

Fossil *Helicosporae*: global diversity, morphological variations and distribution in time and space

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ABSTRACT

Saxena R.K. 2022. Fossil *Helicosporae*: global diversity, morphological variations and distribution in time and space. *Geophytology* 51(1&2): 87–108.

Fossil fungal spores exhibit a variety of morphological variations. These may be unicellate, dicellate, tricellate, multicellate, muriform, filiform, spirally coiled, star-like, etc. The present paper deals with helicospores (spirally coiled) only. The morphological features considered for the identification of these spores are shape, size, symmetry, presence/absence and nature of aperture, nature of coiling and ornamentation of spore wall. Altogether, fossil helicospores have been described under ten legitimately published genera the world over. These are: *Circinoconites* R. Kar et al. 2010 (1 sp.), *Colligerites* K.P. Jain & R.K. Kar 1979 (2 spp.), *Elsikisporonites* P. Kumar 1990 (1 sp.), *Helicominites* Barlinge & Paradkar 1982 (1 sp.), *Helicoonites* Kalgutkar & Sigler 1995 (1 sp.), *Helicosporiates* Kalgutkar & Sigler 1995 (1 sp.), *Involutisporonites* R.T. Clarke 1965 (3 spp.), *Palaeocirrenalia* Ramanujam & Srisailam 1980 (2 spp.), *Paleoslimacomyces* Kalgutkar & Sigler 1995 (3 spp.) and *Retihelicosporonites* Ramanujam & K.P. Rao 1978 (1 sp.). Under these genera, 16 species have so far been described. The dominant genera, both in number and variety, are *Involutisporonites* R.T. Clarke 1965 (3 spp.), *Paleoslimacomyces* Kalgutkar & Sigler 1995 (3 spp.), *Colligerites* K.P. Jain & R.K. Kar 1979 (2 spp.) and *Palaeocirrenalia* Ramanujam & Srisailam 1980 (2 spp.). Other genera are monotypic. Helicospores have been recorded from Antarctica, Canada, India and U.S.A. In India, these have been recorded from many states, e.g. Andhra Pradesh, Gujarat (Kutch and Cambay basins), Kerala, Madhya Pradesh, Maharashtra, Mizoram and Tamil Nadu. Although fungal spores are of limited value in biostratigraphy, these can be useful in the evaluation of the palaeoenvironments, particularly those that can be related to modern taxa.

Keywords –Fossil fungi, fungal spores, *Helicosporae*, global diversity, morphological variations, India.

INTRODUCTION

During the last hundred years, serious efforts have been made on the study of fossil fungi the world over. Kalgutkar and Jansonius (2000) published a synopsis of fossil fungi and tried to streamline taxonomic status of almost all fossil fungal genera and species. In order to include all records of fossil fungal remains from the Indian Tertiary sediments, published till 2005, three catalogues were published (Lakhanpal et al. 1976, Saxena 1991, 2006). In addition, a monographic study

was carried out by Saxena and Tripathi (2011) with the objective to synthesize the available information on Indian fossil fungi.

In the present paper, fossil fungal spores have been treated according to Saccardoan system of grouping the spores (e.g. *Amerosporae*, *Didymosporae*, *Phragmosporae*, *Dictyosporae*, *Helicosporae*, *Staurosporae* and *Scolecosporae*). Here, in this paper, only helicospores are dealt with. These are uni- to multicellate spores, with curved axis, spirally coiled in

one plane or twisted in three planes. Helicospores are not found in all fossil fungal assemblages because they are produced by only a few fungi. Clarke (1965) instituted *Involutisporonites* (Type: *I. foraminus* R.T. Clarke 1965) from the Vermejo Formation coal beds (Late Cretaceous) of Central Colorado, U.S.A. which is similar to extant species of *Cirrenalia* Meyers & R.T. Moore. This confirms the presence of a group of helicoid fungi in the Cretaceous Period. Pirozynski (1978) observed that coiled helicospores are generally more distinctive than dicellate didymospores or unicellate amerospores and recognizability of dispersed ascospores and conidia increases with the complexity of their morphology. Helicoid spores like *Involutisporonites*, *Helicosporiates*, *Helicoonites*, *Palaeocirrenalia* and *Paleoslimacomycetes* are so discrete that they are readily identifiable. Ramanujam and Srisailam (1980) described helicoid spore genus *Palaeocirrenalia* from the Neogene sediments of Kerala, South India. Kalgutkar and McIntyre (1991) described two helicosporous fungal types (now known as *Helicoonites* and *Helicosporiates*) from the Eocene Eureka Sound Formation in the Canadian Arctic. Kalgutkar and Sigler (1995) instituted *Helicoonites* (Type: *H. goosii* Kalgutkar & Sigler 1995), *Helicosporiates* (Type: *H. pirozynskii* Kalgutkar & Sigler 1995) and *Paleoslimacomycetes* (Type: *P. canadensis* Kalgutkar & Sigler 1995). Kar et al. (2010) instituted genus *Circinoconites* (Type: *C. arthrus* R. Kar et al. 2010) from the Bhuban Formation (Miocene) of Mizoram, India. The helicospores are described under different morphologic taxa on the basis of characters associated with shape and size, symmetry, number and nature of cells, septa, pores, nature of coiling, spore wall, etc. Day (1991) published an overview of fossil fungi in the Geodetic Hills Fossil Forest, Axel Heiberg Island, North-West Territories, Canada.

GLOBAL DIVERSITY IN FOSSIL *HELICOSPORAE*

The helicospores recorded so far, the world over, have been allocated to ten genera and 16 species. The

dominant genera, both in number and variety, are *Involutisporonites* R.T. Clarke 1965 (3 spp.), *Paleoslimacomycetes* Kalgutkar & Sigler 1995 (3 spp.), *Colligerites* K.P. Jain & R.K. Kar 1979 (2 spp.) and *Palaeocirrenalia* Ramanujam & Srisailam 1980 (2 spp.). The remaining six genera, viz. *Circinoconites* R. Kar et al. 2010, *Elsikisporonites* P. Kumar 1990, *Helicominites* Barlinge & Paradkar 1982, *Helicoonites* Kalgutkar & Sigler 1995, *Helicosporiates* Kalgutkar & Sigler 1995 and *Retihelicosporonites* Ramanujam & K.P. Rao 1978 are represented by only a single species each.

The fossil helicospore genera, known so far, are described ahead (arranged in alphabetical order). Species are also arranged in alphabetical order under each genus. Following information is provided for genera: Name of the genus with its author(s) and year of publication, Index Fungorum Registration Identifier, Type species, Original Diagnosis (and subsequent Emended Diagnosis, if any), Number of species known and Remarks, wherever required. Similarly, the following information is provided for species: Name of the species with its author(s) and year of publication, Index Fungorum Registration Identifier, Basionym/Synonym, if any, Original Description, Location, Age and Remarks, wherever required. Each species is provided with a hand-drawn illustration.

Genus: *Circinoconites* R. Kar et al. 2010

Index Fungorum Registration Identifier: 541647.

Type species: *Circinoconites arthrus* R. Kar et al. 2010.

Original Diagnosis: Fungal conidia, conidia acrogenous, strongly spiralled, spirals 30–39 × 25–31 μm; solitary, coiled, not in chains or slime, 8–14 septate, fist-shaped, dark brown, constricted at septa, cells increasing in diameter from base to apex, dissimilar, spirally arranged. Monotypic (Kar et al. 2010, p. 246).

Number of species known: One.

Circinoconites arthrus R. Kar et al. 2010

Figure 1

Index Fungorum Registration Identifier: 542238.

Original Description: Conidia arise from tip of conidiophores, helicoid, looking like fist, $42\text{--}30 \times 23\text{--}27 \mu\text{m}$, made up of 10–16 cells, cells increase in size from base to top; basal cell rectangular, $6\text{--}8 \times 4\text{--}6 \mu\text{m}$, 3–4 lower cells straight, rest cells coiled, septate, septa up to $2 \mu\text{m}$ thick, constriction more marked in middle region, individual cells rectangular–wedge shaped, terminal cell oval–subcircular, $11\text{--}18 \times 12\text{--}16 \mu\text{m}$; spore wall about $1 \mu\text{m}$ thick, mostly laevigate, sometimes weakly intrastriated. (Kar et al. 2010, p. 246).



Figure 1. *Circinoconites arthrus* R. Kar et al. 2010. Scale Bar = $10 \mu\text{m}$.

Location: Tlamsam, Champhai District, Mizoram, India.

Age: Miocene (Bhuban Formation).

Genus: *Colligerites* K.P. Jain & R.K. Kar 1979

Index Fungorum Registration Identifier: 21058.

Type species: *Colligerites kutchensis* (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar 1979.

Original Diagnosis: Spores multicellular, coiled, cells generally smaller, rounded in central region and bigger, rectangular in outer region. Spore wall mostly laevigate, sometimes granulose. Pore may be present or absent in each cell (Jain & Kar 1979, p. 110).

Number of species known: Two.

Remarks: According to Jain and Kar (1979), *Colligerites* closely resembles the extant spores of

Hobsonia mirabilis (Peck) Linder illustrated by Subramanian (1971). The spores of the modern species *Vanbeverwijkia spirospora* Agnihotr., *Helicoma mulleri* Corda and *Helicomycetes roseus* Link also broadly resemble this species but all are distinguished by their different coiling nature (Kendrick & Carmichael in Ainsworth et al. 1973).

Colligerites kutchensis (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar 1979

Figure 2

Index Fungorum Registration Identifier: 112205.

Basionym: *Involutisporonites kutchensis* R.K. Kar & R.K. Saxena 1976.

Original Description: Coiled, laevigate, generally monoporate fungal spores. Cells in central region darker with thicker wall and rhomboid-squarish shape, outer cells thinner but longer, having rectangular shape. Holotype $72 \times 72 \mu\text{m}$ (Kar & Saxena 1976, p. 12).

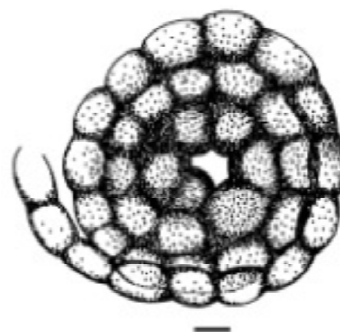


Figure 2. *Colligerites kutchensis* (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar 1979. Scale Bar = $8 \mu\text{m}$.

Location: Bhuj-Lakhpat Road, Matanomadh Village, Kutch District, Gujarat, India (Kar & Saxena 1976), Papanasam and Varkala, Kerala, India (Jain & Kar 1979).

Age: Palaeocene (Kar & Saxena 1976), Miocene (Jain & Kar 1979).

Colligerites trochus B. Samant in R.K. Saxena 2009

Figure 3

Index Fungorum Registration Identifier: 515017.

Synonym: *Colligerites trochus* B. Samant 2000 (nom. inval.) fide Saxena (2009).

Original Description: Fungal spores multicellular; coiled; trochospiral coiling; 47–60 μm in diameter; nonaperturate; first cell smallest, dark in colour and almost indistinct, cells of inner circle dark and fused, cell size gradually increases from centre to outer region, individual cell rectangular in shape; spore wall smooth (Samant 2000, p. 12).

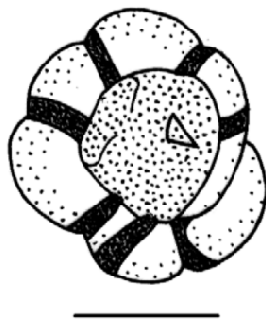


Figure 3. *Colligerites trochus* B. Samant in R.K. Saxena 2009. Scale Bar = 30 μm .

Location: Near Bhavnagar, Cambay Basin, Gujarat, India.

Age: Early Eocene (Kharsalia Clay Formation).

Remarks: Samant (2000) described *Colligerites trochus* but did not validly publish it because its protologue contained no information regarding holotype locations (Turland et al. 2018: Art. 40.7). This name was validated and was ascribed to B. Samant based on the original descriptions and illustrations by Saxena (2009). The holotype was designated by Samant (2000) and is stored in the Geology Department, Nagpur University, Nagpur, India (Dr. Bandana Samant, personal communication).

In addition to the above, the following species originally ascribed to *Colligerites* K.P. Jain & R.K. Kar 1979 has been recombined with *Involutisporonites* R.T. Clarke 1965, as follows.

Colligerites chowdhryi K.P. Jain & R.K. Kar 1979 (Index Fungorum Registration Identifier: 112034). Current name: *Involutisporonites chowdhryi* (K.P. Jain & R.K. Kar) Kalgutkar & Janson. 2000 fide Kalgutkar & Jansonius (2000).

Genus: *Elsikisporonites* P. Kumar 1990

Index Fungorum Registration Identifier: 25441.

Type species: *Elsikisporonites tubulatus* P. Kumar 1990.

Original Diagnosis: Fungal spores monoporate, aseptate, tubular and coiled. Pore at outer end, nozzle-like. Spore wall smooth and pale. Monotypic (Kumar 1990, p. 18).

Number of species known: One.

Remarks: According to Kumar (1990), *Elsikisporonites* resembles the conidiogenous cells (conidia) produced by *Helicosporium* Nees (Kendrick & Carmichael in Ainsworth et al. 1973). The generic name honours Dr. William C. Elsik.

Elsikisporonites tubulatus P. Kumar 1990

Figure 4

Index Fungorum Registration Identifier: 126558.

Original Description: Fungal spores monoporate, aseptate, tubular in shape and coiled. Cell broadest in the middle region, 10–12 μm wide, gradually tapering towards the ends. Pore at free outer end, small, nozzle-like, 1.5 μm wide. Spore wall 1 μm thick, smooth, slightly folded, pale brown. Overall dimensions: ca 36 \times 386 μm (Kumar 1990, p. 18).

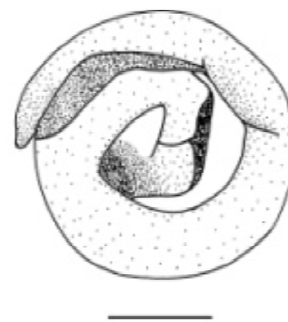


Figure 4. *Elsikisporonites tubulatus* P. Kumar 1990. Scale Bar = 12 μm .

Location: Padappakkara, Kollam District, Kerala, India.

Age: Early-Middle Miocene.

Remarks: *Elsikisporonites tubulatus* is distinguished from other helicosporous species by its lack of septa. *Helicosporites* is characterized by more narrow cylindrical filaments with many concentric spirals.

Genus: *Helicominites* Barlinge & Paradkar 1982

Index Fungorum Registration Identifier: 21126.

Type species: *Helicominites salvinites* Barlinge & Paradkar 1982.

Original Diagnosis: Fungus saprophytic [saprobic]; mycelium septate, branched, hyphae faint in colour; pycnidium and acervulus absent; conidia coiled in loose spirals and narrow at both ends. Monotypic (Barlinge & Paradkar 1982, p. 167).

Number of species known: One.

Helicominites salvinites Barlinge & Paradkar
1982

Figure 5

Index Fungorum Registration Identifier: 108905.

Original Description: Saprophytic fungus found inside *Salvinia intertrappea* megaspores, in space usually occupied by female gametophyte; mycelium 5–6 µm in breadth; conidia loosely, spirally coiled, 21–32 × 20–30 µm, narrow at both ends. Monotypic (Barlinge & Paradkar 1982, p. 167).

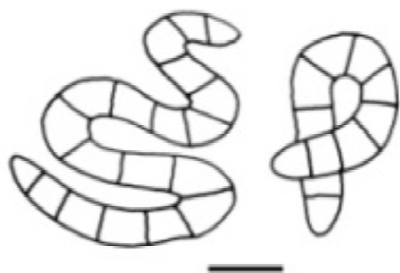


Figure 5. *Helicominites salvinites* Barlinge & Paradkar 1982. Scale Bar = 10 µm.

Location: Mohgaon Kalan, Chhindwara District, Madhya Pradesh, India.

Age: Cretaceous – Maastrichtian (Deccan Intertrappean Series).

Remarks: *Helicominites salvinites* resembles the genus *Helicomina* L.S. Olive of *Dothideomycetes* because of the coiled, thin-walled and hyaline conidia.

Genus: *Helicoonites* Kalgutkar & Sigler 1995 (as ‘*Helicoönites*’)

Index Fungorum Registration Identifier: 622357.

Type species: *Helicoonites goosii* Kalgutkar & Sigler 1995.

Original Diagnosis: Conidia simple, tightly coiled or twisted in three planes to form an ovoid, ellipsoidal (doliiform) to cylindrical or beehive to barrel-shaped spiral; spirals made up of variable numbers of ascending coils or gyres, with each successive gyre usually of smaller diameter; filaments multiseptate, fuscous; cells rectangular. Monotypic (Kalgutkar & Sigler 1995, p. 519).

Number of species known: One.

Remarks: Kalgutkar and McIntyre (1991) described and illustrated these spores as *Helicoon/Helicodendron*-type. Although it is easy to identify a helicosporous conidium because of its distinctively twisted structure, the conidia of some species of *Helicoon* Morgan and *Helicodendron* Peyronel are so similar in appearance that it becomes impossible to separate them on the basis of their morphology alone. *Helicoonites* Kalgutkar & Sigler 1995 is created to encompass all fossil helicosporous conidia with a definite ellipsoidal, ovoid or doliiform shape, and that are loosely to tightly coiled or twisted in three planes. *Helicoonites* differs from *Involutisporonites* R.T. Clarke 1965 emend. Elsik 1968, *Colligerites* K.P. Jain & R.K. Kar 1979, *Helicominites* Barlinge & Paradkar 1982, *Helicosporiates* Kalgutkar & Sigler 1995 and *Paleoslimacomycetes* Kalgutkar & Sigler 1995 by its helically coiled filaments in ellipsoidal to beehive-shaped spirals. Except *Helicominites*, in these genera the conidia are generally flat and coiled in one plane. In *Helicominites* the conidia are bent or twisted in different directions. Goos et al. (1986) mentioned the occurrence of nearly 650-yr old specimens from an archaeological site near Beetley, Norfolk, England, that appear to be

assignable to modern *Helicoon richonis* (Boud.) Linder. The conidia of this subfossil were slightly larger than those of the extant species, but otherwise appeared similar in shape and colour.

Helicoonites goosii Kalgutkar & Sigler 1995

Figure 6

Index Fungorum Registration Identifier: 627571.

Original Description: Conidia simple, smooth, tightly coiled in three planes to form an ellipsoidal (doliiform) to cylindrical spore body; filaments multiseptate, about 5 µm wide, fuscous; cells rectangular, not incurved at the septa, transverse pattern of minute, apparently internal striae commonly present. Conidia 50–75 × 37–45 µm (Kalgutkar & Sigler 1995, p. 520).

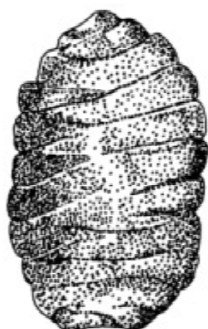


Figure 6. *Helicoonites goosii* Kalgutkar & Sigler 1995. Scale Bar = 10 µm.

Location: Strand Fiord, Axel Heiberg Island, Northwest Territories, Canada.

Age: Early Eocene (Iceberg Bay Formation).

Remarks: According to Kalgutkar & Sigler (1995), *Helicoonites goosii* appears more closely allied to species of *Helicoon* (Goos et al. 1986) such as *H. richonis* than to species of *Helicodendron* (Goos et al. 1985). The species epithet honours Dr. R.D. Goos.

Genus: *Helicosporiates* Kalgutkar & Sigler 1995

Index Fungorum Registration Identifier: 15012.

Type species: *Helicosporiates pirozynskii* Kalgutkar & Sigler 1995.

Original Diagnosis: Conidia simple, pale brown to brown, helicoid; spirals of loose to tightly coiled filaments; filaments slender, multicellular. Conidia usually helically coiled in one plane or somewhat cochleate. Monotypic (Kalgutkar & Sigler 1995, p. 520).

Number of species known: One.

Remarks: Kalgutkar and McIntyre (1991) described and illustrated these spores as *Helicosporium*-type. The conidia of modern *Helicosporium* Nees are very similar to those of *Helicomycetes* Link. The conidia of species of both genera have conidial filaments that are septate or indistinctly septate and broadly to narrowly cylindrical. However, the conidia of *Helicosporium* are mostly brown in contrast to those of *Helicomycetes* which are invariably hyaline. *Helicosporiates* differs from *Involutisporonites* R.T. Clarke 1965 emend. Elsik 1968, in having conidial spirals made up of multicellular filaments consisting of slender cells with sometimes indistinct septa.

Helicosporiates pirozynskii Kalgutkar & Sigler 1995

Figure 7

Index Fungorum Registration Identifier: 413166.

Original Description: Conidia simple, pale brown to brown, smooth, helicoid. Conidial filaments forming the spirals coiled 2–4 times in one plane or cochleate; filaments slender, multicellular, smooth, about 5 µm wide; septa present, or sometimes indistinct; cells cuboid to rectangular, not indented at the septa. Conidia 30–40 µm diameter (Kalgutkar & Sigler 1995, p. 520).

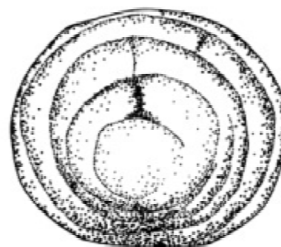


Figure 7. *Helicosporiates pirozynskii* Kalgutkar & Sigler 1995. Scale Bar = 8 µm.

Location: Strand Fiord, Axel Heiberg Island, Northwest Territories, Canada.

Age: Early Eocene (Iceberg Bay Formation).

Remarks: Kalgutkar and Sigler (1995) opined that because of its fuscous and loosely to tightly coiled conidia, *Helicosporiates pirozynskii* appears to be more closely affiliated to *Helicosporium* Nees than to *Helicomycetes* Link. Characteristically, pigmentation appears to be greatest in the outside (peripheral) region of each coil. The species epithet honours Dr. Kris A. Pirozynski.

Genus: *Involutisporonites* R.T. Clarke 1965

Index Fungorum Registration Identifier: 21142.

Type species: *Involutisporonites foraminus* R.T. Clarke 1965.

Original Diagnosis: Fungal spores planispiral, individual cells lobate, septa simple with an opening through each septum (Clarke 1965, p. 90).

Emended Diagnosis: Monoporate, psilate, multiseptate, coiled fungal spores (Elsik 1968, p. 276).

Emended description: Fungal spore coiled, transversely septate, multicellate, individual cells of variable shapes, septal pores may or may not be present, terminal cell if present, may have a single pore, spore wall generally psilate to variously ornamented (Elayaraja & Kumarasamy 2016, p. 8).

Number of species known: Seven (but only three species are accepted as legitimate because four species have been transferred to other genera).

Remarks: Clarke (1965) named the genus in reference to the involute arrangement of the cells. According to Elsik (1968), the presence or absence of a pore in each septum may not be a constant feature. If present, the pore may be obscured in darkly pigmented forms. The septa may also be broken in some specimens, further obscuring the nature of any connecting pores. Song and Cao (1994) instituted *Involutisporonites crassus* (Index Fungorum Registration Identifier: 483775; originally published as *Involutisporonites? crassus*) from Late Cretaceous sediments of King

George Island, Antarctica. The description and illustration of this species could not be assessed for further comments.

Involutisporonites chowdhryi (K.P. Jain & R.K. Kar) Kalgutkar & Janson. 2000

Figure 8

Index Fungorum Registration Identifier: 483410.

Basionym: *Colligerites chowdhryi* K.P. Jain & R.K. Kar 1979.

Original Description: Spores multicellular, coiled once in centre, generally keeping a hollow space. Cells smaller in centre and bigger in outer region. Spore wall granulate. Pore present or absent in cells. Holotype 80 µm (Jain & Kar 1979, p. 110).

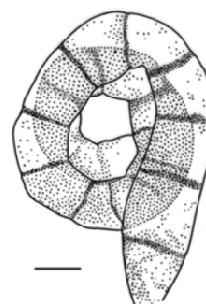


Figure 8. *Involutisporonites chowdhryi* (K.P. Jain & R.K. Kar) Kalgutkar & Janson. 2000. Scale Bar = 10 µm.

Location: Papanasam and Varkala, Kerala, India.

Age: Miocene.

Remarks: *Colligerites kutchensis* (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar 1979 is much coiled and hence is easily differentiated from the present species. Jain & Kar (1979) opined that *Colligerites chowdhryi* resembles closely the spores of *Helicominopsis fici* (illustrated by Subramanian 1971). The spores of *Helicomina caperoniae* are also helicoid but the coilings are not as prominent as in the present species. The species epithet honours Dr. Harsh Chowdhry.

Involutisporonites foraminus R.T. Clarke 1965

Figure 9

Index Fungorum Registration Identifier: 332602.

Original Description: Fungal spores planispiral, individual cells lobate, 8–10 μm diameter, cell wall psilate, 0.5–1 μm thick, septa simple, about 1 μm thick, each cell connected by a 0.5 μm diameter opening through each septum, overall dimensions 28–36 μm (Clarke 1965, p. 90).

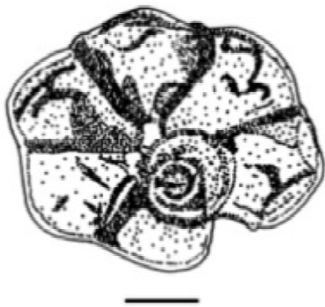


Figure 9. *Involutisporonites foraminus* R.T. Clarke 1965. Scale Bar = 10 μm .

Location: Canon City Coalfield, Fremont County, Colorado, U.S.A.

Age: Late Cretaceous.

Remarks: The species epithet '*foraminus*' refers to the resemblance of the species to planispiral foraminifera.

Involutisporonites trapezoides Kalgutkar 1993

Figure 10

Index Fungorum Registration Identifier: 483881.

Original Description: Distinctive, multicellular, porate, dark brown, helicoid, tightly curled, smooth spores with an open centre. Ten or more cells form a conical helix by having irregularly elongated, trapezoidal

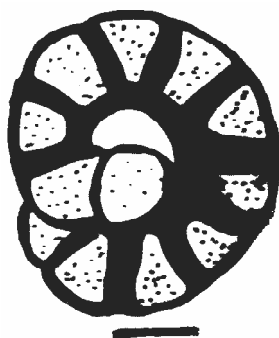


Figure 10. *Involutisporonites trapezoides* Kalgutkar 1993. Scale Bar = 10 μm .

shape, each with outer cell wall much longer than the inner, and separated by thick cross walls (septa). Cells generally not constricted at the septa, 10–12 μm in diameter. Apical cell in the centre, porate but not hyaline; pore simple, rounded. Septa about 2 μm thick, with folds and central (slit-like) openings. Spore size range 33–43 \times 28–35 μm (Kalgutkar 1993, p. 82).

Location: Peel River, Yukon Territory, Canada.

Age: Late Palaeocene-Early Eocene.

Remarks: The species epithet is derived from the Latin, *trapezoideus*, irregularly four-sided.

The following four species, originally ascribed to *Involutisporonites* R.T. Clarke 1965, have been recombined with other genera, as follows.

1. *Involutisporonites kutchensis* R.K. Kar & R.K. Saxena 1976 (Index Fungorum Registration Identifier: 112379). Current name: *Colligerites kutchensis* (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar 1979 fide Jain & Kar (1979).
2. *Involutisporonites minutus* Rouse & Mustard 1997 (Index Fungorum Registration Identifier: 463995) Current name: *Palaeoslimacomyces minutus* (Rouse & Mustard) Kalgutkar & Janson. 2000 fide Kalgutkar & Jansonius (2000).
3. *Involutisporonites putus* P. Ke & Z.Y. Shi 1978 (Index Fungorum Registration Identifier: 115668). Current name: *Paragranatisporites putus* (P. Ke & Z.Y. Shi) Kalgutkar & Janson. 2000 fide Kalgutkar & Jansonius (2000).
4. *Involutisporonites wilcoxii* Elsik 1968 (Index Fungorum Registration Identifier: 315918). Current name: *Paleoslimacomyces wilcoxii* (Elsik) Kalgutkar & Janson. 2000 fide Kalgutkar & Jansonius (2000).

Genus: *Palaeocirrenalia* Ramanujam & Srisailam 1980

Index Fungorum Registration Identifier: 21205.

Type species: *Palaeocirrenalia elegans* Ramanujam & Srisailam 1980.

Original Diagnosis: Spores light brown to reddish brown, inaperturate, helicoid, 1 to 1.25 times

loosely coiled, multicellular, 2– to 6–septate, septa transverse, prominent, as thick and dark bands, cells of unequal size, terminal cell dome-shaped and broader, basal cell usually cuneate, pale-coloured, surface psilate (Ramanujam & Srisailam 1980, p. 124).

Number of species known: Two.

Remarks: Ramanujam and Srisailam (1980) stated that “In their loosely coiled 2– to 6–septate nature with the terminal cell dome-shaped, these spores are remarkably similar to the conidia of the modern dematiaceous hyphomycete *Cirrenalia* (Ellis 1976). The species of *Cirrenalia* are characteristic of brackish to marine habitats and hence are environmentally significant. They are generally found on driftwood. No information is available with regard to the nature of the conidiophores of the fossil specimens, i.e. whether they are simple or branched.” Kalgutkar & Jansonius (2000) opined that the characteristics of a more than hemispherical to globular dark distal cell, the curved longitudinal axis, and an indistinct proximal hilum, define this genus.

Palaeocirrenalia elegans Ramanujam & Srisailam 1980

Figure 11

Index Fungorum Registration Identifier: 109520.

Original Description: Spores light brown to reddish brown, inaperturate, helicoid, 1 to 1.25 times loosely coiled, 4 to 6 septate, maximum width 34–49.3 μm , basal cell cuneate to elongated-cuneate, 10 \times 8.5

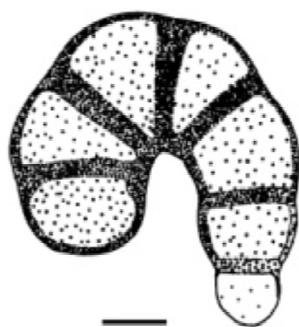


Figure 11. *Palaeocirrenalia elegans* Ramanujam & Srisailam 1980. Scale Bar = 8 μm .

μm , pale-coloured to almost hyaline, terminal cell dome-shaped, 15.3 \times 17 μm in diameter, septa prominent to form thick dark bands up to 5 μm thick, spore wall up to 1.7 μm thick, surface psilate (Ramanujam & Srisailam 1980, p. 125).

Location: Kannur Beach area, Palayangadi and Cheruvattur (southern side of Karingottu River), Kerala, India.

Age: Miocene.

Remarks: According to Ramanujam & Srisailam (1980), these spores exhibit remarkable similarity with the conidia of *Cirrenalia macrocephala* (Kohlm.) Meyers & R.T. Moore 1960 (Ellis 1976).

Palaeocirrenalia oligoseptata Ramanujam & Srisailam 1980

Figure 12

Index Fungorum Registration Identifier: 109521.

Original Description: Spores light brown to light yellowish, inaperturate, helicoid or only partially curved, 2 or 3 septate, maximum width 23.8 \times 68 μm , basal cell smaller than, or of same size as terminal cell, elongated cuneate, pale-coloured, central cells larger than others, 34 \times 23.8 μm , septa as prominent dark bands, up to 6.1 μm thick; spore wall 1.7 μm thick, surface psilate (Ramanujam & Srisailam 1980, p. 125).

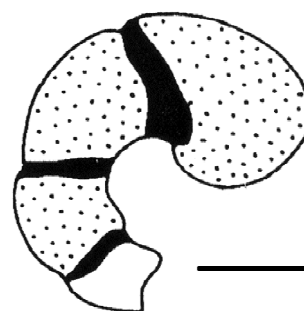


Figure 12. *Palaeocirrenalia oligoseptata* Ramanujam & Srisailam 1980. Scale Bar = 20 μm .

Location: Kannur Beach area, Palayangadi and Cheruvattur (southern side of Karingottu River), Kerala, India.

Age: Miocene.

Genus: *Paleoslimacomyces* Kalgutkar & Sigler 1995

Index Fungorum Registration Identifier: 27617.

Type species: *Paleoslimacomyces canadensis* Kalgutkar & Sigler 1995.

Original Diagnosis: Conidia simple, solitary, helicoid, curved to hemi-circinate, brown to fuscous, smooth. Conidia 2–3-septate; septa dark, often thick; conidial filaments short, made up of 3–4 broadly curved cells; cells, except the apical cell, darkly-pigmented; apical cell hyaline to pale brown. Monotypic (Kalgutkar & Sigler 1995, p. 521).

Number of species known: Three.

Remarks: According to Kalgutkar & Sigler (1995), conidia of *Paleoslimacomyces* show some similarity to the conidia of extant *Slimacomyces monospora* (W.B. Kendr.) Minter, which was originally described by Kendrick (1958) in *Helicoma* Corda. Ellis (1976) transferred this species to *Troposporella* P. Karst. as *Troposporella monospora* (W.B. Kendr.) M.B. Ellis. After re-examination of type material, Minter (1986) concluded that this fungus was different from *Troposporella* in its dispersal mechanism, and in having two types of cells in a filament for performing different functions. One type, having thick-walled cells with thick septa, had a survival function, whereas the second type, having cells with thinner walls with ordinary septa, germinated quickly. He, therefore, placed this fungus in a new genus *Slimacomyces* with *S. monospora* as its type (Kalgutkar & Jansonius 2000, p. 215). Goos (1987) concurred that the biology and morphology of *Slimacomyces monospora* justify its placement in a different genus. *Paleoslimacomyces* conidia are distinguished from spores of all fossil helicosporous genera by their distinctively short, and curved to partially circinate filaments.

Paleoslimacomyces canadensis Kalgutkar & Sigler 1995

Figure 13

Index Fungorum Registration Identifier: 413657.

Original Description: Conidia simple, solitary, generally curved, horse-shoe shaped smooth, brown to fuscous, 2–4 septate, usually with 3 septa; septa dark, often thick, slightly thicker than the cell walls and with central perforations. Apical cell hyaline to pale brown, other cells dark pigmented; terminal cell broadly cylindrical, rounded; cells forming the coiled axis curved with their outer periclinal cell walls much greater in length than the inner periclinal walls. Spores 13–16 μm wide; filaments 5–6 μm thick (Kalgutkar & Sigler 1995, p. 521).

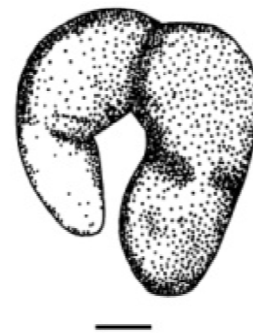


Figure 13. *Paleoslimacomyces canadensis* Kalgutkar & Sigler 1995. Scale Bar = 5 μm .

Location: Kanguk Peninsula, Axel Heiberg Island, Northwest Territories, Canada.

Age: Late Palaeocene or Early Eocene (Iceberg Bay Formation).

Remarks: According to Kalgutkar and Sigler (1995), conidia of *Paleoslimacomyces canadensis* show some similarities with those of extant *Helicoma* Corda, *Helicomina* L.S. Olive and *Trochophora* R.T. Moore. However, in these genera, the conidial filaments are strongly circinate, narrower than those of *Paleoslimacomyces canadensis*, and have several septa. Although conidia of this new fossil species do not show the presence of two types of thick-walled cells, which characterizes the conidia of extant *Slimacomyces monospora*, they appear similar in their general morphological features. According to Kalgutkar and Jansonius (2000), the Late Paleocene *Paleoslimacomyces minutus* (Rouse & Mustard) Kalgutkar & Janson. appears to be similar to *P. canadensis*, and may be a later taxonomic synonym.

The species epithet is derived from the place of its occurrence in Canada.

Paleoslimacomyces minutus (Rouse & Mustard)
Kalgutkar & Janson. 2000

Figure 14

Index Fungorum Registration Identifier:
483499.

Basionym: *Involutisporonites minutus* Rouse & Mustard 1997.

Original Description: Planispiral fungal spores, with few (usually 4) cells encircling a fusiform open area in the centre; outer walls about 0.25 µm thick and laevigate; inner walls of cells about 1.0–1.5 µm; septa about 0.75 µm thick, with a single faint pore. Size range 16–21 µm (Rouse & Mustard 1997, p. 207).

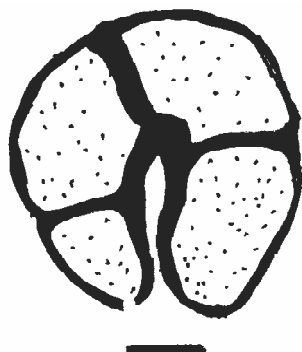


Figure 14. *Paleoslimacomyces minutus* (Rouse & Mustard) Kalgutkar & Janson. 2000. Scale Bar = 5 µm.

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

Age: Late Palaeocene.

Remarks: According to Rouse and Mustard (1997), this species is smaller than the type species *Involutisporonites foraminus*, with fewer and nonlobate cells. It is usually found on fragments of leaf, and hence is likely the spore of an epiphytic fungus. Kalgutkar and Sigler (1995) established *Paleoslimacomyces* to include fossil spores resembling the conidia of modern *Helicoma* Corda, *Helicomina* L.S. Olive, *Slimacomyces* Minter and *Trochophora*

R.T. Moore, which all consist of short hemicircinate filaments made up of 4–5 cells and having middle cells more pigmented than the terminal ones. Spores of *Paleoslimacomyces minutus* appear to be similar to spores of *P. canadensis*, and the latter may be an earlier taxonomic synonym.

Paleoslimacomyces wilcoxii (Elsik) Kalgutkar & Janson. 2000

Figure 15

Index Fungorum Registration Identifier:
483500.

Basionym: *Involutisporonites wilcoxii* Elsik 1968.

Original Description: Coiled, psilate, monoporate fungal spores of 6 cells. Maximum dimension 26 µm. Wall 0.5 µm thick except apical chamber, which has walls about 0.2 µm thick. Wall darkly pigmented except for apical chamber, which is much lighter. Septa twice as thick as wall, two layered. Pore ca. 1 µm in diameter (Elsik 1968, p. 277).



Figure 15. *Paleoslimacomyces wilcoxii* (Elsik.) Kalgutkar & Janson. 2000. Scale Bar = 8 µm.

Location: Strip mine approximately 11 km southwest of Rockdale, Milam County, Texas, U.S.A.

Age: Palaeocene.

Genus: *Retihelicosporonites* Ramanujam & K.P. Rao 1978

Index Fungorum Registration Identifier:
21281.

Type species: *Retihelicosporonites elsikii* Ramanujam & K.P. Rao 1978.

Original Diagnosis: Spores simple, uniseriate, multicellular, inaperturate, basal cell cuneate, other cells rectangular; apical part of spore helical. Spore wall reticulate. Monotypic (Ramanujam & Rao 1978, p. 299).

Number of species known: One.

Remarks: Ramanujam & Rao (1978) recorded helical spores of this kind in the samples collected from the Warkalli Beds of Warkalli and Alleppey and from the Quilon Beds of Padappakkara. They opined that *Involutisporonites* Elsik 1968, although multiseptate and helical, is distinguishable by its monoporate and psilate nature. Helical spores (conidia) are found in various genera of *Hyphomycetes*, viz. *Helicoma* Corda, *Helicomina* L.S. Olive, *Helicoon* Morgan, *Helicodendron* Peyronel, *Hiospira* R.T. Moore and *Xenosporella* Höhn (Barnett 1956, Ellis 1971, Ainsworth et al. 1973). In possessing a reticulate cell wall, the fossil spores show remarkable resemblance to the conidia of the *Hiospira* state of *Brooksia tropicalis* Hansf. *Hiospira* R.T. Moore is commonly found in moist tropical regions. Elsik (1992) considered spores of *Retihelicosporonites* to be monoporate and differentiated them from other multicellate monoporate form genera on their combination of reticulate sculpture and their tendency to be loosely coiled.

Retihelicosporonites elsikii Ramanujam & K.P. Rao 1978

Figure 16

Index Fungorum Registration Identifier: 115089.

Original Description: Spores light to dark brown, multicellular with 3–8 transverse septa, 110–130 μm long, apical part helical; septa very faint or almost absent in the helical region. Cell 10–13.5 \times 5–7.5 μm . Wall two-layered, reticulate, coarsely so in the helical region, meshes hexagonal, lumina smooth (Ramanujam & Rao 1978, p. 299).

Location: Alleppey, Alappuzha District and Kollam and Warkalli, Kollam District, Kerala, India.

Age: Miocene (Quilon and Warkalli beds).

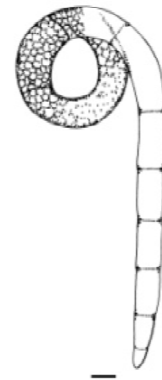



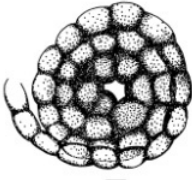
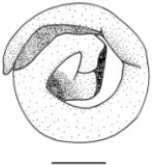
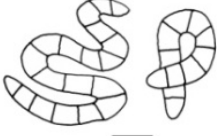

Figure 16. *Retihelicosporonites elsikii* Ramanujam & K.P. Rao 1979. Scale Bar = 20 μm .

Remarks: The species epithet is in honour of Dr. William C. Elsik.

MORPHOLOGICAL VARIATIONS

It is evident from the records of fossil *Helicosporae* that they exhibit a broad range of morphological variations. Since their assignment to modern fungal taxa is seldom possible, these are placed into artificial genera and species based on morphological characters. The shape of the conidia greatly varies, e.g. fist-shaped (*Circinoconites*), circular (*Colligerites*, *Elsikisporonites*, *Helicosporiates*, *Involutisporonites*), wavy to loosely spiral (*Helicominites*), apical part with one coil and remaining part straight (*Retihelicosporonites*), ellipsoidal-barrel-shaped spiral (*Helicoonites*) and horse-shoe shaped (*Palaeocirrenalia*, *Paleoslimacomycetes*). Variations in shape are, in fact, result of variations in coiling pattern. Tightly coiled or twisted in three planes, barrel-shaped spiral are found in *Helicoonites* whereas partially coiled helicospores are represented by *Palaeocirrenalia* and *Paleoslimacomycetes*. *Colligerites* and *Helicosporiates* are tightly coiled several times. The spore wall is psilate to faintly structured in most genera but in *Retihelicosporonites*, it is clearly reticulate. It has been observed that only one genus, e.g. *Elsikisporonites*, is unicellate (non-septate) whereas all other genera are multiseptate with prominent septa. In order to understand morphological variations in fossil *Helicosporae*, the characteristic features of various fossil helicospore genera are summarized in Table 1.

Table 1. Morphological characters of various genera of fossil *Helicosporae* (along with sketch of the holotype of type species of each genus).

Genus	Cells	Shape and Coiling	Pore/ Aperture	Septa	Spore wall	Holotype of the type species
<i>Circinoconites</i> R. Kar et al. 2010	Dissimilar, 10–16 in number, increase in diameter from base to apex, basal cells rectangular, 6–8 × 4–6 μm, straight, rest cells coiled, spirally arranged.	Fist-shaped, constricted at septa, strongly spiralled, solitary, coiled, not in chains or slime.	None observed.	8–14 septate, septa up to 2 μm thick.	Dark brown, about 1 μm thick, laevigate, sometimes weakly intrastructured.	 <i>Circinoconites arthrus</i>
<i>Colligerites</i> K.P. Jain & R.K. Kar 1979	Multicellate, cells generally smaller, rounded in central region and bigger, rectangular in outer region.	Circular, tightly coiled.	Pore may be present or absent in each cell.	Septate.	Mostly laevigate, sometimes granulose.	 <i>Colligerites kutchensis</i>
<i>Elsikisporonites</i> P. Kumar 1990	Unicellate, cells broadest in the middle region, 10–12 μm wide, gradually tapering towards the ends.	Tubular and coiled.	Monoporate, pore at outer end, nozzle-like, 1.5 μm wide.	Non-septate.	Pale, smooth and hyaline, 1 μm thick, slightly folded.	 <i>Elsikisporonites tubulatus</i>
<i>Helicominites</i> Barlinge & Paradkar 1982	Multicellate, branched hyphae, 5–6 μm wide.	Coiled in loose spirals, 21–32 × 20–30 μm, narrow at both ends.	None observed.	Septate.	Faint in colour.	 <i>Helicominites salvinites</i>
<i>Helicoonites</i> Kalgutkar & Sigler 1995	Multicellate, cells rectangular, not incurved at the septa.	Tightly coiled or twisted in three planes to form an ovoid, ellipsoidal (doliiform) to cylindrical or beehive to barrel-shaped spiral. Spirals made up of variable numbers of ascending coils or gyres, with each successive gyre usually of smaller diameter.	None observed.	Multiseptate, septa about 5 μm wide.	Smooth, fuscous, transverse pattern of minute, apparently internal striae commonly present.	 <i>Helicoonites goosii</i>

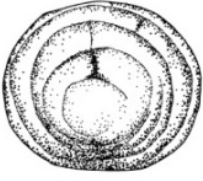

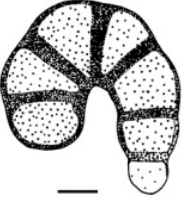
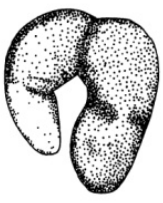
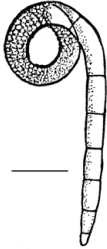
<i>Helicosporiates</i> Kalgutkar & Sigler 1995	Simple, slender, multicellate, cells cuboid to rectangular.	Helicoid, spirals of loose to tightly coiled filaments, usually helically coiled 2–4 times in one plane or somewhat cochleate, not indented at the septa.	None observed.	Septa present or sometimes indistinct.	Pale brown to brown, smooth.		<i>Helicosporiates pirozynskii</i>
<i>Involutisporonites</i> R.T. Clarke 1965	Multiseptate, individual cells lobate.	Coiled, planispiral.	Monoporate.	Transversely septate, septa about 1 µm thick, simple with an opening through each septum.	Psilate to variously ornamented, 0.5– 1 µm thick.		<i>Involutisporonites foraminus</i>
<i>Palaeocirrenalia</i> Ramanujam & Srisailam 1980	Multicellate, cells of unequal size, terminal cell dome- shaped and broader, basal cell usually cuneate.	Helicoid, loosely coiled.	Inaperturate.	2- to 6- septate, septa transverse, prominent, as thick and dark bands.	Spores light brown to reddish brown, basal cell pale-coloured, surface psilate.		<i>Palaeocirrenalia elegans</i>
<i>Paleoslimacomyc</i> <i>es</i> Kalgutkar & Sigler 1995	Multicellate, simple and solitary conidia.	Helicoid, curved to hemi-circinate, horse-shoe shaped, conidial filaments, short, made up of 3– 4 broadly curved cells, filaments 5–6 µm thick.	Inaperturate.	Conidia 2–3- septate, septa dark, often thick with central perforations.	brown to fuscous, smooth, cells darkly- pigmented, except the apical cell which is hyaline to pale brown.		<i>Paleoslimacomyc canadensis</i>
<i>Retihelicosporonit</i> <i>es</i> Ramanujam & K.P. Rao 1978	Multicellate, simple, uniseriate.	Apical part of spore helical, basal cell cuneate, other cells rectangular.	Inaperturate.	Septate, 3–8 transverse septa, very faint or almost absent in the helical region.	Spore wall, two layered, reticulate, coarsely reticulate in the helical region, meshes hexagonal, lumina smooth.		<i>Retihelicosporonites elsikii</i>

Table 2. Showing global distribution of various species of fossil *Helicosporae* and their occurrences in India.

Country (from where first recorded)	Species	Original location and occurrences in India
Antarctica	<i>Involutisporonites crassus</i> Z.C. Song & Liu Cao	King George Island, Antarctica (Song & Cao 1994). Not recorded from India.
Canada	<i>Helicoonites goosii</i> Kalgutkar & Sigler	Strand Fiord, Axel Heiberg Island, Northwest Territories, Canada (Kalgutkar & Sigler 1995). Not recorded from India
	<i>Helicosporiates pirozynskii</i> Kalgutkar & Sigler	Strand Fiord, Axel Heiberg Island, Northwest Territories, Canada (Kalgutkar & Sigler 1995). Not recorded from India
	<i>Involutisporonites trapezoides</i> Kalgutkar	Peel River, Yukon Territory, Canada (Kalgutkar 1993). Indian record: Neyveli lignite mine 1, Cuddalore District, Tamil Nadu (Elayaraja & Kumarasamy 2016).
	<i>Paleoslimacomyces canadensis</i> Kalgutkar & Sigler	Kanguk Peninsula, Axel Heiberg Island, Northwest Territories, Canada (Kalgutkar & Sigler 1995). Not recorded from India
	<i>Paleoslimacomyces minutus</i> (Rouse & Mustard) Kalgutkar & Janson.	Strait of Georgia, eastern Vancouver Island, the Fraser River lowlands of southwest British Columbia, Canada (Rouse & Mustard 1997). Not recorded from India.
India	<i>Circinoconites arthrus</i> R. Kar et al.	Tlansam, Champhai District, Mizoram (Kar et al. 2010).
	<i>Colligerites kutchensis</i> (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar	Matanomadh, Kutch District, Gujarat (Kar & Saxena 1976); around Kollam and Varkala, Kerala (Jain & Kar 1979).
	<i>Colligerites trochus</i> B. Samant in R.K. Saxena	Near Bhavnagar, Cambay Basin, Gujarat (Samant 2000); Cambay Basin, Gujarat (Samant & Tapaswi 2000).
	<i>Elsikisporonites tubulatus</i> P. Kumar	Clay mine section near Kanjantheria House, Padappakkara, Kollam District, Kerala (Kumar 1990).
	<i>Helicominites salvinites</i> Barlinge & Paradkar	Mohgaon Kalan, Chhindwara District, Madhya Pradesh (Barlinge & Paradkar 1982).
	<i>Involutisporonites chowdhryi</i> (K.P. Jain & R.K. Kar) Kalgutkar & Janson.	Around Quilon and Varkala, Kerala (Jain & Kar 1979).
	<i>Palaecirrenalia elegans</i> Ramanujam & Srisailam	Kannur District, Kerala (Ramanujam & Srisailam 1980); Well at Golap on Ratnagiri-Pawas Road, Ratnagiri District, Maharashtra (Phadtare & Kulkarni 1984); Godavari-Krishna Basin, Andhra Pradesh and Palk Bay area in Cauvery Basin, Tamil Nadu (Malleshham et al. 1989); Borewell at Kulasekharamangalam, Kottayam District, Kerala (Rao et al. 1995); Alleppey & Kannur districts, Kerala (Rao 1995); Rajparadi, Cambay Basin, Gujarat (Samant & Phadtare 1997); Near Bhavnagar, Cambay Basin, Gujarat (Samant 2000); Cambay Basin, Gujarat (Samant & Tapaswi 2000).
	<i>Palaecirrenalia oligoseptata</i> Ramanujam & Srisailam	Kannur District, Kerala (Ramanujam & Srisailam 1980).
	<i>Retihelicosporonites elsikii</i> Ramanujam & K.P. Rao	Kollam District, Kerala (Ramanujam & Rao 1978).
U.S.A.	<i>Involutisporonites foraminus</i> R.T. Clarke	Canon City Coalfield, Fremont County, Colorado, U.S.A. (Clarke 1965). Not recorded from India
	<i>Paleoslimacomyces minutus</i> (Rouse & Mustard) Kalgutkar & Janson.	North-western Washington State, U.S.A. (Rouse & Mustard 1997). Not recorded from India
	<i>Paleoslimacomyces wilcoxii</i> (Elsik) Kalgutkar & Janson.	Strip mine approximately 11 km southwest of Rockdale, Milam County, Texas, U.S.A. (Elsik 1968). Indian record: Sindhudurg District, Maharashtra (Saxena & Misra 1990).

GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

It has been observed that helicospores are not as rich as others groups of fungal spores in the fossil fungal assemblages. However, these have been recorded from

widespread areas, e.g. Antarctica, Canada, India and U.S.A. (Table 2, Figure 17). In Antarctica, helicospores were recorded from the Late Cretaceous sediments King George Island. In Canada, these spores were recorded from Strand Fiord and Kanguk Peninsula,

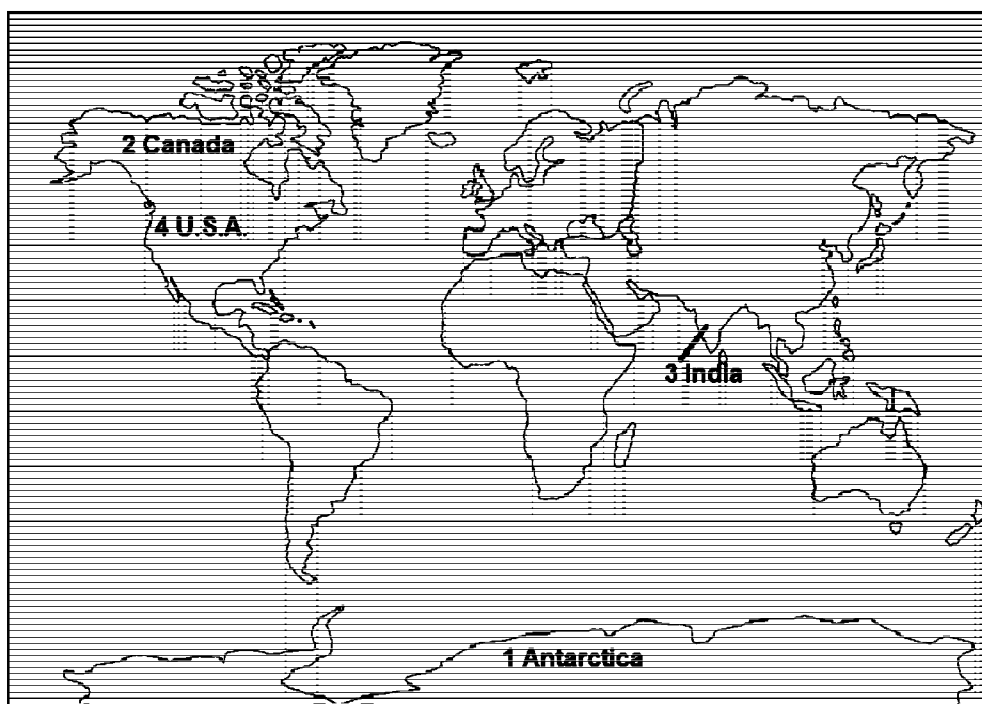


Figure 17. World map showing countries from where fossil *Helicosporae* has been recorded. **1. Antarctica (King George Island):** *Involutisporonites crassus* Z.C. Song & Liu Cao. **2. Canada:** **A.** Strand Fiord, Axel Heiberg Island, Northwest Territories: *Helicoonites goosii* Kalgutkar & Sigler and *Helicosporiates pirozynskii* Kalgutkar & Sigler. **B.** Peel River, Yukon Territory: *Involutisporonites trapezoides* Kalgutkar. **C.** Kanguk Peninsula, Axel Heiberg Island, Northwest Territories: *Paleoslimacomycetes canadensis* Kalgutkar & Sigler. **D.** Strait of Georgia, eastern Vancouver Island, the Fraser River lowlands of southwest British Columbia: *Paleoslimacomycetes minutus* (Rouse & Mustard) Kalgutkar & Janson. **3. India:** **A.** Andhra Pradesh: Godavari-Krishna Basin: *Palaeocirrenalia elegans* Ramanujam & Srisailam. **B.** Gujarat: Kutch District: *Colligerites kutchensis* (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar. Cambay Basin: *Colligerites trochus* B. Samant in R.K. Saxena. **C.** Kerala: Around Kollam and Varkala: *Colligerites kutchensis* (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar. Padappakkara, Kollam District: *Elsikisporonites tubulatus* P. Kumar and *Retihelicosporonites elsikii* Ramanujam & K.P. Rao. Papanasam, Varkala: *Involutisporonites chowdhryi* (K.P. Jain & R.K. Kar) Kalgutkar & Janson. Kannur District: *Palaeocirrenalia elegans* Ramanujam & Srisailam. and *Palaeocirrenalia oligoseptata* Ramanujam & Srisailam. Borewell at Kulasekharamangalam, Kottayam District: *Palaeocirrenalia elegans* Ramanujam & Srisailam. **D.** Madhya Pradesh: Mohgaon Kalan, Chhindwara District: *Helicominites salvinites* Barlinge & Paradkar. **E.** Maharashtra: Ratnagiri District: *Palaeocirrenalia elegans* Ramanujam & Srisailam. Sindhudurg District: *Paleoslimacomycetes wilcoxii* (Elsik.) Kalgutkar & Janson. **F.** Tamil Nadu: Palk Bay area in Cauvery Basin: *Palaeocirrenalia elegans* Ramanujam & Srisailam. Neyveli lignite mine 1, Cuddalore District: *Involutisporonites trapezoides* Kalgutkar. **4. U.S.A.:** **A.** Canon City Coalfield, Fremont County, Colorado: *Involutisporonites foraminus* R.T. Clarke. **B.** North-western Washington State: *Paleoslimacomycetes minutus* (Rouse & Mustard) Kalgutkar & Janson. **C.** Milam County, Texas: *Paleoslimacomycetes wilcoxii* (Elsik.) Kalgutkar & Janson.

Axel Heiberg Island, Northwest Territories; Peel River, Yukon Territory; Strait of Georgia, eastern Vancouver Island, the Fraser River lowlands of southwest British Columbia. In India, these have been recorded from Godavari-Krishna Basin, Andhra Pradesh; various locations in Kutch and Cambay basins, Gujarat; various locations in Kollam, Alappuzha, Kottayam and Kannur districts, Kerala; Mohgaon Kalan, Chhindwara District, Madhya Pradesh, various locations in Ratnagiri and Sindhudurg districts, Maharashtra, Tlamsam, Champhai District, Mizoram and Palk Bay area in Cauvery Basin

and Neyveli lignite mine 1, Cuddalore District, Tamil Nadu. In U.S.A., Canon City Coalfield, Fremont County, Colorado, North-western Washington State and Milam County, Texas (Table 2, Figure 17). Distribution of 8 genera and 10 species of fossil helicospores in India and their stratigraphic unit (geologic age) and areas of occurrence, along with citation of relevant References is shown in Tables 3, 4, Figure 18.

Although most of the fungal spores are long ranging and do not bear much stratigraphical significance, some

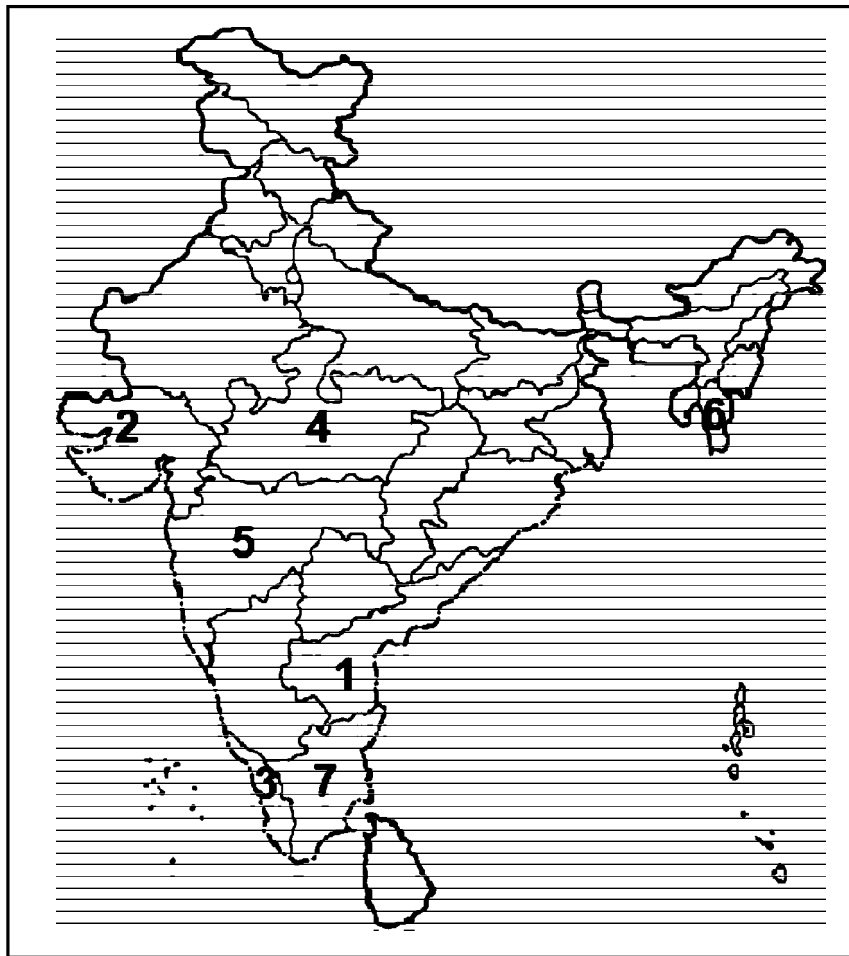


Figure 18. Map of India showing occurrences of species of fossil *Helicosporae* in various states of India. **1. Andhra Pradesh:** Miocene, Godavari-Krishna Basin: *Palaeocirrenalia elegans* Ramanujam & Srisailam. **2. Gujarat:** A. Palaeocene, Kutch District: *Colligerites kutchensis* (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar. B. Eocene, Cambay Basin: *Colligerites trochus* B. Samant in R.K. Saxena and *Palaeocirrenalia elegans* Ramanujam & Srisailam. **3. Kerala:** A. Miocene, around Kollam and Varkala: *Colligerites kutchensis* (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar. B. Miocene, Padappakkara, Kollam District: *Elsikisporonites tubulatus* P. Kumar. C. Miocene, Papanasam, Varkala: *Involutisporonites chowdhryi* (K.P. Jain & R.K. Kar) Kalgutkar & Janson. D. Miocene, Kannur District: *Palaeocirrenalia elegans* Ramanujam & Srisailam. E. Early Miocene, Borewell at Kulasekharamangalam, Kottayam District: *Palaeocirrenalia elegans* Ramanujam & Srisailam. F. Miocene, Kannur District: *Palaeocirrenalia oligoseptata* Ramanujam & Srisailam. G. Miocene, Kollam District: *Retihelicosporonites elsikii* Ramanujam & K.P. Rao. **4. Madhya Pradesh:** Mohgaon Kalan, Chhindwara District: *Helicominites salvinites* Barlinge & Paradkar. **5. Maharashtra:** A. Miocene, Ratnagiri District: *Palaeocirrenalia elegans* Ramanujam & Srisailam. B. Miocene, Sindhudurg District: *Paleoslimacomycetes wilcoxii* (Elsik.) Kalgutkar & Janson. **6. Mizoram:** Miocene Tlamsam, Champhai District: *Circinoconites arthrus* Kar et al. **7. Tamil Nadu:** A. Miocene, Palk Bay area in Cauvery Basin: *Palaeocirrenalia elegans* Ramanujam & Srisailam. B. Neyveli lignite mine 1, Cuddalore District: *Involutisporonites trapezoides* Kalgutkar.

are morphologically distinct and have restricted range in geological time (Kalgutkar & Jansonius 2000). Graham (1962) and Elsik (1970) were amongst the pioneers to suggest the possibility of using fungal spores for supplementing age determinations in palynological studies. Ramanujam (1982) opined that overall diversity in morphology of fungal spore was attained by late

Cretaceous and early Tertiary. An analysis of the global stratigraphic distribution of fossil *Helicosporae* reveals that *Involutisporonites foraminus* and *Helicominites salvinites* are restricted to the late Cretaceous. *Paleoslimacomycetes wilcoxii* and *Paleoslimacomycetes minutus* are restricted to Palaeocene whereas *Involutisporonites trapezoides*,

Table 3. Representation of species of fossil *Helicosporae* in various states of India.

Geographical area	Species recorded (References)
Andhra Pradesh	<i>Palaeocirrenalia elegans</i> Ramanujam & Srisailam: Miocene, Godavari-Krishna Basin, Andhra Pradesh (Mallesham et al. 1989).
Gujarat and Cambay basins)	<i>Colligerites kutchensis</i> (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar: Matanomadh Formation (Palaeocene), Matanomadh, Kutch District, Gujarat (Kar & Saxena 1976). <i>Colligerites trochus</i> B. Samant in R.K. Saxena: Kharsalia Clay Formation (Early Eocene), near Bhavnagar, Cambay Basin, Gujarat (Samant 2000); Cambay Shale (Early Eocene), Cambay Basin, Gujarat (Samant & Tapaswi 2000). <i>Palaeocirrenalia elegans</i> Ramanujam & Srisailam: Tarkeshwar Formation (Early Eocene), Rajparadi, Cambay Basin, Gujarat (Samant & Phadtare 1997); Kharsalia Clay Formation (Early Eocene), near Bhavnagar, Cambay Basin, Gujarat (Samant 2000); Cambay Shale Early (Eocene), Cambay Basin, Gujarat (Samant & Tapaswi 2000).
Kerala	<i>Colligerites kutchensis</i> (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar: Miocene, around Kollam and Varkala, Kerala (Jain & Kar 1979). <i>Elsikisporonites tubulatus</i> P. Kumar: Quilon Beds (Miocene), clay mine section near Kanjantheria House, Padappakkara, Kollam District, Kerala (Kumar 1990). <i>Involutisporonites chowdhryi</i> (K.P. Jain & R.K. Kar) Kalgutkar & Janson.: Miocene, Papanasam, Varkala, Kerala, South India (Jain & Kar 1979). <i>Palaeocirrenalia elegans</i> Ramanujam & Srisailam: Warkalli Beds (Miocene), Kannur District, Kerala (Ramanujam & Srisailam 1980); Early Miocene, Borewell at Kulasekharamangalam, Kottayam District, Kerala (Rao et al. 1995); Tertiary, Alleppey & Kannur districts, Kerala (Rao 1995). <i>Palaeocirrenalia oligoseptata</i> Ramanujam & Srisailam: Warkalli Beds (Miocene), Kannur District, Kerala (Ramanujam & Srisailam 1980). <i>Retihelicosporonites elsikii</i> Ramanujam & K.P. Rao: Quilon and Warkalli Beds (Miocene). Kollam District, Kerala (Ramanujam & Rao 1978).
Madhya Pradesh	<i>Helicominites salvinites</i> Barlinge & Paradkar: Deccan Intertrappean Series (?Late Cretaceous), Mohgaon Kalan, Chhindwara District, Madhya Pradesh (Barlinge & Paradkar 1982).
Maharashtra	<i>Palaeocirrenalia elegans</i> Ramanujam & Srisailam: Ratnagiri Beds (Miocene), well at Golap on Ratnagiri-Pawas Road, Ratnagiri District, Maharashtra (Phadtare & Kulkarni 1984). <i>Paleoslimacomycetes wilcoxii</i> (Elsik) Kalgutkar & Janson.: Ratnagiri Beds (Neogene), Amberiwadi Section, Sindhudurg District, Maharashtra (Saxena & Misra 1990).
Mizoram	<i>Circinoconites arthrus</i> R. Kar et al.: Bhuban Formation (Miocene), Tlamsam, Champhai District, Mizoram (Kar et al. 2010).
Tamil Nadu	<i>Palaeocirrenalia elegans</i> Ramanujam & Srisailam: Miocene, Palk Bay area in Cauvery Basin, Tamil Nadu (Mallesham et al. 1989). <i>Involutisporonites trapezoides</i> Kalgutkar: Neyveli Formation (Miocene), Neyveli lignite mine 1, Cuddalore District, Tamil Nadu (Elayaraja & Kumarasamy D. 2016).

Colligerites kutchensis and *Paleoslimacomycetes canadensis*, although originate in Palaeocene, are found in younger sediments too. *Colligerites trochus*, *Helicoonites goosii* and *Helicosporiates pirozynskii* are found restricted to early Eocene. It is noteworthy that helicospores have not been recorded in any of the fossil fungal assemblages from Oligocene sediments. The following six species are restricted to Miocene, viz. *Retihelicosporonites elsikii*, *Palaeocirrenalia oligoseptata*, *Palaeocirrenalia elegans*, *Involutisporonites chowdhryi*, *Elsikisporonites tubulatus* and *Circinoconites arthrus*. Global stratigraphic distribution of fossil *Helicosporae* species is summarized in Figure 19.

PALAEOENVIRONMENTAL SIGNIFICANCE

Fungi are found in close association with specific

plants and animals and if found in a fossil state are indicative of similar kind of situations during the geologic past. Fossil fungi prefers a warm and humid climate, therefore their rich occurrence indicates such climate with plenty of rainfall. Ramanujam and Srisailam (1980) correlated prevalence of the helicoid spores *Palaeocirrenalia* in Neogene sediments of Kerala to conditions of brackish to marine waters, by comparing them to the similar modern dematiaceous hyphomycete, *Cirrenalia*, which is commonly found in such an environment. Presence of other spores in the same strata, affiliated to *Grallomyces* F. Stevens, *Sporidesmium* Link, *Spagazzinia* Sacc., *Amphisphaerella* (Sacc.) Kirschst., *Isthmospora* F. Stevens, etc., also supports this interpretation of a tropical climate (Ramanujam & Rao 1978, Ramanujam & Srisailam 1980). Kalgutkar and McIntyre (1991)

Table 4. Distribution of species of fossil *Helicosporae* in India with stratigraphic unit (age) and area of their occurrence.

Genus	Species	Stratigraphic unit, age and area (References)
<i>Circinoconites</i> R. Kar et al. 2010	<i>C. arthrus</i> R. Kar et al. 2010	Bhuban Formation (Miocene), Tlangsam, Champhai District, Mizoram (Kar et al. 2010, p. 246, plate 2, figure 10).
<i>Colligerites</i> K.P. Jain & R.K. Kar 1979	<i>C. kutchensis</i> (R.K. Kar & R.K. Saxena) K.P. Jain & R.K. Kar 1979	Matanomadh Formation (Palaeocene), Matanomadh, Kutch District, Gujarat (Kar & Saxena 1976, p. 12, plate 3, figures 37–38); Miocene, around Kollam and Varkala, Kerala (Jain & Kar 1979, p. 110, plate 2, figure 29).
	<i>C. trochus</i> B. Samant in R.K. Saxena 2009	Kharsalia Clay Formation (Early Eocene), near Bhavnagar, Cambay Basin, Gujarat (Samant 2000, p. 12, plate 1, figure 3); Cambay Shale (Early Eocene), Cambay Basin, Gujarat (Samant & Tapaswi 2000, p. 29, figure 2.1).
<i>Elsikisporonites</i> P. Kumar 1990	<i>E. tubulatus</i> P. Kumar 1990	Quilon Beds (Miocene), clay mine section near Kanjantheria House, Padappakkara, Kollam District, Kerala (Kumar 1990, p. 18, plate 1, figures 7–8, text-figure 5).
<i>Helicominites</i> Barlinge & Paradkar 1982	<i>H. salvinites</i> Barlinge & Paradkar 1982	Deccan Intertrappean Series (?Late Cretaceous), Mohgaon Kalan, Chhindwara District, Madhya Pradesh (Barlinge & Paradkar 1982, p. 166–167, text-figures T-V).
<i>Involutisporonites</i> R.T. Clarke 1965	<i>I. chowdhryi</i> (K.P. Jain & R.K. Kar) Kalgutkar & Janson. 2000	Miocene, Papanasam, Varkala, Kerala (Jain & Kar 1979, p. 110, plate 2, figure 30).
<i>Palaeocirrenalia</i> Ramanujam & Srisailam 1980	<i>P. elegans</i> Ramanujam & Srisailam 1980	Warkalli Beds (Miocene), Kannur District, Kerala (Ramanujam & Srisailam 1980, p. 125, plate 1, figures 13–14, plate 2, figure 15); Ratnagiri Beds (Miocene), well at Golap on Ratnagiri-Pawas Road, Ratnagiri District, Maharashtra (Phadtare & Kulkarni 1984, p. 517, plate 1, figure 5); Miocene, Godavari-Krishna Basin, Andhra Pradesh and Palk Bay area in Cauvery Basin, Tamil Nadu (Mallesham et al. 1989, p. 15, plate 1, figures 10–12); Early Miocene, Borewell at Kulasekharamangalam, Kottayam District, Kerala (Rao et al. 1995, p. 374, figure 4); Tertiary, Alleppey & Kannur districts, Kerala (Rao 1995, p. 233); Tarkeshwar Formation (Early Eocene), Rajpardi, Cambay Basin, Gujarat (Samant & Phadtare 1997, p. 68, plate 15, figure 13); Kharsalia Clay Formation (Early Eocene), near Bhavnagar, Cambay Basin, Gujarat (Samant 2000, p. 16, plate 1, figure 27); Cambay Shale (Early Eocene), Cambay Basin, Gujarat (Samant & Tapaswi 2000, p. 29).
	<i>P. oligoseptata</i> Ramanujam & Srisailam 1980	Warkalli Beds (Miocene), Kannur District, Kerala (Ramanujam & Srisailam 1980, p. 125, plate 2, figure 16).
<i>Paleoslimacomycetes</i> Kalgutkar & Sigler 1995	<i>P. wilcoxii</i> (Elsik) Kalgutkar & Janson. 2000	Ratnagiri Beds (Neogene), Amberiwadi Section, Sindhudurg District, Maharashtra (Saxena & Misra 1990, p. 265).
<i>Retihelicosporonites</i> Ramanujam & K.P. Rao 1978	<i>R. elsikii</i> Ramanujam & K.P. Rao 1978	Quilon and Warkalli Beds (Miocene). Kollam District, Kerala (Ramanujam & Rao 1978, p. 299, plate 3, figures 37–38)

interpreted a warm and humid environment in the Canadian Arctic due to the presence of helicosporous fungal types. They described two helicosporous fungal types known as *Helicoonites* and *Helicosporiates* from the Eocene Eureka Sound Formation in the Canadian Arctic, that are morphologically similar to the extant warm-climate, subaqueous generic groups *Helicoon* Morgan-*Helicodendron* Peyronel and *Helicosporium* Nees, and used their presence to postulate pools of open water in a warm, humid paleoenvironment of the region. Kalgutkar and Sigler (1995) instituted *Helicoonites* (Type: *H. goosii* Kalgutkar & Sigler 1995), *Helicosporiates* (Type: *H.*

pirozynskii Kalgutkar & Sigler 1995) and *Paleoslimacomycetes* (Type: *P. canadensis* Kalgutkar & Sigler 1995). Chitale (1978) and Chitale and Yawale (1978) provided valuable palaeoecological information based on the presence of fossil fungal spores in petrified plant materials from the Deccan Intertrappean beds of India. Similar kinds of interpretations were published by Kar et al. (2004a, b, 2005, 2006). These studies emphasize the importance of some fungal spores in evaluation of palaeoenvironment. Studies on fossil fungal remains in coordination with micro- and megafossils of other groups have sometimes been used to infer the

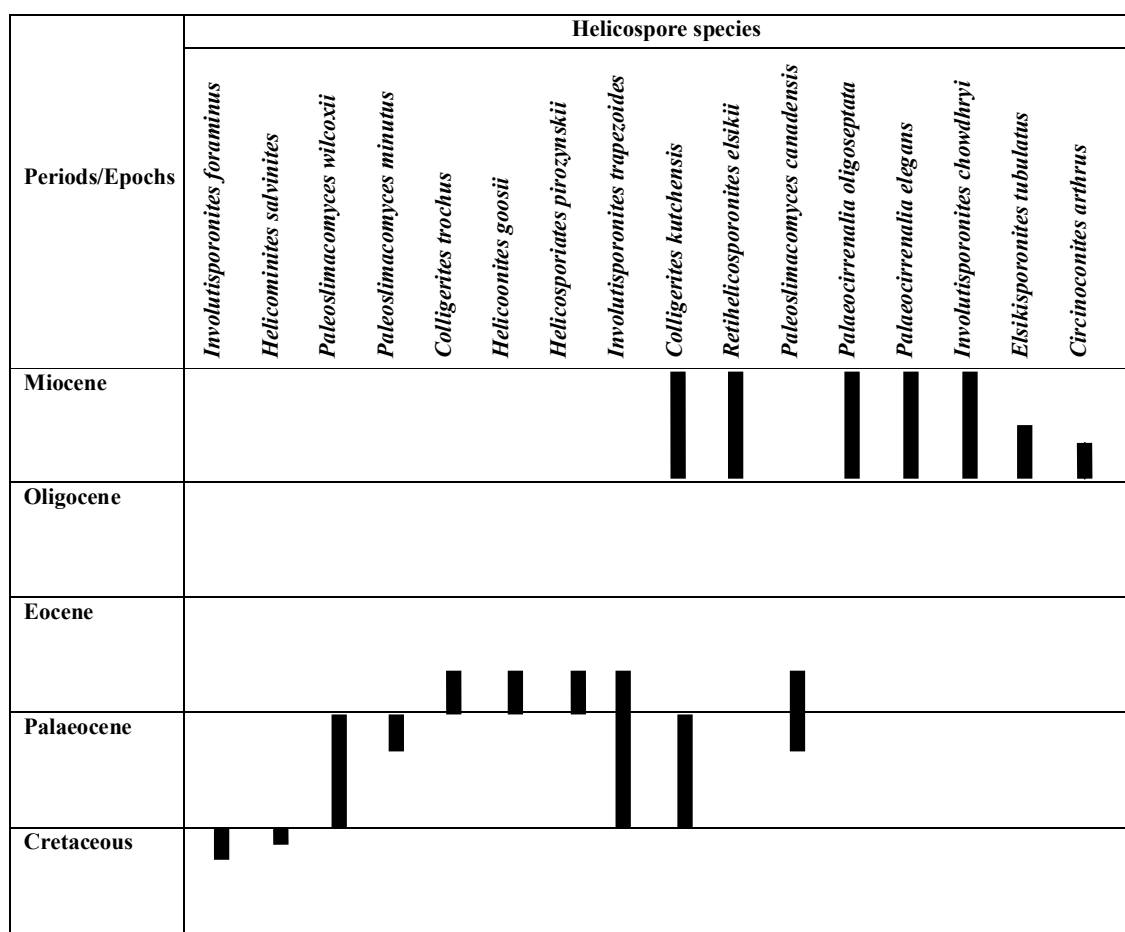


Figure 19. Global stratigraphic distribution of fossil *Helicosporae* species.

palaeoenvironment (Dilcher 1973, Pirozynski 1976, Ramanujam 1982). These assessments are based on the assumption that the palaeoclimatic sensitivity of fossil taxa was similar to that of the comparable modern counterparts. In this regard special stress was laid to explore the possibility of relating fossil fungal spores with those of modern fungi so as to realize their full potential in determining the ancient environment.

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