

Some fossil fungal form-taxa from the Maastrichtian and Palaeogene ages†

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Some distinctive dispersed fungal spores of Maastrichtian to Oligocene age from the Amphitheatre Formation, Yukon Territory, Canada, the Iceberg Bay Formation at Strand Fiord and Kanguk Peninsula on Axel Heiberg Island, Northwest Territories, Canada, and the Deccan Intertrappean Beds of India are described. Except for *Delitschia*-type ascospores, all fungal spores are considered to be conidia. Five new fossil form-genera are described and have been named according to their affinities to modern taxa. *Xylohyphites verrucosa*, with affinity to *Xylohypha*, is described from permineralized fruits of *Viracarpon*. *Ampulliferinites axelheibergi*, *Helicoonites goosii*, *Helicosporiates pirozynskii* and *Paleoslimacomycetes canadensis* are described for *Ampulliferina*-type, *Helicoon*–*Helicodendron*-type, *Helicosporium*-type and *Slimacomycetes*-type conidia. New species in existing fossil genera including *Piriurella alternariata*, *Diporicellaesporites icebergi*, *Brachysporisporites endophragmia* and *Pluricellaesporites excipularis* are described for conidia with affinities to *Alternaria*, *Diplococcium* or *Bispora*, *Endophragmia* and *Excipularia* respectively. Conidia resembling those of the modern genus *Uberispora* are described but not named. *Dicellaesporites delitschiapites* sp. nov. is described for ascospores with affinity to *Delitschia*.

In recent years information on fossil fungi has increased rapidly, providing not only significant data on the diversity of fungi in the fossil record but also on the potential relationships that exist among the major groups of fungi (Taylor & White, 1989). The study of fossil fungi is generally shunned by palaeobotanists and palynologists because of difficulties encountered in identifying and interpreting dispersed material. The geological record of fossil fungi is rich. Progressive studies of their evolutionary history and diversity continue to demonstrate their importance. The application of fossil fungi in biostratigraphy has increased with discoveries of characteristic and unique spores having limited stratigraphic ranges. Remains of fossil fungi are also an important source of information for interpreting past environments if their affinities to extant species have been determined. As familiarity with extant fungi is inevitably necessary to accomplish this purpose successfully, collaborative work with mycologists can assist in obtaining valuable results.

It is now widely accepted that an emphasis on the combined studies of fossil and living fungi is necessary to realize the full potential of fossil fungal palynomorphs as predictors of past environments (Wolf, 1966*a, b*, 1968, 1969; Lange & Smith, 1971; Pirozynski, 1976; Ramanujam & Rao, 1978; Ramanujam & Srisailam, 1980; Jarzen & Elsik, 1986; Pirozynski *et al.*, 1988; Kalgutkar & McIntyre, 1991). Pirozynski (1976) stated that 'evidence accumulates to support

the long-held view that the history of fungi is not marked by change and extinctions but by conservatism and continuity. Thus fungi in fossil remains are likely to be sensitive interpreters of past environments rather than index fossils'.

In the Tertiary, many distinctive fungal spores show affinities to modern genera. At the species level, however, it seems from accumulating work that fossil fungal forms rarely correspond exactly to modern spores. This can be attributed to various factors including the rapid evolution in fungi accompanied by ontogenetic and morphological changes, and the total extinction of species by ecological, edaphic and biotic changes which affected their substrata and consequently their saprotrophic and parasitic modes of nutrition.

This paper describes some distinctive dispersed spores, considered to be either ascospores or conidia of Palaeogene and Maastrichtian age, encountered in specimens collected from the Amphitheatre Formation, Yukon Territory, Canada, the Iceberg Bay Formation at Strand Fiord and Kanguk Peninsula, Northwest Territories, Canada and the Deccan Intertrappean Beds of India (Fig. 1). Characteristics of spore size and shape, septal nature and thickenings, wall sculpture, absence or presence and number and nature of apertures or 'pores', and other characters of diagnostic significance were used to classify them in existing or new fossil form-genera and to assess their possible affinities to modern taxa. In fossil studies, an apparent opening or aperture in a spore is referred to as a 'pore' regardless of its functional attribute, i.e. as germinalus or point of attachment. The form taxa of the Sporae Dispersae (Sheffy & Dilcher, 1971; Elsik, 1976) are

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† Geology Survey of Canada contribution No. 24493.

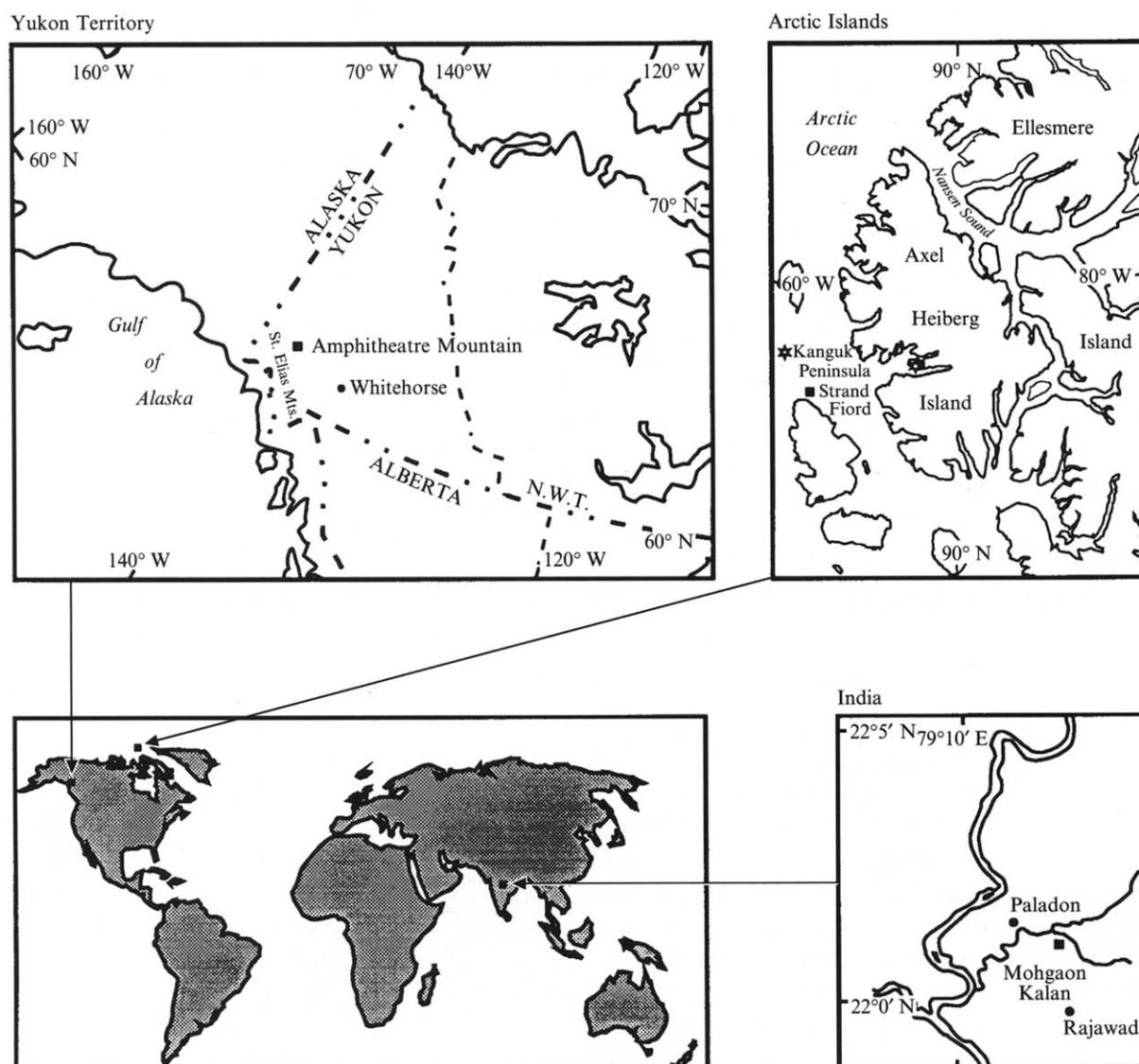


Fig. 1. Map showing locations of samples collected from Amphitheatre Mountain ($61^{\circ} 16' N$, $139^{\circ} 21' W$), Yukon Territory, Strand Fiord ($79^{\circ} 14' N$, $91^{\circ} 21' W$) and Kanguk Peninsula ($79^{\circ} 15' N$, $92^{\circ} 33' W$), Northwest Territories and Mohgaon Kalan ($22^{\circ} 30' N$, $79^{\circ} 20' E$), Chhindwara District, India.

grouped according to Saccardos spore group (Hawksworth, Sutton & Ainsworth, 1983) for convenience.

MATERIALS AND METHODS

Samples were collected from the Iceberg Bay Formation on Axel Heiberg Island at Strand Fiord ($79^{\circ} 14' N$, $91^{\circ} 21' W$; Early Eocene) and Kanguk Peninsula ($79^{\circ} 15' N$, $92^{\circ} 33' W$; late Palaeocene or early Eocene), from the Amphitheatre Formation in southwestern Yukon Territory ($61^{\circ} 16' N$, $139^{\circ} 21' W$; late Eocene or early Oligocene) and from the Deccan Intertrappean Beds of the Maastrichtian Mohgaon Kalan locality, Chhindwara District of India ($22^{\circ} 30' N$, $79^{\circ} 20' E$). The ages given are based on the associated angiosperm pollen and fungal spores. The samples were prepared by using standard palynological procedures, modified by using a weak or diluted Schultze's solution to control the rate of oxidation, a technique found to improve the recovery of fungal spores (Kalgutkar, 1993). The residues of unsieved

(UN), $+45 \mu m$, $+20 \mu m$ and $-20 \mu m$ were mounted on slides. Coordinates of all figured specimens are from a Carl Zeiss transmitted light microscope with camera attachment located at the Institute of Sedimentary and Petroleum Geology in Calgary, Alberta. All slides bearing the figured specimens including the holotypes will be permanently stored in the type collection of the Geological Survey of Canada in Ottawa.

DESCRIPTIONS OF TAXA

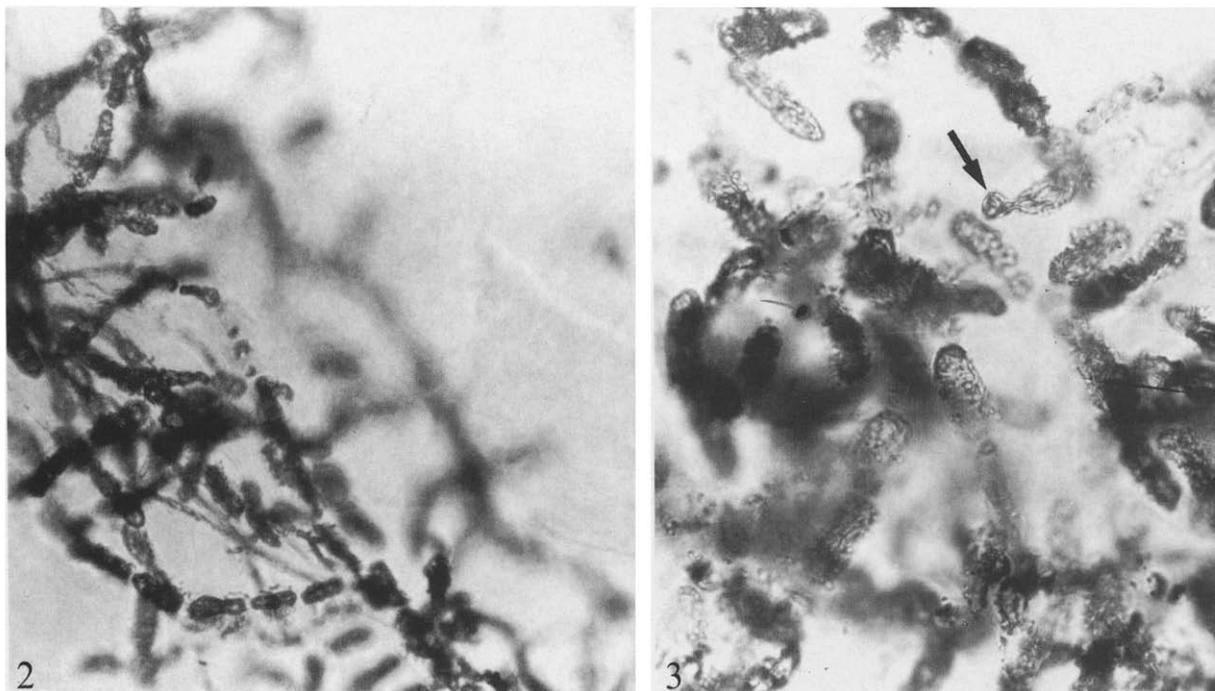
Spore group: Amerosporae

Xylohyphites Kalgutkar & Sigler gen. nov.

Type species: Xylohyphites verrucosa

Conidia in chains formed in acropetal succession, simple, ellipsoidal or cylindrical, pale brown, verrucose, aseptate, occasionally 1-septate; conidia tapering at each end but sometimes with slightly protuberant hilum.

Derivation of name: Affinity to *Xylohypha* (Fr.) E. W. Mason emend. Deighton, 1960.



Figs 2 & 3. *Xylohyphites verrucosa*. **Fig. 2**, holotype. GSC 106532, DI-10, 112·1 × 8·7, GSC loc. DI-10, **Fig. 3**, GSC 106532, DI-10, 112·1 × 8·7, GSC loc. DI-10. Note that in all legends the species name is followed by the GSC type number, the slide number, stage coordinates, the GSC locality. Bar markers = 10 µm; Figs 3, 6–14 and 16–22 are to the same scale (bar on Fig. 14), Figs 2, 4, 5 and 15 are to the same scale (bar on Fig. 15).

Comments: Although the cylindrical form of the conidia and arrangement in chains initially suggested an arthroconidial type of development, the presence of a single bud-like proliferation (Fig. 3, arrow) suggested an affinity to a dematiaceous blastoconidial fungus. Three modern genera in which blastic chains of dematiaceous conidia are formed from more or less undifferentiated hyphae are *Xylohypha*, *Bispora* Corda and *Septonema* Corda. *Xylohypha* is separated from the latter genera by having one-celled conidia (Deighton, 1960), but species within the genus differ in this respect. Conidia of those species which can be grown on agar tend to disassociate with difficulty and there may be fragments of different length and pattern of septation (Hughes, 1972; Padhye *et al.*, 1988; Kwon-Chung, Wickes & Plaskowitz, 1989). Conidia of *Xylohyphites* differ from all modern species of *Xylohypha* in being verrucose.

The occurrence of *Xylohyphites verrucosa* as a saprotroph in fruits of *Viracarpon* and its verrucose conidia in chains also suggest a possible affinity with *Cladosporium*. This modern genus is widely associated with plant materials of various kinds including fruits. However, no evidence could be found of a conidiophore among the tangled chains. Moreover, the conidia lack the prominent hila and detachment scars of typical *Cladosporium* conidia.

Xylohyphites verrucosa Kalgutkar & Sigler sp. nov.
(Figs 2, 3)

Holotype: GSC 106532, GSC loc. DI-10

Characteristics as in generic diagnosis. Conidia 9–16 × 2·5–5·5 µm.

Derivation of name: Verrucose nature of conidia.

Occurrence: In permineralized fruits of *Viracarpon*, a monocotyledonous fruit consisting of a cephalium borne on a peduncle to which compound drupes (phalanges) are attached (Kalgutkar *et al.*, 1993); collected from Deccan Intertrappean Beds of Mohgaon Kalan Locality, India; Age: Maastrichtian; Locality: DI-10.

Comments: Conidia are similar to those of *Xylohypha nigrescens* (Pers.) E. W. Mason in size (mostly 10–13·7 × 3·7–5 µm, fide Hughes, 1972) and shape, but differ in being verrucose.

Spore group: *Didymosporae* or *Phragmosporae*

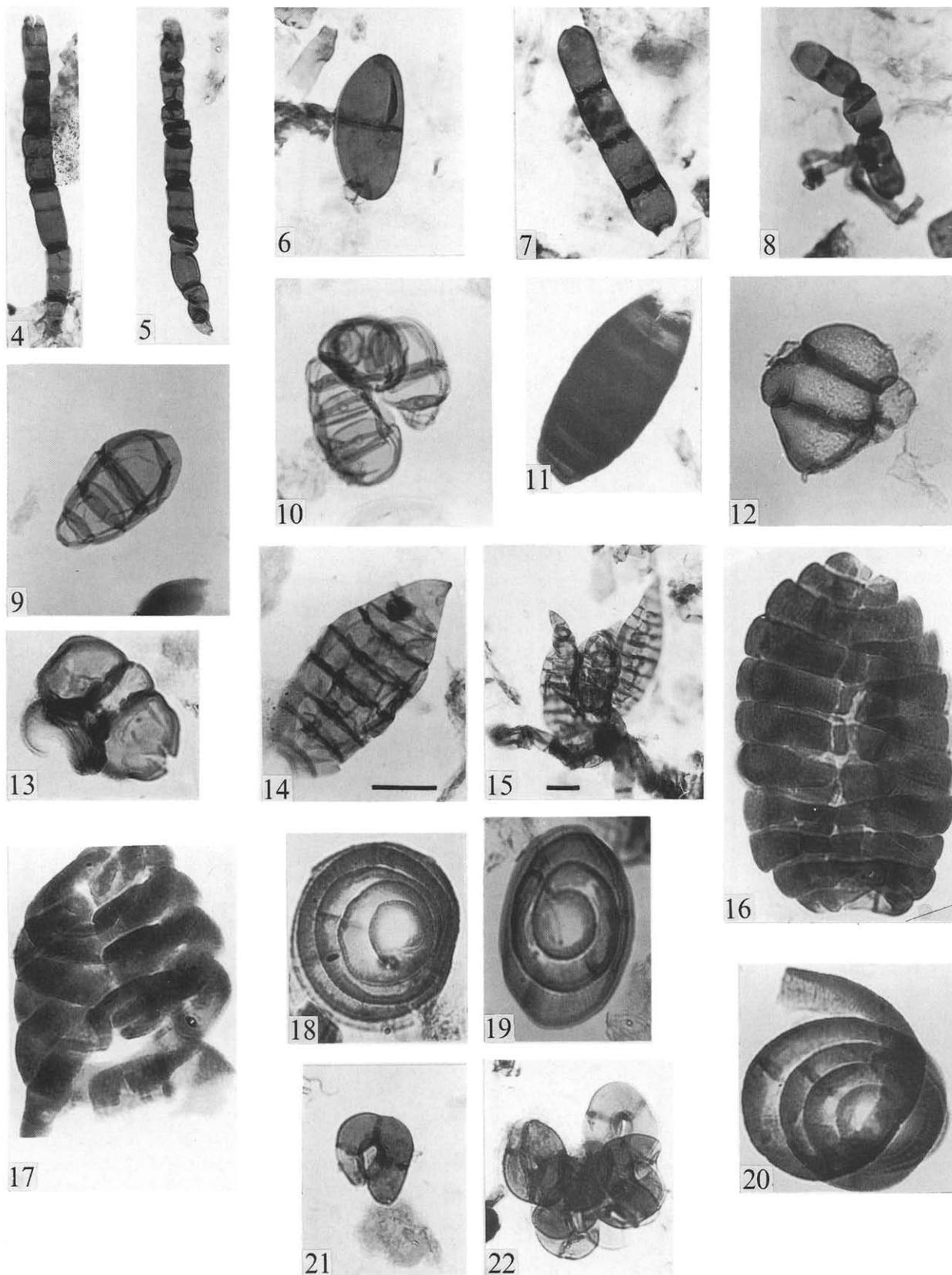
Ampulliferinites Kalgutkar & Sigler gen. nov.

Type species: *Ampulliferinites axelheibergeri*

Fungus filamentous; filaments in short or long, determinate chains of conidia; filaments traversed by thin and thick-walled septa which alternate along the chains; conidia in arthroconidial chains separated by dark, thick septa; didymosporous, not or slightly constricted at median septum and with median septum thinner, smooth, brown, cylindrical with truncate ends except the terminal conidium which is rounded at its apex.

Derivation of name: Affinity *Ampulliferina* B. Sutton.

Comments: *Ampulliferinites* appears to be similar to modern *Ampulliferina* (Sutton, 1969) which has didymosporous, catenate conidia that separate by fragmentation through the thick, dark brown septa along its length of arthroconidial chains. *Ampulliferinites* is also characterized by the presence of a basal cell with an attachment scar similar to one present



Figs 4–22. **Figs 4 & 5.** *Ampulliferinites axelheibergeri*. **Fig. 4**, holotype. GSC 106520, 3473-19 (+20), 96.9 × 19.0, GSC loc. C-189109. **Fig. 5**, GSC 106521, 3473-19 (+20), 100.6 × 14.0, GSC loc. C-189109. **Fig. 6.** *Dicellaesporites delitschiapites*, holotype. GSC 106524, 2614-126 (–20), 98.0 × 3.5, GSC loc. C-112393. **Figs 7 & 8.** *Diporicellaesporites icebergi*. **Fig. 7**, holotype. GSC 106522, 2614-129 (–20), 86.0 × 15.4, GSC loc. C-112397. **Fig. 8**, GSC 106523, 2614-126 (UN), 91.0 × 5.9, GSC loc. C-112393. **Figs 9 & 10.** *Brachysporisporites endophragmia*. **Fig. 9**, holotype. GSC 106525, 2614-126 (UN), 92.1 × 5.9, GSC loc. C-112393. **Fig. 10**, GSC 106526, 2614-126 (UN), 92.1 × 5.9, GSC loc. C-112393.

in *Ampulliferina*. *Bispora* also produces catenate two-celled conidia, but the extension growth is blastic, the conidia are more strongly constricted at the fragmentation septa, and the conidia have very dark brown to black bands at each septum (Ellis, 1971).

Ampulliferinites axelheibergeri Kalgutkar & Sigler sp. nov.
(Figs 4, 5)

Holotype: GSC 106520, GSC loc. C-189109.

Chains comprising 5–8 conidia straight and unbranched and slightly constricted at the thick separating septa. Filamentous chains 79–240 µm long. Didymosporous conidia occurring in arthroconidial chains separated by thick, dark-brown septa which alternate with the thin septa along the length of the filament. Filaments short to long, determinate; subtended by a basal cell. Basal cell pale brown, aseptate, tapering towards the base with an attachment scar left after the detachment of the filament from the mycelium. Conidia two-celled, not or slightly constricted at septum, smooth, brown, truncate at both thickened ends, 16–22 × 7–11 µm. Detached conidia were not found.

Derivation of name: After its type locality on Axel Heiberg Island.

Occurrence: Amphitheatre Formation, Yukon Territory; Age: late Eocene or early Oligocene. Locality: C-189109.

Comments: *Ampulliferinites axelheibergeri* resembles *Alternoseptites elongatus* Rouse (1962) in having filaments indented at every second septum, but in *A. elongatus* the septa are not thickened and filaments are not arthroconidial in nature.

Dicellaesporites Elsik, 1968 emend. Sheffy & Dilcher, 1971

Type species: *D. popovii* Elsik, 1968.

Dicellaesporites delitschiapites Kalgutkar & Sigler sp. nov.
(Fig. 6)

Holotype: GSC 106524, GSC loc. C-112393.

Spores broadly ellipsoid with rounded ends, 2-celled, aporate, brown, without a constriction at the septum; septum nearly median; spores with a furrow or germinal slit; germinal slit lateral, slightly gaping and about two-thirds the length of the spore; spore wall smooth, surrounded by an hyaline, narrow layer. Spores 25–28 × 11–13 µm.

Derivation of name: Affinity *Delitschia* Auersw.

Occurrence: Iceberg Bay Formation at Kanguk Peninsula, Axel Heiberg island, Northwest Territories; Age: late Palaeocene or early Eocene. Locality: C-112393.

Comments: Spores of *Dicellaesporites delitschiapites* are generally similar to the ascospores of the living loculoascomycetous and coprophilous *Delitschia* in the presence of furrows which appear similar to the distinctive germ slits. The ascospores of modern *Delitschia* are generally surrounded by conspicuous gelatinous sheaths. These probably were lost either during fossilization or laboratory processing. A thin hyaline layer around each spore of *Dicellaesporites delitschiapites* is discernible under high magnification (not shown) although its gelatinous nature may be questionable. Jarzen & Elsik (1986) have described *Delitschia*-type spores with good illustrations from river deposits, Luangwa Valley, Zambia.

Diporicellaesporites Elsik, 1968

Type species: *D. stacyi* Elsik, 1968.

Diporicellaesporites icebergi Kalgutkar & Sigler sp. nov.
(Figs 7, 8)

Holotype: GSC 106522, GSC loc. C-112397.

Conidia simple cylindrical, brown, smooth to minutely verruculose, diporate, catenate, 1–3 septate; septa thicker than conidium wall, about 2 µm thick, dark brown, with narrow septal pores in the centre. Septal thickening extending laterally a little along the spore wall on either side. Pores or areas of contact between conidia at both ends dark, simple, slightly convex. Mature conidia 27–42 × 5–7 µm. Two-celled conidia 12–16 × 5–7 µm.

Derivation of name: After Iceberg Bay Formation.

Occurrence: Iceberg Bay Formation at Kanguk Peninsula, Axel Heiberg Island, Northwest Territories; Age: late Palaeocene or early Eocene. Locality: C-112393 and C-112397.

Comments: *Diporicellaesporites icebergi* may be compared with *Diplococcium* Grove 1885 or *Bispora* in which conidia are predominantly two-celled and have a broad, dark-brown band at the septum. The conidia of both *Bispora betulina* (Corda) S. Hughes and *D. spicatum* Grove are borne in chains through pores and are rounded at each end or slightly convex. The septa of *D. spicatum* are marked by conspicuous septal pores, rather similar to those of *Diporicellaesporites icebergi* shown in Figs 7 and 8. There is no evidence of blastic conidial development in the fossil specimen.

2614-126 (–20), 100·7 × 6·8, GSC loc. C-112393. **Fig. 11.** *Pluricellaesporites excipularis*, holotype. GSC 106527, 2614-128 (UN), 85·7 × 9·0, GSC loc. C-112396. **Fig. 12.** *Uberispora*-type A. GSC 106530, 2614-126 (UN), 93·0 × 4·5, GSC loc. C-112393. **Fig. 13.** *Uberispora*-type B. GSC 106531, 2614-134 (UN), 94·1 × 4·9, GSC loc. C-112402. **Figs 14 & 15.** *Piriurella alternariata*. **Fig. 14**, holotype. GSC 106518, 2614-126 (UN), 92·8 × 8·0, GSC loc. C-112393. **Fig. 15**, GSC 106519, 2614-126 (+20), 92·9 × 5·1, GSC loc. C-112393. **Figs 16 & 17.** *Helicoonites goosii*. **Fig. 16**, holotype. GSC 97291, 2614-57 (+20), 87·7 × 13·5, GSC loc. C-111847. **Fig. 17**, GSC 97292, 2614-57 (+20), 79·0 × 15·7, GSC loc. C-111847. **Figs 18–20.** *Helicosporiates pirozynskii*. **Fig. 18**, holotype. GSC 97294, 2614-57 (+20), 76·0 × 3·5, GSC loc. C-111847. **Fig. 19**, GSC 97295, 2614-57 (UN), 101·8 × 6·9, GSC loc. C-111847. **Fig. 20**, GSC 97296, 2614-57 (+20), 86·0 × 12·4, GSC loc. C-111847. **Figs 21 & 22.** *Paleoslimacomycetes canadensis*. **Fig. 21**, holotype. GSC 106528, 2614-126 (UN), 96·8 × 4·2, GSC loc. C-112393. **Fig. 22**, GSC 106529, 2614-126 (UN), 94·8 × 14·4, GSC loc. C-112393.

Spore group: Phragmosporae**Brachysporisporites** R. T. Lange & P. H. Sm., 1971*Type species: B. pyriformis* R. T. Lange & P. H. Sm., 1971.**Brachysporisporites endophragmia** Kalgutkar & Sigler
sp. nov. (Figs 9, 10)*Holotype:* GSC 106525, GSC loc. C-112393.

Conidia simple, obovoid to clavate, brown, smooth. Conidia 2–4 septate, central cells darker than the subhyaline to hyaline cell at the proximal end; cells with broad dark bands at the septa; cell wall slightly notched and thickened at the septa; basal cell with a pore or an attachment scar at the end. Conidia 27–34 μm long, 12–19 μm thick in the broadest part and 5–6 μm wide at the truncate base.

Derivation of name: Affinity *Endophragmia* Duvernoy & Maire, 1920 emend Hughes, 1979.

Occurrence: Iceberg Bay Formation at Kanguk Peninsula, Axel Heiberg Island, Northwest Territories; Age: late Palaeocene or early Eocene. Locality: C-112393.

Comments: The conidia of *Brachysporisporites endophragmia*, with their truncated ends and broad thickened septa, compare favourably with conidia of the living *Endophragmia*. Hughes (1979) revised *Endophragmia* after transferring several of its species to other genera including a number to *Endophragmiella* B. Sutton, (1973). The truncated proximal end and absence of a basal protuberance separate the conidia of *Brachysporisporites endophragmia* from those of *Endophragmiella*.

Pluricellaesporites Hammen, 1954 emend. Elsik & Janson., 1974*Type species: P. typicus* Hammen, 1954.**Pluricellaesporites excipularis** Kalgutkar & Sigler sp. nov. (Fig. 11)*Holotype:* GSC 106527, GSC loc. C-112396.

Conidia solitary, multiseptate, dark brown except for terminal and basal cells which remain distinctively hyaline or pale. Conidia fusiform, 5–6 septate, smooth; septa dark, about 4–5 μm thick. Conidia truncate at point of attachment; basal cell not porate; terminal cell with thin, entire and clear wall. Conidia 46–48 \times 18.5 μm .

Derivation of name: Named for apparent affinity to *Excipularia* Sacc.

Occurrence: Iceberg Bay Formation at Kanguk Peninsula, Axel Heiberg Island, Northwest Territories; Age: late Palaeocene or early Eocene. Locality: C-112396.

Comments: The conidia of *Pluricellaesporites excipularis* appear morphologically similar to those of the modern genus *Excipularia* in shape, septation and in the differentiated hyaline basal and terminal cells.

Spore group: Staurosporae or Phragmosporae**Uberispora**-type A (Fig. 12)*Illustrated specimen:* GSC 106530, GSC loc. C-112393.

Conidia complex, solitary, light brown to subhyaline, composed of three linear and two or more lateral cells; cells

equidistant, terminal cell semi-circular, basal cell triangular and central cell rectangular; basal cell with an apparent apiculus. Conidia thin-walled, subhyaline, characteristically with papillate lateral cells arising from the central cell at the septa. Conidia multi-septate; septa dark and thick. Conidial surface rough and scabrid; overall size about 30 \times 18 μm .

Uberispora-type B (Fig. 13)*Illustrated specimen:* GSC 106531, GSC loc. C-112402.

Conidia complex, solitary, terminal, brown; consist of three linear and one or more lateral cells; cells smooth walled, upper and basal cells rounded, middle cell compressed and seemingly subrectangular. Lateral cells similar to those on the main axis, not papillate or thin-walled. Basal cell with a pore-like opening, indicating the point of attachment of the conidium to a conidiogenous cell. Conidia multi-septate; septa thick and dark. Conidia 31 \times 18 μm .

Occurrence: Iceberg Bay Formation at Kanguk Peninsula, Axel Heiberg Island, Northwest Territories; Age: late Palaeocene or early Eocene. Locality: C-112393.

Comments: Both *Uberispora*-type A and *Uberispora*-type B spores are distinctive and peculiar in the fossil fungal assemblage from this site. *Uberispora*-type A differs from *Uberispora*-type B in the nature of the cell wall, and in the development of lateral cells. In the former, the surface is rough and scabrid, and the spores have papillate, thin-walled lateral cells whereas in *Uberispora*-type B the surface is smooth and lateral cells are larger, thicker and non-papillate. They resemble living *Uberispora simplex* (Ichinoe) Piroz. & Hodges in their lateral branching pattern and characteristic form. This affinity was noted also by Drs K. Pirozynski (pers. comm. 1992) and S. J. Hughes (pers. comm. 1992). Pirozynski & Hodges (1973) established *Uberispora* with type species *U. simplex* after determining and redescribing the fungus *Arachnophora simplex* Ichinoe originally described from Japan (Ichinoe, 1972). Hughes (1979) also briefly described *Uberispora* as having *Endophragmiella*-like proliferations after rhexolytic secession of the conidia. *Uberispora simplex* is characterized by a central, thick-walled, dark-brown angular cell, one apical and three lateral hyaline, thin-walled conical cells and a pale brown conico-truncate basal cell. In *Uberispora*-type A and *Uberispora*-type B the main axis consists of three cells and irregularly budding lateral cells arise mainly from the central cell. Both fossil types are larger than the conidia of *U. simplex*.

Spore group: Dictyosporae**Piriurella** Cookson & Eisenack, 1979*Type species: Piriurella elongata* Cookson & Eisenack, 1979.**Piriurella alternariata** Kalgutkar & Sigler sp. nov. (Figs 14, 15)*Holotype:* GSC 106518, GSC loc. C-112393.

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 conical beak about 9–11 μm , broad with a conspicuous dark thickened tip probably representing the point of origin (attachment scar) of the successive spore in the conidial chain. Conidia when cicatrized, with a scar at the proximal end at the point of attachment to the conidiophore. Conidia 42–74 μm long, 18–27 μm wide in the broadest part.

Derivation of name: Affinity to *Alternaria* Nees, 1817.

Occurrence: Iceberg Bay Formation at Kanguk Peninsula, Axel Heiberg Island, Northwest Territories; Age: late Palaeocene or early Eocene. Locality: C-112393.

Comments: Cookson & Eisenack (1979) described *Piriurella* and the type species *P. elongata* from the Cretaceous of the Eucla basin, Australia as an algal form similar to modern *Lambertia*. Smith & Chaloner (1979) demonstrated the difference in structure between *Piriurella* and *Korshikovella schaefernai* (= *Lambertia schaefernai*) and concluded that *Piriurella* is a conidium of *Alternaria*. Elsik (1992) indicated its similarity to *Alternaria* and commented that it has priority in the event a form genus is created, assuming it is considered a fossil and not a modern contaminant.

As *Piriurella* is considered to include fossil fungal spores with an affinity to modern *Alternaria*, the *Alternaria*-type conidia described here are described under *Piriurella*. However, the senior author is not convinced that the type species, *Piriurella elongata*, has the essential characters that distinguish *Alternaria* conidia, i.e. a broader basal region with transverse and longitudinal septation and a distally tapering short or cylindrical beak with or without a dark thickened tip. The antapical tapered portion described for *P. elongata* appears like a remnant or residual portion of a conidiophore or a hypha subtending the spore. Re-examination of the holotype of *P. elongata* is necessary to resolve this question and if it should prove to lack the essential characteristics of an *Alternaria* phragmospore, a new genus would be required for fossil *Alternaria*-like dispersed spores.

The taxonomy of modern *Alternaria* is difficult due to the variability in shape, size and septation of conidia even within the species (Barron, 1983). Emphasis on sporulation patterns in species determination (Simmons & Roberts, 1993) makes assessment of affinities between fossil forms and modern taxa difficult. Solitary conidia, however, can possibly be identified as allied to *Alternaria* if they are mature and have diagnostic features such as the beaks similar to those found in modern species. The muriform conidia with short conical beaks and dark thickened tips suggest this affinity for *Piriurella alternariata*.

The conidia of *Piriurella elongata* differ from those of *P. alternariata* in being elongate with a rather long, tapered, gradually differentiated, antapical end. Also, the spore is not muriform and lacks a thickened beak. Trevedi & Verma (1970) described *Alternaria malayensis* from the Eocene of Malaya and strongly suggested the affinity of its spores to the conidia of *Alternaria*. However, the description and illustrations (p. 71, pl. 1, fig. 13; text-figs 14–16) do not appear similar or even closely related to the conidia of *Alternaria*. Spores of *Staphlosporonites* species described and illustrated by Takahashi (1991, pl. 1, figs 10–11) appear similar to the conidia of extant

Alternaria with distally extended beaks. Ediger (1981) described the new fossil genus *Transeptaesporites* to include spores resembling the conidia of *Alternaria*. However, it becomes a synonym of *Piriurella*.

Spore group: *Helicosporae*

The characteristic and distinctively coiled, septate spores found in the samples from Strand Fiord and Kanguk Peninsula in Axel Heiberg Island are easily recognized as conidia of helicosporous fungi. The genera to which they are referred belong to a group of aero-aquatic Hyphomycetes, which have peculiar conidia devised to trap air. This assists in their dispersal when the substratum is submerged under water (Webster, 1980). These fungi do not sporulate when submerged but do so at the moist interface between air and water. Helicosporous fungi have a wide geographical distribution and apparently form the most conspicuous fungal biota on submerged leaves decaying under relatively anaerobic conditions and on wood and bark lying on the ground (Kalgutkar & McIntyre, 1991).

In an extensive account of the helicosporous Hyphomycetes, Goos (1987) commented on the occurrence of a unique helicoid conidial structure which can be easily recognized and used to circumscribe this group of fungi. Extant helicosporous genera and species are classified on the basis of the morphology and ontogeny of their conidiophores and conidia and the nature and development of their mycelia. However, when the fungus and its substratum are dispersed during deposition as in the fossil sediments, the conidia are usually the only part of the organism that can be recognized.

Three forms of helicosporous conidia are described which resemble conidia of the modern genera of either *Helicoon* Morgan or *Helicodendron* Peyronel, *Helicosporium* Nees and *Slimacomycetes* Minter. These affinities were suggested by Pirozynski (pers. comm. 1992) and Goos (pers. comm. 1993). Although similar helicosporous fossil genera have been described previously, including *Involutisporonites* R. T. Clarke (1965) emend. Elsik (1968), *Colligerites* K. P. Jain & R. K. Kar (1979), and *Helicominites* Barlinge & Paradkar (1979), the morphological characteristics of the conidia from the present samples are sufficiently distinct to require new genera. Elsik (1992) recorded conidia such as these, having a coiled axis forming a planispiral to conical helix, but has not yet validly published a new genus.

Kalgutkar (1993) indicated how fossil fungal types, which are morphologically similar to modern equivalents and have a limited habitat preference, could be important in assessing the palaeoenvironment by relating the known environment of the extant taxa to similar fossil forms. In this context, the importance of helicosporous fungi in palaeoenvironmental interpretations has been demonstrated by Ramanujam & Rao (1978), Ramanujam & Srisailam (1980), Gray (1985), Sherwood-Pike (1988) and Kalgutkar & McIntyre (1991).

Helicoonites Kalgutkar & Sigler gen. nov.

Type species: **Helicoonites goosii**

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 diam.; filaments multiseptate, fuscous; cells rectangular.

Comments: Described and illustrated previously as *Helicoon*–*Helicodendron*-type (Kalgutkar & McIntyre, 1991, their Figs 1–3). Although it is easy to identify a helicosporous conidium because of its distinctively twisted structure, the conidia of some species of *Helicoon* and *Helicodendron* are so similar in appearance that it becomes impossible to separate them on the basis of their morphology alone. The most significant character separating the two extant genera is the mode of conidial development. In *Helicodendron*, the conidia are proliferating, forming catenate chains, or tangled masses or clusters, whereas in *Helicoon* the conidia are produced singly. In both genera, the conidia could be acrogenous or acropleurogenous and doliiform with tightly coiled spirals. In fossil sediments, however, during deposition such secondary conidial aggregates are unlikely to be retained on the mycelial tissue or conidiophores and are generally preserved in scattered condition. Therefore, the tightly coiled conidia of species of *Helicodendron* are extremely difficult to distinguish from the similar conidia of *Helicoon* (Kalgutkar & McIntyre, 1991). *Helicoonites* is created to encompass all fossil helicosporous conidia with a definite ellipsoidal, ovoid or doliiform shape and which are loosely to tightly coiled or twisted in three planes.

Helicoonites differs from *Involutisporonites*, *Colligerites* and *Helicominites*, and from *Helicosporiates* gen. nov. and *Paleoslimacomycetes* gen. nov. 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 a nearly 650-yr-old specimen from an archaeological site near Beetley, Norfolk, England, which appeared to be assignable to modern *Helicoon richonis* (Boud.) Linder (1929). 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 sp. nov.**

(Figs 16, 17)

Holotype: GSC 97291, GSC loc. 111847.

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.

Derivation of name: In honour of Dr R. D. Goos.

Occurrence: Iceberg Bay Formation at Strand Fiord, Axel Heiberg Island, Northwest Territories; Age: early Eocene. Locality: C-111847.

Comments: *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).

***Helicosporiates* Kalgutkar & Sigler gen. nov.**

Type species: ***Helicosporiates pirozynskii***

Conidia simple, pale brown to brown, smooth, helicoid; spirals of loose to tightly coiled filaments; filaments slender, multicellular. Conidia usually helically coiled in one plane or somewhat cochleate.

Comments: Previously described and illustrated as *Helicosporium*-type (Kalgutkar & McIntyre, 1991, their figs 4–6). The conidia of modern *Helicosporium* 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.

Modern concepts of the genera also place emphasis on development of conidia or conidiophores. In *Helicosporium*, the conidia are borne on differentiated (macronematous) conidiophores which are mononematous, tall, slender, brown, septate, simple or loosely branched and bear pale to dark, coiled or somewhat cochleate, pleurogenous or acropleurogenous conidia. In *Helicomycetes*, conidia are generally hyaline, usually tightly coiled, acrogenous, and are borne terminally on sessile denticles on repent mycelium, or on short, simple, hyaline conidiophores which arise from the mycelium as lateral branches.

Helicosporiates differs from *Involutisporonites* in having conidial spirals made up of multicellular filaments consisting of slender cells with sometimes indistinct septa. Spores of *Involutisporonites* usually have a limited number of spirals consisting of thickened broad cells with distinct septa and a porate or aporate terminal cell. In *Colligerites* multicellular compactly coiled spores are differentiated into a central region consisting of generally smaller, rounded cells and an outer region with larger, rectangular cells. This feature separates *Colligerites* from other fossil helicosporous genera including *Helicosporiates*. The multicellular and multiseptate spores of *Helicominites* are tortuous and coiled in very loose spirals with narrow ends, hence are easily distinguished from the conidia of *Helicosporiates*.

***Helicosporiates pirozynskii* Kalgutkar & Sigler sp. nov.**

(Figs 18–20)

Holotype: GSC 97294, GSC loc. 111847.

Conidia simple, pale brown to brown, smooth, helicoid. Conidial filaments forming the spirals coiled 2–4 times in one plane (Figs 18 & 19) or cochleate (Fig. 20); 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 diam.

Derivation of name: In honour of Dr Kris A. Pirozynski.

Occurrence: Iceberg Bay Formation at Strand Fiord, Axel Heiberg Island, Northwest Territories; Age: early Eocene. Locality: C-111847.

Comments: Because of its fuscous and loosely to tightly coiled conidia, *Helicosporiates pirozynskii* appears more closely affiliated to *Helicosporium* than to *Helicomycetes*.

Paleoslimacomycetes Kalgutkar & Sigler gen. nov.*Type species: Paleoslimacomycetes canadensis*

Conidia simple, solitary, helicoid, curved to hemi-circinate, brown to fuscous, smooth. Conidia 2–3 septate; septa dark, often thick; conidial filaments short and made up of 3–4 broadly curved cells; cells, except the apical cell, darkly pigmented; apical cell hyaline to pale brown.

Comments: Conidia of *Paleoslimacomycetes* show some morphological similarity with the conidia of extant *Slimacomycetes monospora* (W. B. Kendr.) Minter which was originally described by Kendrick (1958) in *Helicoma* Corda. In a revision of *Helicoma*, Ellis (1976) transferred it to *Troposporella* P. Karst. as *T. monospora* (W. B. Kendr.) M. B. Ellis. After re-examining type material, Minter (1986) concluded that the 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 *Slimacomycetes* with *S. monospora* as type. Goos (1987) concurred that the biology and morphology of *S. monospora* justify its placement in a different genus.

Paleoslimacomycetes conidia are distinguished from spores of all fossil helicosporeous genera by their distinctively short and curved to partially circinate filaments.

Paleoslimacomycetes canadensis Kalgutkar & Sigler sp. nov. (Figs 21, 22)*Holotype:* GSC 106528, GSC loc. C-112393.

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.

Derivation of name: From its occurrence in Canada.

Occurrence: Iceberg Bay Formation at Kanguk Peninsula, Axel Heiberg Island, Northwest Territories; Age: late Palaeocene or early Eocene. Locality: C-112393.

Comments: Conidia of *Paleoslimacomycetes canadensis* show some similarities with those of extant *Helicoma*, *Helicomina* L. S. Olive and *Trochophora* R. T. Moore. In these genera, however, the conidial filaments are strongly circinate, narrower than those of *Paleoslimacomycetes canadensis*, and have several septa. Although conidia of this new fossil species do not show the presence of two types of thick-walled cells that characterize the conidia of extant *Slimacomycetes monospora*, they appear similar in their general morphological features.

The authors wish to thank Dr Art Sweet of the Geological

Survey of Canada for reviewing the manuscript and making useful comments. Drs Vasu Nambudiri and William Tidwell kindly let us use the prepared slides of the fungal material from the Deccan Intertrappean beds of India. Drs William C. Elsik, R. D. Goos, S. J. Hughes and Kris Pirozynski are thanked for suggesting affinities to some modern taxa. Financial support from the Natural Sciences and Engineering Research Council, Canada, to L. Sigler is acknowledged.

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(Accepted 27 August 1994)