Plate 1, figure 10

Material

UNSP-SM 3154c: Y15/1.

Description

A young ascoma (Plate 1, figure 10 – black arrow) is recognised beneath a fragmented, more or less rounded, thyriothecium. In close proximity a 2-septate spore (Plate 1, figure 10 – white arrow) is distinguished, germinating through each of its three cells. A hook-like appressorium, similar to that illustrated in Vishnu et al. (2017), is recognised on one of the hyphae (Plate 1, figure 10 – black arrowhead).

Dimensions

Spore: 9 × 14 µm, hyphae up to 4 µm wide, initial of ascoma 25 µm in diameter.

Remarks

This specimen is similar to *Ascodesmisites malayensis* figured in Kalgutkar and Jansonius (2000, pl. 34, fig. 7).

Specimen 8

Plate 1, figure 11

Material

UNSP-T 2223b: N56/2.

Description

Thyriothecia medium to dark brown, triangular in lateral view, irregular in outline and ostiolate, with a black neck of 5 µm in height (Plate 1, figure 11 – black arrow). Around the ostiole, a darkened zone of around 30 µm in diameter can be clearly recognised.

Dimensions

Thyriothecia 60 µm in height, 110 µm in width, ostiole *ca.* 10 µm in diameter.

Remarks

This is a mature ascoma shown in lateral view. It resembles the schematic figure shown in Ellis (1977, fig. 9A) of the extant *Trichothyrina salicis* Ellis. In Quaternary sediments it may also be recognised as HDV-8B-d (van Geel 1978).

5. Discussion

Ascomycetes growing on the surface of plants are collectively known as epiphyllous fungi. The group is polyphyletic as it contains members of distantly related orders such as the Asterinales and Meliolales (Hongsanan et al. 2016). Alvin and Muir (1970) described an epiphyllous fungus from the Lower Cretaceous in the Isle of Wight, UK, considering it to be the oldest member of the order Microthyriales. Recently, García Massini et al. (2012) described several specimens from the Jurassic in Argentina, which are now considered the earliest fossil records of epiphyllous fungi (Taylor et al. 2015). Hongsanan et al. (2016) analysed data from sequences and molecular clock calibration and then estimated the evolution of the group to have occurred as early as the Permian. However, it is not until the Cretaceous when records of these fungi become common; consequently, they are considered to be valuable indicators of age and ecological conditions (e.g. Smith 1980; Traverse 2007; Taylor et al. 2015).

From palynological samples of sedimentary rocks of the Ñirihuau Basin (Middle Eocene–Oligocene), we recovered a high concentration of remains that are very similar morphologically to the modern epiphyllous ascomycetes, mainly to members of the Asterinales and Microthyriales. Among them are fungal structures commonly assigned to *Desmidiospora willoughbyi*. The easiest solution would have been to use this name in the same way that it has been used repeatedly in palynological studies, but as we found several discrepancies in the literature, the question arose as to what precisely is meant by *Desmidiospora willoughbyi*.

The genus *Desmidiospora* was established by Thaxter (1891) for a single, entomopathogenic species. The fungus, named *Desmidiospora myrmecophila*, was found growing on the queen of the cosmopolitan ant *Camponotus*. Its distinguishing character was the huge brown macroconidia (up to 100 µm) which were described as dichotomously lobulate. This odd species, closely related to the entomopathogenic genus *Ophiocordyceps* Petch, is rare, and since it was originally described it has only been collected occasionally, although it is presently known from three continents (Evans and Samson 1984; Clark and Prusso 1986; Saltamachia 2018).

In 1967, Bradley described lobulated structures from Eocene samples as the sporangia of a chytrid genus, naming them *Entophlyctis willoughbyi*. Pirozynski (1976, p. 243) criticised Bradley's assignation of those forms to the Chytridiales, saying they 'resemble developing fructifications and juvenile conidiophores of certain leaf-litter hyphomycetes, or appressoria of, for example, *Gaeumannomyces*'.

Ethridge Glass et al. (1986) found similar structures while they were studying Upper Eocene lignites from the Manning Formation. They believed they were the same as those Bradley (1967) had described. These structures had been previously noticed by Edwards (1922), Dilcher (1965), Lange and Smith (1971, 1975) and Elsik and Dilcher (1974) who considered them to be non-conidial fungal propagules. Although some of these contributions were mentioned by Ethridge Glass et al. (1986), the fact that the structures had no septae led them to conclude that the materials had a strong similarity to the macroconidia of *Desmidiospora*. Although they were not associated with ants and they were significantly smaller than the macroconidia of *D. myrmecophila*, Ethridge Glass et al. (1986) believed that the material had enough similarities to create a new combination, *Desmidiospora willoughbyi*. Kalgutkar (1997) went further and described a third fossil species, *D. marginiconvoluta*, from the Paleogene of Canada.

From Ethridge Glass et al. (1986) to now, this epithet has been widely used to name fungal remains in palynological samples with similar lobulate morphology (e.g. Kalgutkar 1993, 1997; Norris 1997; Parsons 2000; Ramírez 2004; Traverse 2007; Ratanasthien et al. 2008; García Massini and Jacobs 2011; Shumilovskikh et al. 2015; Silva et al. 2015). Even when several authors identified them as germlings (viz. Romero and Castro 1986; Ediger and Allişan 1989; Head 1993; Conran et al. 2016), the use of *D. willoughbyi* and its description as a spore have prevailed, generating greater confusion. As examples of intermediate positions, García Massini and Jacobs (2011) use the name '*Desmidiospora* propagules' whereas Bannister et al. (2016) do not use the name *D. willoughbyi* but describe the structures as spores.

In our opinion, *Desmidiospora* must be considered a monotypic genus, restricted to entomopathogenic fungi, that could be merged with *Ophiocordyceps*, as suggested by Saltamachia (2018). This opinion is shared by Wilk et al. (2012); however, they proposed the creation of a separate form genus in which to place the current *D. willoughbyi and D. marginiconvoluta*. We strongly disagree with the erection of a new form genus on two grounds: (i) no new information about the taxa would be generated (Seifert 2017); and (ii) the creation of such form genera would only introduce more nomenclatural and systematic chaos, and indeed would violate the 'one fungus one name' precept of the current ICN for algae, fungi, and plants (Hawksworth 2011; Wingfield et al. 2012; Turland et al. 2018). Therefore, we think it is time that a formal proposal to dismiss both *D. willoughbyi* Ethridge Glass, Brown and Elsik 1986 and *D. marginiconvoluta* Kalgutkar 1997 should be drafted and submitted to IMA Fungus.

We agree with Conran et al. (2016) that many materials named under these taxa represent immature forms of Microthyriaceae, so they should be considered thyriothecium propagules. In the case of *D. marginiconvoluta*, it is morphologically the same as the forms ranked as Types I–II by Lange (1976). We also agree with van Geel (1978) and Wilk et al. (2012) that others do not seem to be immature microthyriaceous ascomata. Therefore, as these elements are part of the life cycle of epiphyllous fungi belonging to different families, a proper assignation to a definite, single species is not possible for them. For the purposes of palaeoecology, until such time as proper assignations can be made, employing Lange types or lab codes (Miola 2012) as operational taxonomic units may be useful.

Regardless of taxonomic placement, these forms may still provide important information about past ecological conditions. They are known from *Sphagnum* and *Polytrichum* leaves in bogs, are ubiquitous in Cenozoic lignite samples and are known as dispersed particles in siliciclastic sediments (van Geel 1978; Kalgutkar 1997; Wilk et al. 2012), and thus may be indicative of humid, wet conditions.

Several researchers (Dilcher 1965; Lange and Smith 1971; Lange 1978, 1980; Smith 1984; Wells and Hill 1993) considered them useful indicators for palaeoenvironmental reconstruction based on similarities to modern epiphyllous fungi. Lange (1976) made a comprehensive comparison between fossil germlings and their living equivalents on leaf-litter from Australasia and assigned the various types to precipitation ranges. Smith (1984) employed Lange's types and their frequencies in fossil cuticles and palynological samples from British Paleogene strata to infer wet palaeoclimatic conditions. Conran et al. (2016) used the same approach to perform a detailed study of fungal fossils associated with angiosperm leaves recovered from a Late Eocene New Zealand rain forest and to make inferences about climate. The application of Lange's categories combined with an analysis of leaf physiognomy allowed them to reinforce their subtropical, ever-wet and humid palaeoclimatic interpretation. In all cases, the abundance of higher grade of germlings (Type IV–V) seems to be a better indicator of high rainfall/humidity conditions than of a latitudinal temperature gradient.

Regardless of how germlings are used to perform palaeoclimatic interpretations, all authors agree that their utility is greater and the most reliable inferences are made when these structures are found associated with the host cuticle. When they are recovered only from palynological samples, a multi-proxy analysis should be performed.

6. Conclusions

The study of Paleogene fungal remains recovered from outcrop samples of the El Foyel Group, Argentina, led us to conclude that the lobulate remains found in palynological samples and frequently identified as *Desmidiospora* in fact represent part of the life cycle of at least two different groups of epiphyllous ascomycetes; thus, *Desmidiospora* as presently defined is strongly polyphyletic in origin.

We propose that fungal remains of this kind should be maintained in an open assignation and treated as germlings. This criterion attempts to bring nomenclatural order to the assignment of these structures, which have recognised palaeoecological utility during the Cenozoic.

Despite the overrated importance that palynologists assign to formal names, a confusing, inaccurate or dubious assignation can lead to erroneous ecological inferences. The recognition of the function or the role a structure plays in a biological cycle is more valuable than the name itself where a reliable assignation cannot be made, and therefore more reliable palaeoenvironmental and palaeoclimatic reconstructions can be obtained.

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Disclosure statement

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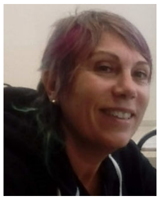
Notes on contributors



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