

# Relationship of the fossil fungal spore genus *Polycellaesporonites* Anil Chandra et al. 1984 with extant *Alternaria* Nees 1816

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## ABSTRACT

Saxena R.K., Nuñez Otaño N.B. & O’Keefe J.M.K. 2022. Relationship of fossil fungal spore genus *Polycellaesporonites* Anil Chandra et al. 1984 with extant *Alternaria* Nees 1816. *Geophytology* 50(1&2): 61–72.

The objective of the present paper is to establish the relationship between fossil fungal spores of the genus *Polycellaesporonites* Anil Chandra, R.K. Saxena & Setty 1984 and those of extant *Alternaria* Nees 1816. Based on morphological comparisons, *Polycellaesporonites* is considered to be a later taxonomic synonym of *Alternaria*. Consequently, seven species of *Polycellaesporonites* have been transferred to *Alternaria* as new combinations, viz. *Alternaria acuminata* (Rouse & Mustard), *Alternaria alternariata* (Kalgutkar & Sigler), *Alternaria bella* (Anil Chandra, R.K. Saxena & Setty), *Alternaria clavellata* (Z.-C. Song & G.-X. Li in Song et al.), *Alternaria psilata* (A. Gupta), *Alternaria saxenae* (A. Gupta) and *Alternaria sirmaurensis* (A. Gupta). In order to understand nomenclatural status of fossil taxa vis-a-vis extant ones, various provisions of the current Shenzhen Code (ICNafp) as well as those in previous Codes have been discussed.

**Keywords:** *Polycellaesporonites*, *Alternaria*, modern analog, nomenclature, deep time, palaeoecology, paleoenvironment.

## INTRODUCTION

Mycopalynology is an increasingly important aspect of palynology due to the utility of fungal palynomorphs as palaeoenvironmental indicators, regardless of the age of the sediments or rocks under study. Advances in the past 30 years, primarily through molecular clock evolutionary studies of fungal lineages (Tedersoo et al. 2018, Berbee et al. 2017) as well as collaborations between palynologists and modern mycologists (e.g. van Geel & Aptroot 2006, Hawksworth et al. 2016,

Nuñez Otaño et al. 2017, Shumilovskikh et al. 2017, Pound et al. 2019) have indicated that not only do many fungal lineages have extremely deep roots in geologic time but it is also possible to apply modern names, especially for families and sometimes genera, to fossil specimens. This has permitted a proliferation in fungal palaeoecology, primarily in studies of Quaternary-aged rocks and sediments (Gelorini et al. 2012, Musotto et al. 2017, Loughlin et al. 2021, Shumilovskikh et al. 2021), but beginning to extend well into the Cenozoic

and deeper in time (Pound et al. 2019, Smith et al. 2020, Romero et al. 2021). These developments and the establishment of Chapter F of the International Code of Nomenclature for Algae, Fungi, and Plants have resulted in a change in approach to fossil fungal nomenclature (Aime et al. 2021, O’Keefe et al. 2021). The most modern approach tries to avoid the use of morpho-taxonomic names (Elsik 1976, Kalgutkar & Jansonius 2000, Saxena et al. 2021, among others) wherever possible as this form-taxonomic system, while widely applied in biostratigraphy where there is a need to organize specimens by stratigraphic occurrence, is not useful for palaeoecology (Nuñez Otaño et al. 2021, Romero et al. 2021) and in some cases may introduce taxonomic instability by inadvertently giving extant taxa a different name in the fossil record (O’Keefe et al. 2021). Rather, it applies an extant classification where possible and assigns an identifying acronym where impossible, unless the case can be made that a morpho-taxonomic name is absolutely necessary. We acknowledge that this practice is not feasible in many cases due to a lack of identifying characters preserved in fossil spores, and pleomorphism present in several fungal taxa, especially among the *Ascomycota* (Wijayawardene et al. 2022). However, studies on fossil fungal spores in the light of new mycological developments provide stronger fossil tie-points for phylogenetic studies and the evolution of modern fungal assemblages worldwide (Pirozynski & Weresub 1979, Wingfield et al. 2012, O’Keefe et al. 2021).

The fossil fungal spore genus *Polycellaesporonites* was described by Chandra et al. (1984) with the following diagnosis: “Capsular fungal spores; inaperturate; one end of the spore is rounded while the other gives rise to a tube-like projection; multicellate; cells arranged in clusters, and not in a row or along a single axis; spore wall laevigate.” Kalgutkar and Jansonius (2000) emended the diagnosis of this genus as follows “Muriform spores with a hilum, and distally with an elongated, knob-like or beaked, extension; overall structure as that in the modern *Alternaria*”. Gupta (2002) again emended the diagnosis as follows: “Capsular spore, one end of the spore gives rise to tube like projection, multicellate, inaperturate, cells

arranged in clusters and not in a row or along a single axis, spore wall laevigate to ornamented”. Specimens of this type range from the Paleocene to the late Quaternary and species are known from the Arabian Sea, Canada, China, India and the U.S.A. (Chandra et al. 1984, Song et al. 1989, Kalgutkar & Sigler 1995, Kalgutkar & Jansonius 2000, Gupta 2002). This fossil genus greatly resembles the extant fungus *Alternaria*, and the range of its type species (*Polycellaesporonites bellus*) into the late Quaternary, raises issues with the original application of a fossil name, as most Quaternary taxa encountered in palynology are considered to be extant, thus a modern name should have been applied (O’Keefe et al. 2021).

The genus *Alternaria* is cosmopolitan and contains more than 700 species with saprobic, endophytic, and pathogenic lifestyles in a wide range of substrates (Woudenberg et al. 2013). This genus was described by Nees (1816) based on *A. tenuis*. Von Keissler (1912) synonymized *A. tenuis* with *Torula alternata* (Fries 1832) and established *Alternaria alternata* as the type species for this genus. *Alternaria* species are characterized as having “conidia catenate or solitary, dry, ovoid, obovoid, cylindrical, narrowly ellipsoid or obclavate, beaked or non-beaked, pale or medium olivaceous-brown to brown, smooth or verrucose, with transverse and with or without oblique or longitudinal septa. Septa can be thick, dark and rigid and an internal cell-like structure can be formed” (Woudenberg et al. 2013: 183). Also, the sexual state produces ascospores that are “muriform, ellipsoid to fusoid, slightly constricted at septa, yellow brown, without guttules, smooth, 3–7 transverse septa, 1–2 series of longitudinal septa through the two original central segments, end cells without septa, or with 1 longitudinal or oblique septum, or with Y-shaped pair of septa” (Woudenberg et al. 2013: 183).

While *Polycellaesporonites*’ spore affinity with *Alternaria* conidia was noted in its establishment (Chandra et al. 1984, Kalgutkar & Jansonius 2000), formal steps to transfer the fossil genus to *Alternaria* have not been made until now. We present the nomenclatural act of transference of the fossil genus *Polycellaesporonites* following the modern approach in line with the San Juan Chapter F (May et al. 2019,

O'Keefe et al. 2021). The results of this study indicate that this fossil genus is a later taxonomic synonym of the extant genus *Alternaria*.

## MATERIAL AND METHODS

The accepted fossil species of *Polycellaesporonites* and extant *Alternaria* species examined in this study were identified from published database records, including the Kalgutkar and Jansonius Database of Fossil Fungi ([https://advance.science.sfu.ca/fungi/fossils/Kalgutkar\\_and\\_Jansonius/index.php?-link=Home](https://advance.science.sfu.ca/fungi/fossils/Kalgutkar_and_Jansonius/index.php?-link=Home)), Index Fungorum ([www.indexfungorum.org](http://www.indexfungorum.org)), Species Fungorum ([www.speciesfungorum.org](http://www.speciesfungorum.org)), and MycoBank ([www.mycobank.org](http://www.mycobank.org)). The original descriptions for fossil and extant species were extracted from the articles noted in the databases (Chandra et al. 1984, Song et al. 1989, Kalgutkar & Sigler 1995, Rouse & Mustard 1997, Kalgutkar & Jansonius 2000, Gupta 2002, Simmons 2007, Woudenberg et al. 2013, among others). Known ranges of fossil taxa were cross-checked with the John Williams Index of Palaeopalynology (JWIP) housed at the Natural History Museum, London (Riding et al. 2012) and with more recent publications from India (Saxena et al. 2021).

## SYSTEMATIC MYCOLOGY

**Kingdom:** *Fungi*

**Phylum:** *Ascomycota*

**Class:** *Dothideomycetes*

**Order:** *Pleosporales*

**Family:** *Pleosporaceae*

**Genus:** *Alternaria* Syst. Pilze (Würzburg): 72 (1816) [1816–17]

**Type species:** *Alternaria alternata* (Fr.) Keissl., Beihefte zum Botanischen Centralblatt 29: 433 (1912) [MB#119834]

*Alternaria alternata* (Fr.) Keissl., Beihefte zum Botanischen Centralblatt 29: 433 (1912)

**MycoBank No.:** MB#119834

**Basionym:** *Torula alternata* Fr., Systema Mycologicum 3: 500 (1832) [MB#452904]

## Synonyms:

=*Embellisia* E.G. Simmons, Mycologia 63: 380 (1971) [MB#8149]

=*Alternaria* sect. *Embellisia* Woudenb. & Crous, Studies in Mycology 75: 190 (2013) [MB#803737]

=*Ulocladium* Preuss, Linnaea 24: 111 (1851) [MB#10346]

=*Alternaria* sect. *Ulocladium* Woudenb. & Crous, Studies in Mycology 75: 205 (2013) [MB#803747]

=*Chmelia* Svob.-Pol., Biológia Bratislava 21: 82 (1966) [MB#7626]

=*Macrosporium* Fr., Systema Mycologicum 3: 373 (1832) [MB#8821]

=*Nimbya* E.G. Simmons, Sydowia 41: 316 (1989) [MB#25376]

=*Alternaria* sect. *Nimbya* Woudenb. & Crous, Studies in Mycology 75: 197 (2013) [MB#803742]

=*Allewia* E.G. Simmons, Mycotaxon 38: 260 (1990) [MB#25500]

=*Lewia* M.E. Barr & E.G. Simmons, Mycotaxon 25 (1): 289 (1986) [MB#25583]

=*Elosia* Pers., Mycologia Europaea 1: 12 (1822) [MB#8147]

=*Prathoda* Subram., Journal of the Indian Botanical Society 35 (1): 73 (1956) [MB#9526]

=*Rhopalidium* Mont., Annales des Sciences Naturelles Botanique 6: 30 (1836) [MB#9743]

=*Trichoconiella* B.L. Jain, Kavaka 3: 39 (1976) [MB#10279]

=*Crivellia* Shoemaker & Inderbitzin, Canadian Journal of Botany 84 (8): 1308 (2006) [MB#522560]

=*Alternaria* sect. *Crivellia* Woudenb. & Crous, Studies in Mycology 75: 189 (2013) [MB#803735]

=*Ybotromyces* Rulamort, Bulletin de la Société Botanique du Centre-Ouest 17: 192 (1986) [MB#11225]

=*Chalastospora* E.G. Simmons, CBS Biodiversity Series 6: 668 (2007) [MB#505051]

-*Alternaria* sect. *Chalastospora* (E.G. Simmons) Woudenb. & Crous, *Studies in Mycology* 75: 188 (2013) [MB#803733]

=*Teretispora* E.G. Simmons, *CBS Biodiversity Series* 6: 674 (2007) [MB#505053]

-*Alternaria* sect. *Teretispora* Woudenb. & Crous, *Studies in Mycology* 75: 202 (2013) [MB#803745]

=*Botryomyces* de Hoog & C. Rubio, *Sabouraudia* 20: 19 (1982) [MB#7424]

=*Brachycladium* Corda, *Icones fungorum hucusque cognitorum* 2: 14 (1838) [MB#7439]

=*Sinomyces* Yong Wang bis & X.G. Zhang, *Fungal Biology* 115 (2): 192 (2011) [MB#513490]

=*Undifilum* B.M. Pryor, Creamer, Shoemaker, McLain-Romero & Hambl., *Botany* 87 (2): 190 (2009) [MB#540855]

-*Alternaria* sect. *Undifilum* Woudenb. & Crous, *Studies in Mycology* 75: 206 (2013) [MB#803748]

=*Polycellaesporonites* Anil Chandra, R.K. Saxena & Setty, *Biovigyanam* 10: 49 (1984) [MB#25604]

#### **Diagnosis for the conidia of *Alternaria* (Fr.)**

**Keissl.:** Conidia catenate or solitary, dry, ovoid, obovoid, cylindrical, narrowly ellipsoid or obclavate, beaked or non-beaked, pale or medium olivaceous-brown to brown, smooth or verrucose, with transverse and with or without oblique or longitudinal septa. Septa can be thick, dark and rigid and an internal cell-like structure can be formed.

**Section: *Alternata*** D.P. Lawr., Gannibal, Peever & B.M. Pryor, *Mycologia* 105: 538, figure 4. 2013.

**Type species:** *Alternaria alternata* (Fr.) Keissl.

**Diagnosis:** "Section *Alternata* contains straight or curved primary conidiophores, short to long, simple or branched, with one or several apical conidiogenous loci. Conidia are obclavate, long ellipsoid, small or moderate in size, septate, slightly constricted near some septa, with few longitudinal septa, in moderately long to long, simple or branched chains. The conidium body can narrow gradually into a tapered beak or secondary conidiophore. Secondary conidiophores can be formed

apically or laterally with one or a few conidiogenous loci." (Woudenberg et al. 2013:185)

***Alternaria alternata*** (Fr.) Keissl., *Beihefte zum Botanischen Centralblatt* 29: 433 (1912)

=*Alternaria tenuis* Nees, *System der Pilze und Schwämme*: 68, t. 5:68 (1817) [MB#211928]

=*Macrosporium fasciculatum* Cooke & Ellis, *Grevillea* 6 (37): 6 (1877) [MB#190904]

=*Alternaria fasciculata* (Cooke & Ellis) L.R. Jones & Grout, *Bull. Torrey bot. Club*: 257 (1897) [MB#445678]

=*Macrosporium erumpens* Cooke, *Grevillea* 12 (61): 32 (1883) [MB#183250]

=*Alternaria erumpens* (Cooke) P. Joly, *Encyclopédie Mycologique* 33: 199 (1964) [MB#326041]

=*Macrosporium polytrichi* Peck, *Annual Report on the New York State Museum of Natural History* 43: 77 (1890) [MB#243404]

=*Macrosporium meliloti* Peck, *Annual Report on the New York State Museum of Natural History* 33: 26 (1883) [MB#246007]

=*Macrosporium seguierii* Allesch., *Hedwigia* 33: 75 (1894) [MB#246499]

**Comments:** *Polycellaesporonites* is a synonym of the genus *Alternaria*. The fossil genus included seven species, with *Polycellaesporonites bellus* as the type species. The fossil spore's original description as a psilate to ornamented multicellular spore with one end giving rise to tube-like projection coincide with *Alternaria* conidia description despite slight differences in its length and width due to intraspecific variations. The extant genus currently has more than 700 species which are sub-divided into continually revised sections due to ever-increasing availability of molecular phylogenetic data and analyses (Lawrence et al. 2013, Woudenberg et al. 2013, 2015, Dettman & Eggerston 2021). Many of these species have high intraspecific variability of their asexual spores (Woudenberg et al. 2013), which makes use of spore character alone for assignment in a single taxon within *Alternaria*, much less a section, difficult.

### NEW COMBINATIONS

*Alternaria acuminata* (Rouse & Mustard) R.K. Saxena, Nuñez Otaño & O’Keefe **comb. nov.**

Figure 1

**Mycobank No.:** MB#843345.

**Basionym:** *Multicellaesporites acuminatus* Rouse & Mustard, *Palynology* 21: 208 (1997) [MB#463998].

**Homotypic Synonyms:** *Piriurella acuminata* (Rouse & Mustard) M.G. Parsons & G. Norris: 139 (1999) [MB#483924]; *Polycellaesporonites acuminatus* (Rouse & Mustard) Kalgutkar & Janson.: 249, A.A.S.P. Contributions Series 39: 249, plate 16, figure 16 (2000) [MB#483526].



**Figure 1.** *Alternaria acuminata* (Rouse & Mustard) R.K. Saxena, Nuñez Otaño & O’Keefe **comb. nov.** Scale Bar = 20  $\mu$ m.

**Original Diagnosis:** Fusiform fungal spores, consisting of 5–6 thin septa in each half; each septum with a small central pore; septa supporting an inner membranous body that is closely appressed to the outer wall in central regions, but contracted away from the outer wall towards the two pointed extremities; wrinkles occur sporadically on the inner wall that appear as elongate irregular plicae. Dimensions: range of length 62–68  $\mu$ m; of diameter 17–25  $\mu$ m.

**Location and age:** Strait of Georgia, eastern Vancouver Island, the Fraser River lowlands of southwest British Columbia, Canada and the North-western Washington State, U.S.A.; Late Palaeocene.

*Alternaria alternariata* (Kalgutkar & Sigler) R.K. Saxena, Nuñez Otaño & O’Keefe **comb. nov.**

Figure 2

**Mycobank No.:** MB#843343.

**Basionym:** *Piriurella alternariata* Kalgutkar & Sigler, *Mycol. Res.* 99(5): 518, Figure 14 (1995) [MB#413840].

**Homotypic Synonyms:** *Polycellaesporonites alternariatus* (Kalgutkar & Sigler) Kalgutkar & Janson., A.A.S.P. Contributions Series 39: 249, plate 16, figure 3 (2000) [MB#483527].



**Figure 2.** *Alternaria alternariata* (Kalgutkar & Sigler) R.K. Saxena, Nuñez Otaño & O’Keefe **comb. nov.** Scale Bar = 15  $\mu$ m.

**Original Diagnosis:** Conidia arising singly or in clusters; multicellate, muriform, solitary, ovoid to obclavate, rostrate, cicatrized or not, pale brown to brown, smooth. Conidia with a short conical beak and 8–12 transverse and several longitudinal or oblique septa; transverse septa more prominent and thicker than the longitudinal or oblique septa; terminal [apical] conical beak about 9–11  $\mu$ m broad, with a conspicuous dark thickened tip that probably represents the point of origin (attachment scar) of the next apical spore in the succession of a conidial chain. Conidia, when cicatrized, with a scar at the proximal end at the point of attachment to the conidiophore. Conidia 42–74  $\mu$ m long, 18–27  $\mu$ m wide in the broadest part.

**Location and age:** Kanguk Peninsula, Axel Heiberg Island, Northwest Territories, Canada; Late Paleocene or Early Eocene (Iceberg Bay Formation).

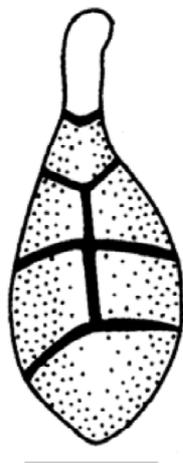
**Remarks:** This species has also been recorded from the intertrappean beds (Early Palaeocene) exposed at about 5 km west of Naredi, on Naliya-Narayan Sarovar Road, Kutch District, Gujarat, India (Saxena & Ranhotra 2009).

*Alternaria bella* (Anil Chandra, R.K. Saxena & Setty) R.K. Saxena, Nuñez Otaño & O'Keefe  
**comb. nov.**

Figure 3

**Mycobank No.:** MB#843342.

**Basionym:** *Polycellaesporonites bellus* Anil Chandra, R.K. Saxena & Setty, Biovigyanam 10(1): 49, plate 2, figure 20, text-figure 2. slide no. 6302/2. Repository: Museum, Birbal Sahni Institute of Palaeosciences, Lucknow, India (1984) [MB#107183].



**Figure 3.** *Alternaria bella* (Anil Chandra, R.K. Saxena & Setty) R.K. Saxena, Nuñez Otaño & O'Keefe **comb. nov.** Scale Bar = 15  $\mu$ m.

**Original Diagnosis:** Fungal spore with a capsular body and a tube-shaped unicellular appendage emerging from one end; size range 45–68  $\times$  13–15  $\mu$ m; main body of spore 33–48  $\times$  13–15  $\mu$ m; tube-like projection hyaline, 12–20  $\mu$ m long, multicellate individual cells rectangular, not arranged along one axis; inaperturate; spore wall 1–1.5  $\mu$ m thick, psilate.

**Location and age:** Sediment core no. 1 (Lat. 17°57.92 N; Long. 70°46.02 E), Arabian Sea; Late Quaternary.

**Remarks:** Chandra et al. (1984) suggested possible affinity of this species to *Alternaria* sp. This

taxon, whose definition is based on Late Quaternary spore remains, is morphologically identical to spores produced by the extant *A. alternata*. However, presently we are following the precedent of O'Keefe (2017) and Nuñez Otaño et al. (2017) in choosing not to equate the species given the age of the fossil material, the high degree of intraspecific variability of spore produced by many *Alternaria* species, and the need for detailed concurrent stratigraphic and molecular genetic study of the taxon, which is beyond the scope of this paper. This species has also been recorded from the Pinjor Formation (Pliocene) of Ambala District, Haryana, India (Saxena et al. 1988); Lower Siwalik-Nahan and Upper Siwalik (Middle Miocene-Pliocene) of Sirmour District, Himachal Pradesh, India (Saxena & Bhattacharyya 1987) and Dharmsala Group (Oligocene-Early Miocene) near Dharmsala, Kangra District, Himachal Pradesh, India (Saxena & Bhattacharyya 1990).

*Alternaria clavellata* (Z.-C. Song & G.-X. Li in Song et al.) R.K. Saxena, Nuñez Otaño & O'Keefe  
**comb. nov.**

Figure 4

**Mycobank No.:** MB#843347.

**Basionym:** *Pluricellaesporites clavellatus* Z.-C. Song & G.-X. Li in Song et al., Early Tertiary spore-pollen assemblages from the Dongpu region: 40, plate 2, figure 21 (1989) [MB#485254].



**Figure 4.** *Alternaria clavellata* (Z.-C. Song & G.-X. Li in Song et al.) R.K. Saxena, Nuñez Otaño & O'Keefe **comb. nov.** Scale Bar = 20  $\mu$ m.

**Homotypic Synonym:** *Polycellaesporonites clavellatus* (Z.-C. Song & G.-X. Li in Song et al.) Kalgutkar & Janson., A.A.S.P. Contributions Series 39: 250, plate 16, figure 1 (2000) [MB#483528].

**Original Diagnosis:** Spores clavate with a long stipe and wide middle part, tapering toward both ends; about 100 µm in length, widest part about 18 µm in width. Spores multicellular, cells flat, some middle cells appear to be subdivided [by longitudinal septa]. Septa generally without septal folds and pores. Stipe of one cell, about 30 µm in length, with an attachment scar or pore at the [proximal] end. Spore wall less than 1 µm in thickness, surface smooth.

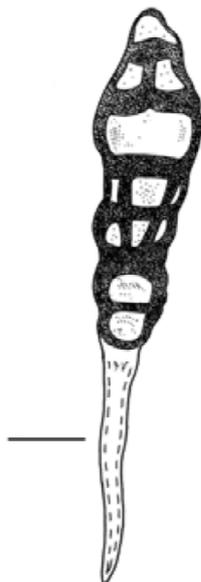
**Location and age:** Heze County and Shenxian County of Shandong Province, China; Middle-Late Oligocene (Shahejie and Dongying formations).

*Alternaria psilata* (A. Gupta) R.K. Saxena, Nuñez Otaño & O’Keefe **comb. nov.**

Figure 5

**Mycobank No.:** MB#843341.

**Basionym:** *Polycellaesporonites psilatus* A. Gupta, Tertiary Research 21(1–4): 146, plate 4, figure 7, slide no. BSIP 10294/1, coordinates 20.0 × 96.7. Repository: Museum, Birbal Sahni Institute of Palaeosciences, Lucknow, India (2002) [MB# 540760].



**Figure 5.** *Alternaria psilata* (A. Gupta) R.K. Saxena, Nuñez Otaño & O’Keefe **comb. nov.** Scale Bar = 10 µm.

**Original Diagnosis:** Spores multicelled, elongate, showing cells arranged in clusters along more than one axis at one end and a tube-like appendage at other, inaperturate, 37–78 µm long, number of cells across its width of cell clusters ranges up to 3 or more, psilate, surface folded.

**Location and age:** Dadahu Road Section, Sirmaur District, Himachal Pradesh, India; Late Palaeocene to Early Oligocene (Subathu Formation).

**Remarks:** The species was named after its psilate spore wall.

*Alternaria saxenae* (A. Gupta) R.K. Saxena, Nuñez Otaño & O’Keefe **comb. nov.**

Figure 6

**Mycobank No.:** MB#843340.

**Basionym:** *Polycellaesporonites saxenae* A. Gupta, Tertiary Research 21(1–4): 145, plate 4, figure 4, slide no. BSIP 10339/6, coordinates 26.2 × 103.3. Repository: Museum, Birbal Sahni Institute of Palaeosciences, Lucknow, India (2002) [MB# 540761].



**Figure 6.** *Alternaria saxenae* (A. Gupta) R.K. Saxena, Nuñez Otaño & O’Keefe **comb. nov.** Scale Bar = 5 µm.

**Original Diagnosis:** Spores multicelled, elongate, showing cells arranged in clusters along more than one axis at one side and a tube-like appendage at other, inaperturate, measuring 35–75 µm long, three or more cells across width, granulate, sculptural elements distinct at cell clusters but indistinct at appendage, surface folded.

**Location and age:** Jamtah Road Section, Sirmaur District, Himachal Pradesh, India; Late Palaeocene to Early Oligocene (Subathu Formation).

**Remarks:** The species was named to honour Dr. Ramesh K. Saxena, Birbal Sahni Institute of Palaeosciences, Lucknow, India.

*Alternaria sirmaurensis* (A. Gupta) R.K. Saxena, Nuñez Otaño & O’Keefe **comb. nov.**

Figure 7

**Mycobank No.:** MB#843339.

**Basionym:** *Polycellaesporonites sirmaurensis* A. Gupta, Tertiary Research 21(1–4): 145, plate 4, figure 3, slide no. BSIP 10311/4, coordinates 28.2 × 92.4. Repository: Museum, Birbal Sahni Institute of Palaeosciences, Lucknow, India (2002) [MB# 540762].



**Figure 7.** *Alternaria sirmaurensis* (A. Gupta) R.K. Saxena, Nuñez Otaño & O’Keefe **comb. nov.** Scale Bar = 15 µm.

**Original Diagnosis:** Spores multicelled, elongate, showing cells arranged in clusters along more than one axis at one side and a tube-like appendage at other, inaperturate, measuring 26–58 µm long, number of cells across the width of cells cluster ranges up to 2, largely granulate, sculptural elements distinct at cluster but indistinct at appendage, surface folded.

**Location and age:** Dadahu Road Section, Sirmaur District, Himachal Pradesh, India; Late Palaeocene to Late Eocene (Subathu Formation).

**Remarks:** The species was named after Sirmaur district, where its type locality is situated.

## DISCUSSION

The morphological characters of fossil and extant

*Alternaria* spores are identical, as noted by many authors, including Cookson and Eisenack (1979), Mustard and Rouse (1994), Parsons and Norris (1999) and Kalgutkar and Jansonius (2000). However, these authors, along with Elsik (1992), questioned the occurrences of deep-time *Alternaria* in large part based on assumptions that extant taxa represent recent evolutionary innovations and that evolutionary convergence may cause ancient extinct lineages to resemble modern lineages. That said, the erection of the genus *Polycellaesporonites* for material obtained in 1972 from “Late Quaternary” sediments – an age range that now encompasses the Holocene and Late Pleistocene (Cohen et al. 2013, rev. 2021) – is itself problematic. Common practice in palynology is to treat Quaternary and younger organisms as members of extant taxa (O’Keefe et al. 2021). From this perspective, *Polycellaesporonites* should not have been erected. The Code is retroactive (Gravendyck et al. 2021; Turland 2018). However, making examination of the version of the Code which was active at the time of erection of *Polycellaesporonites* can throw light on the validity of its erection at that time. The Sydney Code (1983) does not prevent the erection of form-genera for fossils, or for fungal anamorphs (see articles 3.3, 7.16, 11.1 and 58), and does permit the use of descriptions or figures to designate types (see article 9.3) and article 11.1 implies that separate names for form-taxa of *Fungi* and form-genera of fossils are allowable, even though they violate the “... earlier part of the provision – each family or taxon of lower rank with a particular circumscription, position, and rank can bear only one correct name...” To this point, the erection of *Polycellaesporonites* seems reasonable. The 1983 code further notes in Article 13.3 that “fossil material is distinguished from non-fossil material by stratigraphic relations at the site of original occurrence. In case of doubtful stratigraphic relations, provisions for non-fossil taxa apply.” This brings the question of where within stratigraphy are palynomorphs considered “fossils?” There is no consensus answer to this question.

For *Polycellaesporonites*, this is especially challenging, as the stratigraphy of the holotype is not well-reported. Chandra et al. (1984) reported that it came from sample 3 (~56cm) and sample 8 (~144cm)

of Core 1 (USC & GSS Oceanographer Global Expedition OPR-476, Bombay-Bombay leg, Station Serial Number 29, depth to top 649 m with a total core length of 175 cm) (Setty 1972). Setty (1972) notes that the materials at both sampling horizons are unconsolidated clay with ooids, and that slump features are present throughout the section. Neither sets of authors report radiometric age dates for material from Core 1, but do report two dates from Core 2 (USC & GSS Oceanographer Global Expedition OPR-476, Bombay-Bombay leg, Station Serial Number 43, depth to top 2960 m with a total core length of 190 cm) (Setty 1972): sample 1 (~2cm) is  $9830 \pm 180$  years BP, while sample 7 (~100cm) is  $20940 \pm 450$  BP, and assume a “normal” depositional rate (Chandra et al. 1984), which can be calculated as approximately 0.0082 cm/yr. They also present a correlation of the cores, assuming that the tops are co-eval, as they represent the sea-floor surface. If we then apply the age-depth model based on linear interpolation to Core 1, this produces dates of ~6,829 BP and ~17,560 BP for Core 1 samples 3 and 8, respectively, placing them in the middle Holocene and Late Pleistocene. Most palynologists would agree that palynomorphs from this range of ages are not “fossils” per se and likely represent extant taxa.

Within the current code (the Shenzhen Code and San Juan Section F) (Turland et al. 2018; May et al. 2019), this is even more clearly stated – the provisions of the code apply to all fungi, whether fossil or extant (Preamble 8). This inadvertently places fossil names given to presumably extant taxa in competition for priority with non-fossil names. In this case, the genus *Alternaria* (Syst. Pilze (Würzburg) 1816) has priority over the genus *Polycellaesporonites* Anil Chandra, R.K. Saxena & Setty 1984, thus it was equated, above. Handling the species is more challenging. At present, there is no clear provision in the code (Chapter 2, Section 4, Article 13.3) for when in geologic time or at what depth within the stratigraphy an organismal remain is considered a fossil, nor is there consensus among paleontologists. As it stands, there is an apparent gap of more than 6,000 years between the earliest described fossil species and the extant species which produces virtually identical spores. While dispersed

parts of a whole organism can and are used to define fungal taxa (Pirozynski & Weresub 1979), this approach is considered outdated and polyphasic approaches are preferred (Lücking et al. 2020, Aime 2021). It is presently impossible to conduct a combined molecular, genetic and morphological study on young fossils of *Alternaria*, which may contain viable nuclear material, much less ancient fossils which no longer contain viable nuclear material, thus they cannot be reliably placed in any extant species. We therefore have chosen to follow the precedent of O’Keefe (2017) and Nuñez Otaño et al. (2017) and transfer the validly defined species of *Polycellaesporonites* to new fossil species within *Alternaria*.

With the transfer of *Polycellaesporonites* to *Alternaria*, the range of that genus is extended to the late Palaeocene (Gupta 2002, Riding et al. 2012). This range is consistent with the time-calibrated phylogeny for the *Pleosporaceae* presented by Beimford et al. (2013), and with the divergence time for *Alternaria* from *Pyrenophora* of 50.4 MA, as calculated by Hou et al. (2016). No fossil tie-point was used for the origin of *Alternaria* in this phylogeny; the similar origin times indicated by molecular genetics and fossil occurrences highlights the utility of clarifying evolutionary relationships between fossil-taxa and extant organisms and elimination of competing generic names for long-ranging taxa.

## CONCLUSION

As *Polycellaesporonites* spores are morphologically identical to extant *Alternaria* spores, we consider *Polycellaesporonites* Anil Chandra, R.K. Saxena & Setty 1984 to be a later taxonomic synonym of *Alternaria* Nees 1816. However, as molecular studies of *Alternaria* have demonstrated that it is a highly diverse genus with interspecific variation in spore characters (Joly 1964, Simmons 2007, Wang et al. 2011, Lawrence et al. 2012, Woudenberg et al. 2013, 2015, Dettman & Eggerston 2021), and for the sake of taxonomic stability at the present time, we transfer previously defined species of *Polycellaesporonites* to the genus *Alternaria* as new fossil species. A necessary next step in the study of the genus *Alternaria* is a

polyphasic examination of near-surface Holocene (and older) fossil specimens that contain amplifiable nuclear material in conjunction with a detailed morphological study of dispersed reproductive parts.

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