MORPHOLOGICAL RELATIONSHIPS OF *ANCYROSPORA* SPECIES FROM THE GIVETIAN AND FRASNIAN DEPOSITS OF THE PAN-ARCTIC REGION

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Introduction

The occurrence of miospores with ornamentation elements possessing distinctive bifurcate terminations are a characteristic component of Middle and Upper Devonian assemblages from the Arctic regions of both Canada and Russia. Originally recognised in Scotland, this type of miospore ornamentation is also common in deposits of similar age from France, Germany, Spitsbergen, USA and Australia. Records from the northern part of Gondwana are however rare. The earliest records of this distinctive ornamentation are from the latest Emsian and the final examples become extinct at the Devonian–Carboniferous boundary.

Although originally recorded by Lang (1925) as Spore Type G from the late Eifelian of Cromarty, Scotland, several other workers reported miospores with potentially similar ornamentation patterns from related palaeobotanical investigations. Arnold (1936) recorded miospores similar to Lang's Type G from the *Archaeopteris* beds of Scaumenac Bay, Canada and Høeg (1942) noted their presence in the Middle–Upper Devonian sediments of Spitsbergen. Eisenack (1944) however was the first worker to assign a formal binomial

nomenclature with his placement of these forms in the genus *Triletes*. The comprehensive documentation of Devonian miospores in Russia by Naumova (1953) reported several species potentially possessing ornamentation elements with bifurcate terminations. Several were assigned to Naumova's genus *Archaeotriletes* but in general their definition and circumscription are deemed inadequate by modern standards. A degree of confusion still exists in relation to the compatibility of taxa described using the Naumova (1953) classification and the more widely applied system of Potonié and Kremp (1954), brought about by differences in the structural and morphological terminology employed, the lack of defined holotypes and formal reference specimens and the potentially subjective nature of the line drawing illustrations.

Significant developments in the resolution of the taxonomic status of this group of miospores were made in two separate studies in 1960. McGregor investigated an assemblage from a Givetian coal seam on Melville Island, in the Canadian Arctic and described the genus *Hystricosporites* to accommodate azonate miospores with an ornament of processes with "bifurcate grapnel-like tips". Richardson working on miospore assemblages associated with the fish bands in the Middle Devonian of Cromarty, Scotland described the genus *Ancyrospora* to accommodate monosaccate specimens with a broadly comparable type of ornamentation. The structural distinction between these two genera remains clearly in place but both have been subject to significant re-interpretation in the past sixty years. The present study attempts to review the current status of the interpretation of *Ancyrospora* and to establish the taxonomic relationships of certain Canadian and Russian species from that genus.

The overall morphological concept of structure of *Ancyrospora* as either a zonate, pseudozonate or monosaccate genus has been accepted by Devonian palynostratigraphers for

many years. Recent ultrastructural analysis of the type species *Ancyrospora grandispinosa* (Wellman, 2002) in addition to *A. ancyrea* (Wellman, 2002), *A. ampulla* (Telnova, 2007) and *A. melvillensis* (Telnova, 2017) demonstrate that all four of these taxa are pseudozonate (*sensu* Wellman 2001). The spores consist of an inner body entirely enclosed within an outer layer that is extended at the equator to form a pseudozona. However, the description of an increasing number of species has suggested that it might be necessary to further emend the circumscription of the genus or even consider its subdivision to avoid taxonomic confusion.

Material and Method of Study

The specimens examined in the current study were recovered from a small number of samples from the Canadian Arctic and the Timan-Pechora province (TPP) of northern Russia. These specimens (TPP) have been studied by light microscopy (BIOLAM-I) and scanning electron microscopy (JSM 6400 Jeol) at the Institute of Geology, Syktyvkar, Russia, transmission electron microscopy observations were carried out on a Hitachi H600 TEM at the Biology Faculty of Moscow State University.

In addition to the conventional investigation of strew mounts of the total assemblages, selected individual specimens were curated as single grain mounts picked into glycerol jelly before being sealed in wax. All figured material is housed in the Palynological Collections in the Department of Animal & Plant Sciences of the University of Sheffield. Suites of reference specimens from the same sample material are curated in the School of Ocean and Earth Science, University of Southampton and the Institute of Geology, Komi Science Centre Russian Academy of Sciences (Ural Division).

Samples investigated:

1. Key Point 0.51 Well, Depth 449 m, northwest coast of Isle Vanier (76°14'N, 104º 15' W) off the northwest coast of Bathurst Island, Northwest Territories Canada; Hecla Bay Formation (see Whiteley 1980).

2. Southern limb of Robertson Point Anticline, some 10 km northeast of Beverley Inlet, Melville Island, Northwest Territories, Canada, GSC Locality No. 7559; Griper Bay Formation; lower part of Unit 6.

3. Southern limb of Robertson Point Anticline, 10 km northeast of Beverley Inlet, Melville Island, Northwest Territories, Canada, GSC Locality No 7581, Griper Bay Formation, lower part of Unit 8.

4. 1.5 km north of Stevens Head, west coast of Melville Island, Northwest Territories, Canada, GSC Locality No. 5116: Griper Bay Formation.

5. Locality details for samples 13, 14 and 18 is the northeast East-European Platform, (the Timan-Pechora province TPP), the Southern Timan, Ukhta area. Outcrop 13, 14, 18 on the right bank of Ukhta river, near Vodniy settlement. Timan–Ust'yarega Formations (Fig.1). Further details for Arctic Canada are in Owens (1971) and Christie and McMillan (1994).

Systematic Palynology

Turma TRILETES Reinsch, 1881, emend. Dettmann, 1963

Subturma ZONOTRILETES Waltz, 1933

Infraturma CINGULATI Potonié & Klaus, 1954 emend. Dettmann, 1963

Subinfraturma GRAPNELZONATI Tiwari & Schaarschmidt, 1975

The structural interpretation of the genus *Ancyrospora* is complex with a number of proposals resulting in major changes in the supra-generic assignment of the genus.

Ancyrospora was originally described by Richardson (1960) as a "monosaccate" genus. It is clear from Richardson's description and diagrammatic reconstruction of *A. grandispinosa* (Richardson, 1960, Text-fig. 6c) that he interpreted the spores as consisting of a "bladder" enclosing a central body, with the two layers attached at the proximal and distal surfaces, but the "bladder" extending equatorially with cameration (i.e. a gap) between the proximal and distal surface. Subsequent thin section studies reported by Richardson (1962, Plate 27, fig. 4) prompted a reinterpretation of the spore structure, emendation of the generic diagnosis and transfer of the genus from the Subturma *Monosaccites* to *Incertae sedis*. Richardson reinterpreted the spores as bilayered, but with no cameration between the central body (intexine) and bladder (exoexine), and with the exoexine extended at the equatorial margin forming a thick flange or pseudoflange. Richardson provided an emended diagrammatic reconstruction of *A. grandispinosa* (Richardson, 1962, Text-fig. 4) based on his reinterpretation.

Urban (1969) emended the genus *Ancyrospora* following detailed SEM analysis of a number of species from Devonian strata from Iowa and Missouri, USA. He described the wall structure based on fractured and degraded specimens, and suggested that characteristic wrinkling of the proximal surface (a common feature of *Ancyrospora* previously noted by Richardson, 1960, 1962) was a manifestation of the wall structure. He also noted that although the presence of bifurcate-tipped spines is a primary taxonomic criterion in the original diagnosis, spines are sometimes multifurcate. McGregor and Camfield (1982) suggested that Urban's emendaton was "too detailed and restrictive".

Turnau (1974) rejected Richardson's interpretation of the equatorial extension of the exoexine as a thickened flange or pseudoflange and reverted to the original interpretation of a flattened monosaccate structure. This was based on examination of latest Emsian spore

assemblages from southern Poland in which she noted that in broken specimens of *Ancyrospora* "… the flange is double and so it represents the compressed pseudosaccus. Thus the original diagnosis of Richardson (1960) was correct though the relationship between the exine and intexine was not clearly defined". Turnau (Plate IV, fig. 3) illustrates a broken specimen of *Ancyrospora kedoae* (Riegel) Turnau 1974 to demonstrate the "double nature of the zona". However, this observation is not entirely apparent from the published photograph. Furthermore, it should be noted that Turnau's material is poorly preserved and coalified and subjected to extensive oxidation. The double layered zona she observed could just as easily be a pseudozona with the two layers fortuitously separated during the fossilisation or oxidation process. Turnau transferred the genus back into Subturma Pseudosaccitriletes.

The significance of an ornamentation of processes with bifurcate terminations as important components in Devonian miospore populations was highlighted by Tiwari and Schaarschmidt (1975). Those authors noted the similarities between this genus and *Hystricosporites* but suggested that the former was restricted to zonate miospores whilst the latter was azonate. They transferred the genus into the Infraturma Cingulati and established a new Subinfraturma, the Grapnelizonati specifically to accommodate *Ancyrospora*.

This proposal might initially appear extreme but it could have a wider application. McGregor and Camfield (1982) have already noted that up to 50 species of miospores with ornamentation consisting of processes with bifurcate terminations have already been described in the literature and have been assigned to several genera including *Archaeozonotriletes, Calyptosporites, Grandispora, Hymenozonotriletes, Samarisporites, Ocksisporites* and *Perotrilites*. Without further formal emendation of the generic concept of each of these genera, none of these species fit conclusively within those generic units. The

suggestion may therefore be justified to provide greater flexibility to the supra-generic framework to allow the broader grouping of miospores with bifurcate processes.

McGregor and Camfield (1982) and Raskatova (1989) both preferred the structural interpretation of Richardson (1962). The emendation of Raskatova (1989) reverted to the interpretation *sensu* Richardson (1962) of an acavate zonate spore with a thick, wide, equatorial zona ornamented with processes that possess bifurcate terminations. No suprageneric assignment was proposed by Raskatova but use of the term zonate suggests broad agreement with the position suggested by Tiwari and Schaarschmidt (1975). No formal evidence was presented by either Raskatova (1989) or Jurina and Raskatova (2007) to prove the acavate (acamerate) nature of the exoexine/intexine relationship and for that reason, the emendation of the genus by Raskatova (1989) is not accepted here.

The issue of the structure of *Ancyrospora* has been clarified with evidence obtained from detailed Transmission Electron Microscopy analysis of ultrathin sections of various species of this taxon including the type species (Wellman, 2002; Telnova, 2007; 2017). Ultrastructural analysis of the type species *Ancyrospora grandspinosa* (Wellman, 2002) in addition to *A. ancyrea* (Wellman, 2002) and *A. ampulla* (Telnova, 2007), *A. melvillensis* (Telnova, 2017) demonstrate that all four of these taxa are pseudozonate (*sensu* Wellman, 2001). The spores consist of an inner body entirely enclosed within an outer layer that is extended at the equator to form a pseudozona. The inner body and outer layer are in direct contact in both the proximal and distal wall. In the equatorial region, a pseudozona is formed by the outer layer extending away from the inner body, before folding back on itself to continue over the inner body. There is no (or little) cameration either between: (i) the inner body/outer layer in the proximal and distal wall; (ii) the outer layer where it extends out and folds back on itself to

form the pseudozona. This essentially conforms to the emended diagnosis of the genus provided by Richardson (1962).

Evidence from the study of ultrathin sections of *A. ampulla* documented by Telnova (2007) indicates that the exine is divisable into two clearly defined layers, the inner thick dense and lamellar and a thick, friable outer layer with loop-like lamellae. The structure of the outer layer appears comparable to that described by Telnova (2007) from the miospores of the Devonian lycopsid *Kossoviella timanica* Petrosjan

Genus ANCYROSPORA (Richardson, 1960) Richardson, 1962, emend.

1960 *Ancyrospora* Richardson, p. 55.

1962 *Ancyrospora* Richardson, p.175.

Type species: *Ancyrospora grandispinosa* Richardson 1960

Emended diagnosis:

Radial, trilete, acamerate, or partially camerate, zonate miospores. Amb circular, subcircular or rounded triangular with irregular equatorial margin modified by projecting ornament. Intexine forming inner body of variable thickness, normally laevigate. Exoexine variable in thickness, extended in the equatorial plane to form zona of variable width, which may be uniform or variable in thickness. Trilete mark distinct, laesurae often accompanied by elevated exoexinal folds which may form an apical prominence. Exoexine of the equatorial portions of the proximal and entire distal surfaces ornamented with variably shaped processes, with bifurcate terminations.

Discussion:

Several authors including McGregor and Camfield (1982) have commented on the proliferation of species, which have been assigned to the genus and the need for a comprehensive review of all species with this characteristic ornamentation pattern. Such a review is beyond the scope of the present investigation which is aimed at trying to establish justified morphological relationships between certain species described from the Canadian Arctic region with those documented in northern Russia.

It is accepted that many of the proposals made might be regarded speculative since most of the Russian species were described by Naumova (1953) and when contrasted with more modern publications lack detailed descriptions, illustrations and designated reference specimens to facilitate direct comparison. However, as with western schools of palynology there is a direct academic lineage from the species concepts and identifications used by Naumova to today's researchers. They know the species of Naumova.

A superficial examination of the description of species assigned to *Ancyrospora* reveals two consistently variable morphological features, the form and structure of the extended equatorial flange and the nature of the ornamentation. The equatorial flange appears to be of two types, either of more or less uniform thickness or in some cases differentiated into an inner thicker and outer thinner zones to produce a strongly bizonate structure. Variation in the nature and form of the exoexinal sculpture has been utilised by many authors as the primary basis for speciation. However, the potential for confusion is high. Most species descriptions reveal considerable variation and potential intergradation in both the form and size of the processes and in the nature of the terminal bifurcation. In order to avoid unnecessary synonymy, it is essential that all species descriptions should follow the practice of Owens

(1971), Tiwari and Schaarschmidt (1975) and McGregor and Camfield (1982) and include profile illustrations of the processes to provide details of their size, shape and the nature of the bifurcate terminations. It is also desirable to adopt a standard descriptive terminology for the different styles of terminations. For the purposes of the present study, the authors have followed the framework scheme proposed by Owens (1971).

The authors have examined specimens of a number of other species from localities elsewhere in Europe and North America in addition to the species involved in this study. In most cases the exoexine forming the equatorial flange appears to be closely appressed to the intexine forming the inner body over both proximal and distal surfaces. This observation is therefore in agreement with Richardson (1962) and Jurina and Raskatova (2007) and indicates an acamerate condition. In other species however, there is evidence of variable separation of the two exine layers, particularly in the equatorial plane and adjacent regions which necessitates widening the concept of the genus to include potentially camerate forms as suggested by Turnau (1974). A future comprehensive review of all species assigned to the genus might conclude that the distinction between acamerate and camerate forms or separation of forms with a uniform or bizonate flange could provide the basis for further subdivision.

Several authors including Urban (1969) and McGregor and Playford (1992) have commented on the obvious morphological intergradation between many of the species described in the literature. McGregor and Playford suggested that groups of similar species could be conveniently grouped together as morphons. The *Ancyrospora simplex* Morphon proposed by those authors was suggested to include at least one of the species, *Ancyrospora melvillensis* Owens 1971, included in the present study.

Comparisons:

Hystricosporites McGregor 1960 possesses a superficially similar ornament of processes with distinctive bifurcate terminations but is readily distinguished by being acamerate, azonate and possessing a characteristic set of radially orientated, thickened folds on the contact area. Like *Ancyrospora,* both genera show a frequent tendency for the development of elevated folds accompanying the laesurae which may form an apical prominence. *Samarisporites* Richardson 1965 is zonate with the development of either an undifferentiated or bizonate flange ornamented with simple cones and spines, the bases of which may fuse laterally into short irregular groups. *Archaeotriletes* (Naumova) Potonié 1958 clearly includes several species which can be potentially accommodated within *Ancyrospora.* Those species are zonate and appear to possess an ornament of processes with bifurcate terminations. A final judgement must however be withheld until representative material can be re-examined and the precise structure and ornamentation of the genus established.

Nikitinisporites Chaloner, 1959 is significantly larger and described as a two layered megaspore although the structural relationship between the intexine and exoexine was not defined. Representatives of the genus are typically gulate and carry an ornamentation of extremely long, slender processes tipped with distinctive reflexed bifurcate terminations. This bifurcate tip is not part of a gradually tapering process but rather a separate element on the blund ended main spine. *Grandispora* Hoffmeister, Staplin and Malloy, 1955 is camerate with the exoexine ornamented typically with a wide range of simple or biform cones and spines. Specimens of *Grandispora eximia* and *G.* sp. cf. *G. eximia* (Allen) McGregor and Camfield 1982 (pl. 10, figs.2, 6 & 7 and pl. 10, figs 3 & 4 respectively) display some processes with small bifurcate terminations.

Ancyrospora ampulla Owens

1971 *Ancyrospora ampulla* Owens, pp. 73–74, Pl. 24, figs.1–4, text fig.13.

2007 *Ancyrospora ampulla* Owens, *in* Telnova, Pl. 3.11.

Description.

Radial, trilete, acamerate, zonate miospores. Amb rounded triangular to subcircular. Exine composed of two layers, the intexine which forms a rounded triangular inner body and the exoexine which is normally closely appressed to the intexine and extended in the equatorial plane to form a wide flange. Trilete mark distinct, laesurae extending to equator of inner body, frequently obscured by thin, elevated, flexuous folds of the exoexine, up to 15μ high at the pole, which extend to the equator. Intexine up to 2.5μ thick, laevigate. Exoexine variable in thickness, proximal surface thin with slightly roughened, shagreen or punctate appearance. Exoexine extended in the equatorial plane to form a wide, sometimes weakly bizonate, flange up to 44μ in width, the maximum extension occurring variably in either the radial or interradial positions. Maximum thickness of the exoexine developed over the distal polar regions and extending just beyond the equatorial margin of the inner body to produce a differentially thickened, weakly bizonate flange. Distal surface of the exoexine ornamented with distinctive broad based processes with narrow bifurcate or multifurcate terminations arranged in a loosely concentric manner. Processes variable, either broad based, steeply tapering coni or spinae or shorter, gently tapering or parallel-sided stout baculae, all with a narrow, bi- or multifurcate termination. Height of processes 8–15μ, basal diameter 3–8μ, width of bifurcate termination 2.5–3μ. Up to 30 processes project at the equatorial margin. Processes compressed on the distal surface appear to have bulbous bases. Small spines up to 4μ high occur on the distal surface between the larger processes.

Dimensions.

Maximum equatorial diameter excluding the projecting ornament 90–132μ (mean 114μ), maximum equatorial diameter of inner body 40–66μ.

Comparison.

Ancyrospora argutus (Naumova) nov. comb. is superficially similar in size and general construction but differs by possessing a more prominent bizonate flange and lacking the development of elevated exoexinal folds accompanying the laesurae. Direct comparison of the ornament is impeded by the lack of detail in the original description but the specimen illustrated by Naumova (1953, pl. 9, fig. 9) possesses a similar ornament of broad based conical processes with narrow bifurcate or rounded terminations. Some of the elements in the equatorial region may be broader and longer than those in *A. ampulla*. The specimens of *A.* cf. *argutus* illustrated by Taugourdeau-Lantz (1960, pl 3, fig.36 and 1962, pl. 1, figs. 1–2) are distinguished by possessing more numerous, larger conical processes in the equatorial region although similar sized bulbous based elements may be developed in the polar region. *Hymenozonotriletes polyacanthus* Naumova (1953, pl. 4, figs 11, 12) is distinguished by possessing a proportionately larger spore body, a well developed bizonate flange and a more densely distributed ornament of slender conate elements. Elements are arranged in a broadly concentric manner and may have narrow bifurcate terminations. *Ancyrospora grandispinosa* Richardson is larger (174–276μ), and possesses a wider undifferentiated flange with an ornament of longer, bulbous based processes with more slender shafts and wider laterally extended bifurcate terminations. *A. ancyrea* var. *ancyrea* Richardson (1962, pl.25, figs. 6–7)

has a larger inner body and a wide flange which bears an ornament of longer, slender processes with wider, laterally extended and reflexed bifurcate terminations.

Stratigraphic distribution.

The species was originally described from the Frasnian Griper Bay Formation on Melville Island, Arctic Canada. Subsequent studies by McGregor & Camfield (1982) have encountered forms referred to *A.* cf. *ampulla* from the underlying Givetian Hecla Bay Formation in the same area, whilst Whiteley (1980) reported the species from both formations in subsurface sections in the Parry Islands of the Canadian Arctic. Specimens illustrated as *Ancyrospora* sp. cf. *A. ampulla* by McGregor & Playford (1992) from the early Frasnian Fram Formation on Devon Island, Arctic Canada and the Gogo Formation of late Givetian–early Frasnian age in the Canning Basin of Western Australia probably represents extreme variants of this species. Obukhovskaya (2000) has illustrated specimens assigned to this species from the Gelon Beds of the Lansk Horizon and the Sarjansk Beds of the Sargaevo Horizon in Belarus. This interval was included in her *Acanthotriletes bucerus – Archaeozonotriletes varibilis insignis* miospore Zone which was assigned an early Frasnian (*falsiovalis – transitans* conodont zones) age. This species was also recorded by Telnova, 2007 from the upper part of Timan and lower part of Ust'yarega Formations (*A. binodosa – A. rotundiloba* regional conodont zones) of northeast Russian Platform (Timan-Pechora province, southern Timan).

Ancyrospora melvillensis Owens

1971 *Ancyrospora melvillensis* Owens, pp.72–73, pl. 23, figs. 5–6.

2007 *Ancyrospora melvillensis ??* Owens, *in* Telnova, Pl. 3.9, fig. 4

Description.

Radial, trilete, acamerate, zonate miospores. Amb rounded triangular to triangular. Exine composed of two layers, the intexine forming the wall of the inner body and the exoexine which is closely appressed to the intexine and extended in the equatorial plane to form a wide, thin, undifferentiated flange. Trilete mark distinct, laesurae simple, straight, extending to the equatorial margin of the inner body, commonly obscured by thin, elevated folds of the exoexine, up to 10μ high in the polar region and extending to the equatorial margin. Intexine thin and laevigate. Exoexine thin, minutely roughened by very fine punctation which may impart a fine striation to the surface of the spore and the ornamentation. Distal surface and equatorial region of the exoexine ornamented with coarse conate and baculate processes with small bifurcate terminations. In the equatorial region, the processes consist of coarse, broad based cones and spines with gently tapering sides and blunt or truncated tips which may bear very small bifurcate terminations. Over the more polar portions of the distal surface, the processes consist mainly of parallel-sided baculae with slightly expanded bases and small reflexed or laterally extended bifurcate terminations. Processes occurring in the polar region are normally smaller than those in the equatorial region and always more slender. Surface of the processes commonly finely striated. Up to 25 processes project at the equatorial margin. Height of processes 9–30 μ, basal diameter 3–15 μ.

Dimensions.

Maximum equatorial diameter excluding projecting ornament 92–116 μ (mean 99 μ). Maximum diameter of inner body 56–86 μ (mean 69 μ).

Comparison.

Ancyrospora simplex Guennel is closely comparable in overall structure and in the form of the processes ornamenting the exoexine. It may however be distinguished by its smaller size (generally in the range of 60–90 μ in diameter excluding any projecting ornament) and in the type material by the lack of bifurcate terminations to the processes and the lack of any differentiation of the ornament in the distal polar regions. A number of authors have referred specimens to *A. simplex* which may represent intermediate forms to *A. melvillensis*. Vigran (1964) assigned specimens to *A.* cf. *simplex* which range up to 150 μ in size but appear from the illustrations to possess a weakly bizonate flange. Specimens illustrated by McGregor and Playford (1992) as A. sp. cf. *A. simplex* (pl. 2, figs. 5–6) are closely comparable to *A. melvillensis* in possessing more slender processes in the more polar regions but differs by possessing clearly developed laterally extended bifurcate terminations to the processes. *Ancyrospora argutus* (Naumova) nov. com. is superficially similar to *A. melvillensis* but is distinguished by its markedly bizonate flange and the ornament of broad based, sharply tapering cones with either blunt or narrow bifurcate terminations. The conate elements at the equator are smaller and more densely distributed than those on A. *melvillensis* whilst the more polar regions are ornamented with small, blunt topped cones rather than long baculose elements. The specimen of *A. argutus* illustrated by Tuzova (1959) appears to have a closely comparable ornament in the equatorial region to *A. melvillensis* but the polar regions bear an ornament of small cones. Specimens illustrated by Taugourdeau-Lantz (1960, 1962) as *Hymenozonotriletes* cf. *argutus* bear only a superficial similarity to *A. melvillensis* having a more densely distributed ornament of smaller conate elements. *Ancyrospora incisa* (Naumova) Raskatova & Obukhovskaya possesses an ornament in the equatorial region composed of broad based, blunt topped spines without any indication of terminal bifurcations. The specimen illustrated by Naumova (1953) appears to have a more densely distributed

conate ornament at the equator but does show isolated baculose elements in the polar region and appears closely related to *A. melvillensis*. The specimen of *A. incisa* illustrated by Turnau and Racki (1999, pl. 3, fig. 1) bears longer processes (up to 30μ) which are described as having narrow bifurcate terminations. This specimen appears to be intermediate between *A. melvillensis* and *A. incisa sensu* Naumova. The densely distributed ornament of shorter, sharply tapering, broad based cones, frequently arranged in a sub-concentric manner readily distinguishes *A. laciniosa* (Naumova) Mantsurova from this species. No positive evidence is available to demonstrate that this species bears bifurcate terminations to the cones although many of the specimens illustrated (Turnau and Racki, 1999, pl.33, fig.5 and Avkhimovitch *et al.*, 1993, pl.12, fig.9) commonly display a terminal constriction. The original specimen illustrated by Naumova (1953, pl. 9, fig.12) appears to possess stout baculose elements on the distal polar region that are similar to those of *A. melvillensis.*

Stratigraphic distribution.

The species was originally reported from the Griper Bay Formation (early Frasnian) on Melville Island, Arctic Canada. The specimen illlustrated by McGregor and Uyeno (1972) from an alternative section on Melville Island as *Ancyrospora* n. sp. 1 is here considered to belong to this species. Whiteley (1980) recorded the species from both the Hecla Bay Formation (late Givetian) and the Griper Bay Formation from subsurface sections in the Parry Islands.

Two records exist of this species in Russia. Avkhimovitch *et al.* 1993 illustrated one specimen from the *Acanthotriletes bucerus – Archaeozonotriletes variabilis insignis* Subzone of the *Contagisporites optivus – Spelaeotriletes krestovnikovii* (OK) Zone which occurs in the Timan and Sargaevo horizons of the Timan - Pechora Basin. This miospore zone probably

equates with the *hermanni – cristatus* to late *falsiovalvis* conodont zones of late Givetian – early Frasnian age. In South Timan, the species appears at the top of the Timan Formation and it is also known in the sediments of Ust'yarega Formation (Telnova, 2007).

Obukhovskaya (2000) reported the species from the *Ancyrospora incisa – Geminospora micromanifesta* Zone in the Ubortsk Beds of the Lansk Horizon in Belarus and probably equates with the *hermanni – cristatus* conodont zone of late Givetian age. The only probable Southern Hemisphere record is from the late Givetian – early Frasnian Devonian Reef Complexes in the Canning Basin, Western Australia by Grey (1992).

Ancyrospora simplex Guennel

1963 *Ancyrospora simplex* Guennel, p. 257, fig. 13.

1966 cf. *Ancyrospora simplex* McGregor & Owens, pl. 24, figs. 8–9 & 12.

Description.

Radial, trilete, acamerate or partly camerate, zonate miospores. Amb triangular to subcircular. Exine composed of two layers, the intexine, 2–4 μ thick, forming the wall of the rounded triangular inner body and the exoexine which is closely appressed to the intexine and extended in the equatorial plane as an undifferentiated flange of variable width. Trilete mark distinct, laesurae sometimes open, extend to the equator of the inner body and commonly accompanied by elevated folds of the exoexine which continue to the equatorial margin of the spore. Equatorial and distal portions of exoexine ornamented with large spinose processes up to 25 μ in length. Processes in the more polar region may on compression appear to have bulbous bases. Processes commonly have rounded terminations but may develop narrow

bifurcate tips. Surface of the exoexine, including the surface of the processes finely shagreen or infrareticulate.

Dimensions.

Equatorial diameter including the projecting ornament 100–134 µ. Diameter of inner body 50–58 µ.

Comments.

A wide range of variation is observed in the form of the processes projecting at the equatorial margin. The holotype (Guennel, 1963, fig.13) and the specimen illustrated by Hashemi and Playford (2005, pl. 11, fig. 6) are characterised by broad based, uniformly tapering, rounded conical processes with little or no evidence of bifurcate terminations. The specimens from Canada and Australia illustrated by McGregor and Playford (1992, pl. 2, figs. 5, 6 and pl.3, figs. 1, 2) as *A.* sp. cf. *A. simplex* differ by possessing significantly longer processes which have comparable broad bases but more sharply tapering shafts with laterally extended bifurcate terminations. The specimens referred to *Ancyrospora* cf. *A. simplex* by Hodgson (1969, pl.8, figs 9–11) appear to possess both types of processes on the same specimen (fig. 10). This may support the original view of Guennel that the absence of bifurcate terminations in the holotype was the result of damage. Hodgson (1969) considered that there was no extension of the exoexine in the equatorial plane and that the pseudoflange was formed from the fusion of the bases of the broad based spinose processes.

Comparison.

Ancyrospora melvillensis Owens is comparable in overall structure but may be distinguished by its slightly larger size (92–116 μ), longer and broader based spinose processes and the development of more slender baculose elements over the more polar portions of the distal surface. *Ancyrospora arguta* (Naumova) nov. comb. differs by having a well developed bizonate flange and an ornament of predominantly smaller broad based, rounded, coni. Some of the larger equatorial elements illustrated by Naumova (1953, pl.9, fig. 9) are closely comparable to those of A. *simplex* in shape and size but possess small, narrow bifurcate terminations. *Ancyrospora incisa* (Naumova) Raskatova & Obukhovskaya is in part similar. The specimen illustrated by Avkhimovitch *et al.* (1993, pl. 10, fig. 1) appears closely comparable to *A. simplex* in structure and the style of the processes whereas the original specimen illustrated by Naumova (1953, pl. 9, fig.11) possesses a more densely distributed ornament of more rounded conical elements in the equatorial plane.

Stratigraphic distribution.

The species was originally described from late Mid Devonian fissure deposits in the Silurian Tilden Reef in southern Illinois, USA by Guennel (1963) and was subsequently reported in the USA by Sanders (1968) from the Cedar Valley Coal (Givetian) of Iowa and by Urban (1969) from the Calloway Formation in Missouri. McGregor and Owens (1966) illustrated specimens referred to as cf. *Ancyrospora simplex* from the Escarpment Member of the Hay River Formation of mid Frasnian *albertensis* Zone age in the Great Slave Lake region of the Northwest Territories. Elsewhere in Canada, McGregor and Playford (1992) reported this species from the early Frasnian Beverley Inlet Formation from southwest Melville Island in the Arctic Archipelago and the Escuminac Formation in Gaspé, Quebec.

Late Givetian records of the species were made by Turnau and Racki (1999) from the Nieczulice Beds in the Holy Cross Mountains of central Poland whilst Frasnian records in Europe were made by Taugourdeau-Lantz (1971) from the Boulonnais in northeast France and by Vigran (1964) from the Upper Svalbardia Sandstone at Mimerdalen, Spitsbergen. In Australia, McGregor and Playford (1992) have recorded the species from the upper Givetian to early upper Frasnian in the Pillara Limestone in the Canning Basin, Western Australia and Hashemi and Playford (2005) have reported it from the Etonvale Formation in the Adavale Basin, Queensland in beds of late Givetian – early Frasnian age that were correlated with the *optivus – triangulatus* and *ovalis – bulliferus* zones of the Old Red Sandstone continent.

Ancyrospora incisa (Naumova) M. Raskatova & Obukhovskaya

1953 *Hymenozonotriletes incisus* Naumova, p.68, pl. 9, fig.11

1959 *Hymenozonotriletes incisus* Naumova, *in* Tuzova, p. 147, pl. 12, fig. 7.

1981 *Hymenozonotriletes incisus* Naumova, in Kedo & Obukhovskaya, l. 21, fig. 4.

1993 *Ancyrospora incisa* (Naumova) M. Raskatova & Obukhovskaya, *in* Avkhimovitch *et al*., pl. 10, fig. 1.

2000 *Ancyrospora incisa* (Naumova) M. Raskatova & Obukhovskaya, *in* Obukhovskaya, fig.4.1

2007 *Ancyrospora incisa* (Naumova) M. Raskatova & Obukhovskaya, *in* Jurina &Raskatova, pl. 22, figs. 3, 8.

2007 *Ancyrospora incisa* (Naumova) M. Raskatova & Obukhovskaya, *in* Telnova, pl. 3.10

Description modified from Naumova, 1953

Spores rounded triangular in outline. Exoexine (perispore) significantly larger than the intexine forming the inner body and forming an equatorial flange. Surface of the exoexine rough, shagreen, bearing several sets of large spine-like protuberances with broad bases. Inner body triangular. Trilete mark distinct, simple, laesurae extending to equatorial margin of the exoexine

Expanded description after Turnau and Racki (1999)

Miospores radial, trilete. Amb, excluding projecting ornament, rounded triangular. Trilete mark distinct, laesurae accompanied by elevated folds of the exoexine which extend almost to the equatorial margin of spore. Intexine forms rounded triangular to subcircular inner body, commonly obscured by thicker exoexine and ornamentation. Exoexine spongy in appearance and extended in the equatorial plane to form the flange, variable in width but not usually exceeding ⅓ of spore radius. Proximal surface smooth, distal surface 12 μ wide at the base, 12–30 μ long, tapering moderately for most of the length and abruptly near the top to form a short neck before widening into a slender bifurcate tip. Bifurcate processes commonly broken. Longest elements occur in the equatorial and subequatorial regions, elements in more polar portion of distal surface smaller

Description from Telnova (2007, pl. 3.10)

Miospores radial, trilete, acamerate, zonate. Amb is triangular and rounded-triangular. Trilete mark distinct, simple, laesurae extending to equatorial margin of the exoexine. Surface of the exoexine ornamented with large spinose processes. Scanning Electron Microscopy demonstrates a complex multi-layered sculpture – finely shagreen, porous and baculate

processes with small bifurcate terminations (Pl. 3.10, fig. 2–5). Processes are 6–10 μ wide at the base, 8–18 μ long. Size of miospores: 70–100 μ.

Dimensions.

Equatorial diameter of spore, probably excluding projecting ornament 80–90 μ. No details of the size of the inner body or ornamentation elements provided.

Specimens in Turnau and Racki (1999) measured 90–104 μ.

Comments.

The original description by Naumova (1953) of lower Frasnian material from the Lower Shigrovski horizon of the Kaluga Region of the Russian Platform includes no detailed information concerning the form of the exoexinal processes. No mention is made of any bifurcate termination to these processes. Closely comparable specimens are illustrated by Tuzova (1959) from the lower Frasnian of Eastern Tataria and Ozolina (1961) from the Frasnian of Latvia but neither provides any details of the terminations of the processes. Kedo & Obukhovskaya (1981) illustrated specimens with bifurcate terminations to the processes from the lower Frasnian of western region of Russian Platform. However, the SEM illustrations of specimens of *Ancyrospora incisa* from the Upper Frasnian Ustbezmoshitsa Formation of Cheshskaya Guba Bay, Barents Sea, northern Timan in Jurina & Raskatova (2007) provide positive evidence that the processes bear bifurcate terminations. Although no detailed morphological description of the species is provided, these authors comment that "*A. incisa* is characterised by wide conical appendages and starlike, rounded or triangular tips". Naumova (1953) described the trilete mark as simple but there are clear indications on the specimens illustrated by both Naumova (pl. 9, fig. 11) and Tuzova (pl. 12, fig. 7) that the

laesurae are accompanied by relatively low, elevated folds of the exoexine which extend almost to the equatorial margin of the spore.

Comparison.

Ancyrospora melvillensis differs from the specimen of *A. incisa* illustrated by Naumova (1953, pl. 9, fig. 11) by possessing a more sparsely distributed ornament of processes which have narrower bases and narrow bifurcate terminations. The specimen illustrated by Turnau & Racki (1999, pl. 3, fig.1) appears closer to the circumscription of *A. melvillensis* having fewer but longer processes with narrow bifurcate terminations projecting at the equatorial margin. This specimen is probably intermediate between the two species. The characteristic baculose elements described on the polar portion of the distal surface of *A. melvillensis* do not appear to be present in *A. incisa. Ancyrospora laciniosa* (Naumova) Mantsurova is broadly similar but might be distinguished by possessing a slightly denser distribution of processes which are arranged in a sub-concentric manner. The concentration of elements on the distal surface underneath the margin of the inner body creates a bizonate appearance to the flange.

Stratigraphic distribution

This species was originally reported by Naumova (1953) from the Lower Shigrovski Horizon (Early Frasnian) in the Kaluga region of the Russian Platform. Avkhimovitch *et al*. (1993) utilised the appearance of this species at the base of the Pashiya Horizon or its equivalents in central Europe as one of the two subzonal indices for the *Ancyrospora incisa – Geminospora micromanifesta* (IM) Subzone of the *Contagisporites optivus – Spelaeotriletes krestovnikovii* (OK) Zone of Early Frasnian age. The upper limit of its range was noted in the mid late Frasnian in the middle part of the *Cristatisporites deliquescens – Verrucosisporites*

evlanensis (DE) Zone. The species has the same stratigraphic range in the Timan-Pechora province (Telnova, 2007).

In Belarus, Obukhovskaya (2000) recorded the range of this species in the ?late Givetian - Frasnian Lansk and Sargaevo Horizons. The lower part of the Lansk Horizon was assigned to the *Ancyrospora incisa – Geminospora micromanifesta* Zone and the upper part of the Lansk and entire Sargaevo horizons to the *Acanthotriletes bucerus – Archaeozonotriletes variabilis insignis* Zone. Jurina and Raskatova (2007) illustrated a specimen of *A. incisa* from the Ustbezmoshitsa Formation in northern Timan. Elsewhere in Europe, Taugourdeau-Lantz (1960, 1962) reported the species from the lower Frasnian of Boulonnais, northeast France and Turnau and Racki (1999) recorded it from the Nieczulice Beds in the Holy Cross Mountains, central Poland which were considered on conodont evidence to correlate with the Late Givetian *hermanni – cristatus* Zone.

Ancyrospora arguta (Naumova) nov comb.

1953 *Hymenozonotriletes argutus* Naumova, p. 67, pl. 9, fig. 9.

Non 1953 *Hymenozonotriletes argutus* Naumova, p.41, pl. 4, fig. 10.

1955 *Hymenozonotriletes argutus* Naumova, *in* Kedo, p. 32, pl. 4, fig. 4.

1959 *Hymenozonotriletes argutus* Naumova, *in* Tuzova, p. 128, pl. 12, fig. 3

Description modified from Naumova, 1953 (p. 67, pl. 9, fig. 9).

Spore outline rounded triangular. Exoexine (perispore) filmy, somewhat larger in diameter than the spore body (intexine). Surface of the exoexine covered by relatively large spine-like

protuberances. Spore body rounded triangular, dense with a thickened margin. Trilete mark simple with the laesurae extending to the margin of the exoexine (perispore).

Dimensions.

Equatorial diameter of spore, probably excluding projecting ornament 90–100 μ. No indication of size of the inner body or ornamentation elements provided.

Comments.

Naumova (1953) illustrated two specimens which she assigned to this species, the descriptions of both specimens are limited but interpretation of the line drawn illustrations clearly suggests that they could belong to two different species. The specimen of lower Frasnian age from the Semiluk Layer at North Petino in the Voronezh Region, illustrated as pl. 9, fig. 9, appears closely related to *Ancyrospora ampulla* in possessing a differentiated bizonate flange which bears an ornament of broad based conate processes with indications of bifurcate terminations. The ornament in the more distal polar regions consists of smaller processes which may be more densely distributed. The specimens illustrated by Kedo (1955, pl. 4, fig. 4.) from the Luga-Oredezh Beds of latest Givetian to earliest Frasnian age from Vitebsk Province, Belarus and by Tuzova (1959, pl. 12, fig.3) from the late Givetian and early Frasnian of Tataria are closely comparable to Naumova's specimen. Both possess a clearly differentiated flange but lack definitive evidence of any bifurcate termination to the processes. The second specimen illustrated by Naumova (pl. 4, fig. 10) possesses a similar differentiated bizonate flange but the exoexine is more or less uniformly ornamented by densely distributed small cones.

Hymenozonotriletes polyacanthus Naumova (1953, p. 41, pl. 4, figs. 11 & 12) described from the uppermost part of the Starooskol Beds (late Givetian - early Frasnian) of the Kuluga Region of the Russian Platform is superficially similar in organisation but is distinguished by possessing a densely distributed ornament on the equatorial portion of the flange of slender simple spines which lack bifurcate terminations. Elements in the more polar regions are smaller and may possess bulbous bases.

Comparison.

Ancyrospora ampulla Owens appears closely comparable but may be distingushed by possesing a less prominent bizonate flange and lacking any development of elevated exoexinal folds accompanying the laesurae. The ornament of the two species is similar in style but the elements in the equatorial region of *A. ampulla* are shorter and narrower whilst those in the polar region have more prominent bulbous bases.

The specimen of *Hymenozonotriletes* cf. *argutus* illustrated by Taugourdeau-Lantz (1962, pl. 1, figs 1, 2.) appears to differ by possessing more numerous, longer, stouter processes in the equatorial region which are rounded terminations.

Ancyrospora polyacantha (Naumova) nov. comb. is distinguished by its relatively narrower equatorial flange and ornament of more numerous, longer and narrower conical processes.

Stratigraphical distribution.

Naumova (1953) described the species (as interpreted here) from the Semiluk Layer of early Frasnian age from the North Petino district of the Voronezh region of the Russian Platform. An apparently morphologically similar form was reported by Tuzova (1959) from Givetian deposits in Eastern Tataria. In the Gorodok district of the Vitebsk Province of

Belarus, Kedo (1955) reported the species occurring in the Luga - Oredezh beds of Givetian and earliest Frasnian age. Avkhimovitch *et al.* (1993) in the summary of Devonian palynostratigraphy in the eastern European area extending from the Pripyat Depression in the west to the Volga – Ural region in the east, refined these earlier records. They indicated its appearance in the late early Frasnian at the base of their *Geminospora semilucensa – Perotrilites donensis* (SD) Zone at the base of the Semilouky Horizon and extending to the mid-part of the *Cristatisporites deliquescens – Verrucosisporites evlanensis* (DE) Zone at the top of the Evlanov Horizon in the middle part of the late Frasnian.

Taugourdeau-Lantz (1960, 1962) illustrated specimens referred to *Hymenozonotriletes* cf. *argutus* from the lower Frasnian in the Boulonnais, northeast France. The specimen illustrated by Hamid (1974) with the same identification from the Brandenberg Schichten (Eifelian) of the Bergischen Landes, Germany is too poorly preserved to be confirmed.

Ancyrospora laciniosa (Naumova) Mantsurova

1953 *Hymenozonotriletes laciniosus* Naumova, p. 68, pl. 9, fig.12.

1993 *Ancyrospora laciniosa* (Naumova) Mantsurova, *in* Avkhimovitch et al. Pl. 12, fig.9.

2000 *Ancyrospora laciniosa* (Naumova) Mantsurova, *in* Obukhovskaya, Fig.5–11.

2007 *Ancyrospora laciniosa* (Naumova) Mantsurova, *in* Telnova. Pl. 3.6, figs. 4, 5.

Description modified from Naumova (1953)

Spore outline irregular rounded triangular. Exoexine (perispore) forms thin, filmy flange up to twice the diameter of the spore body. Distal surface of the exoexine bears an ornament of long spine-like protuberences arranged in loosely concentric rows and projecting at the

equatorial margin. Intexine forming the spore body dense and laevigate. Trilete mark distinct, laesurae simple, straight, extending to equator of spore body.

Dimensions.

Equatorial diameter probably excluding the projecting ornament, 85–100 μ

Comparison.

Distinguished from *Ancyrospora incisa* by its denser ornamentation of broad based conical processes which are arranged in a loose concentric manner. The specimen illustratetd by Naumova (1953, pl. 9, fig. 12) appears to possess longer, more slender spinose and rounded baculose elements on the more polar portions of the distal surface. The ornament on specimens illustrated by Turnau and Racki (1999, pl. 3, fig.5) and Avkhimovitch *et al.* (1993, pl. 12, fig. 9) display a more uniform broad based conate ornament that is similar to that illustrated by Naumova for *A. incisa.* Complete morphological intergradation probably exists between the two species.

A. melvillensis differs by possessing an ornament of sparser, longer, more slender processes which are arranged randomly over the distal surface of the spore. Bifurcate terminations to the processes of *A. laciniosa* are discernable only on the specimen illustrated by Avkhimovitch *et al.* (1993) which appear to be small, slightly expanded features, similar in size but different in style to those of *A. melvillensis.*

Stratigraphical distribution.

Originally described by Naumova (1953) from the upper Frasnian Semiluki Beds at North Petino in the Voronezh region of the Russian Platform, this species was also recorded by

Tuzova (1959) from Frasnian deposits in Eastern Tataria. Avkhimovitch *et al.* (1993) illustrated a specimen assigned to this species from the late early Frasnian *Geminospora semilucensa – Perotrilites donensis* (SD) Zone from the Volga Basin which they suggested correlates with the *asymmetricus* conodont zone in the Timan - Pechora Basin. In the Timan-Pechora province, this species was recorded in the upper part of Timan Ust'yarega and Domanik Formations (Telnova, 2007).

In Belarus, Obukhovskaya (2007) recorded the species in the *Acanthotriletes bucerus – Archaeozonotriletes variabilis insignis* Zone from the upper part of the Lansk and Sargaevo horizons which were correlated with the *falsiovalvis – transitans* conodont zones of early Frasnian age. Turnau and Racki (1999) reported the species from the late Givetian Nieczulice Beds in the Holy Cross Mountains of central Poland.

Ancyrospora polyacantha (Naumova) nov. comb

1953 *Hymenozonotriletes polyacanthus* Naumova, p. 41, pl. 4, figs. 11,12.

1955 *Hymenozonotriletes polyacanthus* Naumova, *in* Kedo, p. 29, pl. 3, figs. 5, 6.

1959 *Hymenozonotriletes polyacanthus* Naumova, *in* Tuzova*,* p. 127, pl.6, fig. 3.

1981 *Hymenozonotriletes polyacanthus* Naumova, in Kedo & Obukhovskaya, pl. 16, fig. 1.

Description (modified after Naumova, 1953).

Spore outline circular or rounded triangular. Exoexine (perispore) filmy, variable in thickness, extended in equatorial plane to form bizonate flange with the thickest exoexine developed over the distal and subequatorial parts of the inner body. Distal surface of exoexine ornamented with large broad based spines arranged in concentric rings. Spines may be expanded into narrow bifurcate terminations. Elements in the distal polar region shorter.

Intexine laevigate, forms rounded triangular inner body, up to ¾ of spore radius in width. Trilete mark distinct, laesurae extend to margin of spore body and are accompanied by slightly elevated exoexinal folds which taper to the equatorial margin of the spore.

Dimensions.

Equatorial diameter (probably excluding projecting ornament) 80–90 μ.

Comparison.

The specimen illustrated by Kedo (1955, pl. 3, fig. 6) has an ornament of more sparsely distributed, shorter, broad based conate elements ornamenting the distal surface of the spore. Many of the elements in the more polar regions of the distal surface appear to have bulbous bases and none of the elements have any indication of bifurcate terminations. *Ancyrospora arguta* (Naumova) nov. comb. and *A. ampulla* Owens are distinguished by possessing a wider bizonate flange and a more sparsely distributed ornament of longer, broad based conate elements with narrow bifurcate terminations.

Stratigraphic distribution.

Naumova (1953) described this species from the late Givetian – early Frasnian deposits at the base of the Upper Terrigenous Complex (top of the Starooskol Beds) in the Kaluga region of the Russian Platform. Kedo (1955) reported a broad Mid Devonian age for the records of this species in the Luga – Oredezh Beds of the Vitebsk Provence, Belarus.

Morphons:

Ancyrospora melvillensis Morphon.

The genus *Ancyrospora* represents one of the most morphologically complex groups of Devonian miospores with variation taking place in the structure of the equatorial zona, the form of the various ornamentation elements and the extent and diversity of their bifurcate terminations. Several authors including Urban (1969) and McGregor and Camfield (1982) have commented that on the over-speciation of taxa assigned to this and other ancyrate genera. McGregor and Playford (1992) comment that in part the situation is further complicated by the tendency of workers to force variants and intermediate forms into existing species resulting in a "ballooning" of the concept of taxa. Those authors also make an important general point that is applicable to a wide range of complex Devonian taxa that authors might provide adequate detailed written descriptions but fail to illustrate the true range of variation. The need still exists for a critical re-evaluation of all species assigned to the genus *Ancyrospora* and that study must also address the formal integration of those taxa originally assigned by Russian workers to *Archaeotriletes* and *Hymenozonotriletes* which conform to the structural model established for *Ancyrospora*.

McGregor and Playford (1992) were the first workers to suggest that it was possible to group together certain *Ancyrospora* species sharing common morphological features into morphon units as defined by van der Zwan (1979) for "groups of species united by continuous variation of morphological characters". They regarded morphons as informal convenient groupings of taxa circumscribed by morphological features that might need to be emended and upgraded as new data emerged and new variants described. They proposed two broad groups based on the character of the zonate structure and the nature of the bifurcate exoexinal processes. Their *Ancyrospora longispinosa* Morphon which accommodates several species recorded in the Frasnian of the Canadian Arctic including *A. pulchra* Owens (1971), *A. furcula* Owens (1971) and *A. involucra* Owens (1971) is characterised by possessing tapered

processes with broad contiguous bases arising from the equatorial and distal regions. The component species appear zonate as a result of the equatorial concentration of the variably confluent process bases. Elevated exoexinal folds commonly accompany the laesurae.

The *Ancyrospora simplex* Morphon which also accommodated *A. melvillensis* Owens (1971) and A. *ampulla* Owens (1971) is characterised by possessing a slightly or strongly scalloped zona bearing discrete, evenly tapering processes. Whilst by definition these two morphon groups were easily distinguished, McGregor and Playford (1992) confirmed that transitional forms, as variants of *A. langii* (Taugourdeau-Lantz) Allen (1965), might bridge the gap between the morphons.

The choice of criteria utilised to circumscribe the morphons of any genus is clearly dependent on the degree of morphological complexity which is exhibited. Van Veen (1980/1981) in his definition of the *Diducites* Morphon distinguished common characteristics from those features which were found to be more variable. The same distinctions could be drawn for any *Ancyrospora* Morphon. Common or Primary Criteria might include the development of an undifferentiated or bizonate zona, the possession of exoexinal folds accompanying the laesurae and the gross form of the ornamentation. Variable or Secondary Criteria could include the nature of the bifurcate terminations and the detailed form of the ornamentation, although these are features which are found to be most variable even on individual specimens.

Examination of the Pan-Arctic assemblages investigated in the present study suggests close similarities with the *Ancyrospora simplex* Morphon documented by McGregor and Playford (1992). However, rather than being the central component of a multi-directional range of variation trends, the relationships encountered in the Pan-Arctic assemblages suggests than *A. simplex* might be an intermediate component in a lineage from *A. melvillensis* (Fig 3). Further

lineages of morphological variation from the same *A. melvillensis* source can be proposed which reflect variation in other aspects of the morphology of the genus. For the purposes of the current study the morphon is renamed the *A. melvillensis* Morphon and three distinct lineages are proposed. The authors accept that these three lineages are hypothetical and future studies might reveal links with other taxa. Intermediate forms between the named components in all three lineages are known to exist. Their purpose in the current investigation is to explore their potential stratigraphic value

Lineage A: *A. melvillensis – A. arguta – A. laciniosa* Transition

Spores assigned to this lineage are characterised by possessing a wide undifferentiated equatorial flange and an ornament on the distal surface which projects in the equatorial region consisting of broad based conate and baculose processes with gently tapering sides and blunt or rounded tips which may have small, narrow, bifurcate terminations. In *A. melvillensis*, the processes are relatively long and sparsely distributed. Over the more polar portions of the distal surface, the ornament consists of slender, widely spaced, baculose elements. In the equatorial regions, the elements are widely spaced and produce a fluted margin to the spore. Towards *A. arguta,* there is a marked tendency for the ornament projecting at the equatorial margin to become smaller but more elements project at the equatorial margin. Scattered isolated baculose elements may still occur in the distal polar region but these are accompanied by the development of further broad based conate elements in the region immediately underlying the equatorial margin of the inner body. This trend to develop conate elements in the area underlying the margin of the inner body becomes accentuated towards *A. laciniosa* where these processes become elongated and are commonly arranged as a sub-concentric ring.

Slender baculose elements continue to occur in the distal polar regions whilst the broad based conate elements at the equatorial margin remain small.

Lineage B: *A. melvillensis – A. incisa – A. ampulla* Transition

The lineage between *A. melvillensis* and *A. incisa* is more speculative. It involves the progressive reduction in the size of the ornament on the distal surface and at the equatorial margin at the same time as the progressive change in the development of a weakly bizonate flange. In *A. incisa*, the ornament in the polar regions of the distal surface is reduced to sparsely distributed, low rounded cones whilst the equatorial portion of the flange bears a slightly denser ornament of shorter, rounded cones. A small proportion of these conate processes may display narrow bifurcate terminations. The trend towards *A. ampulla* is marked by the progressive development of a coarser conate ornament of the more polar portions of the distal surface with the majority of the elements displaying characteristic bulbous bases and narrow bifurcate terminations. The ornament on the distal surfaces of both *A. incisa* and *A. ampulla* is arranged in a loosely concentric style.

Lineage C: *A. melvillensis – A. simplex – A.* sp. cf. *A. simplex* McGregor & Playford Transition

A close morphological relationship exists between *A. melvillensis* and *A. simplex*. The difficulties encountered in distinguishing between the two species can probably be traced back to the original description of *A. simplex* from poorly preserved corroded sample material. The principal differences between the two species are the apparent absence of any baculose or conate processes in the more distal polar region of *A. simplex* in contrast to *A. melvillensis* and the faint differentiation of the equatorial zona in *A. simplex* where a slightly thickened narrow

band is developed in many specimens, on the distal surface adjacent to the margin of the inner body. This thickening probably extends over the entire distal polar region. The ornamentation of the exoexine is similar in style in both species but the elements in *A. simplex* tend to be shorter. The end member of the lineage as described here is comparable to the forms reported by McGregor and Playford (1992) as *Ancyrospora* sp. cf. *A. simplex*. Representatives of this member are characterised by possessing a zona which compares closely with that of the *A. simplex* group but is distinguished by the development of well formed small, laterally extended bifurcate terminations to the processes.

Phylogenetic relationships

Wellman (2002) has reviewed the evidence from all the major Devonian plant groups and spores *in situ* in an attempt to establish the most probable affinity of *Ancyrospora*. He compared spore dimensions, morphology and wall ultrastructure of well preserved and reliably identified material from the Devonian of Scotland. He concluded that the evidence from the bryophytes, rhyniophytes, zosterophylls and barinophytes failed to generate any conclusive support for them being the parental stock for *Ancyrospora*. Evidence from lycopsids however is more compelling. Wellman suggested that the wide range in size between some members of the genus could be interpreted as similar morphologies being developed in both miospores and megaspores. Lycopsid spores include a wide range of structures including both zonate and camerate types and grapnel tipped sculptural elements have been reported in some members of the group. Wall ultrastructure however provides more compelling evidence of a phyllogenetic relationship. The spore wall is largely lamellate with anatomising elements enclosing voids.

Based on the similarity of the external layer of the exine of miospores recovered from *Kossoviella timanica* Petrosjan and *Ancyrospora ampulla,* it is possible that both were

produced by lycopsid plants. The miospores of *K. timanica* which are similar to dispersed spores of the genus *Cristatisporites,* are rounded – triangular in outline and commonly occur within the 100–140 μ size range although specimens up to 300 μ may be recorded. The exine is dense with the proximal and distal surfaces distinguished by the form and size of the sculptural elements developed. The proximal surface bears a fine tuberculate sculpture whilst the distal surface is characterised by a roughened pitted surface which is ornamented with large biform elements consisting of a bulbous base surmounted by a short curved papillae up to 0.8 μ high and up to 0.3 μ in width. The trilete mark is distinct, variably thickened and elevated up to 3 μ in height.

In TEM section, the main part of the exine is represented by the thick, cellular, friable ectexine composed of anastomosing lamellae. In the area adjacent to the trilete mark, the ectexine is thickened with chains of cells arranged parallel to the suture. Large air cavities may occur at the contact between the ectexine and the endexine. Sculptural elements of the ectexine are commonly friable and may also contain air cavities. The endexine is dense and homogeneous.

The dispersed miospores of *Ancyrospora ampulla* display some similarities to the miospores of the plant *K. timanica* but only in the structure of the ectexine. Essential distinctions in the ultrastructure of the endexine of the two groups probably reflect different reproductive strategies of the parent plants of these two spores. The plant *K. timanica* which was the first Upper Devonian plant in the Timan – Pechora Province to yield heterospores, was described from exposures of the Gruboruchey and Ustbezmoshitsk Formations (Sargaevo and Voronezh regional stages of the Russian Platform) in northern Timan (Petrosian, 1988). In contrast, *A. ampulla* was recorded only from the older upper part of the Timan and lower part of the Ust'yarega Formations.

Biostratigraphy

In the Timan-Pechora province, the most complete sequence of Givetian-Frasnian deposits is located in the Ukhta area of southern Timan (Fig.1). Frasnian deposits here are well exposed and characterized in detail by different groups of fauna and miospores. The history of research in this area has been documented with varying degrees of detail in numerous scientific publications (House, Menner, Becker *et al*., 2000; Ovnatanova et al., 2017).

On the Russian Platform, the lower boundary of the Frasnian is traditionally taken at the base of the Pashiya regional horizon. This horizon is correlated with the *hermanni-cristatus* conodont zone (Rzonsnitskaya, 1988) and the *Contagisporites optivus – Spelaeotriletes krestovnikovii* palynozone (Chibrikova, 1991, 2008; Avkhimovich *et al*., 1993).

Following the decision of the Subcomission on Devonian Stratigraphy, the lower boundary GSSP of the Upper Devonian is drawn at the base of Lower *asymmetricus* conodont zone. In the Devonian sections of the Timan-Pechora province, the base of this zone is located at the base of the Sargaevo Horizon and equates with the Ancyrodella rotundiloba local conodont zone (Ovnatanova, Kononova, Menner, 2005). In the deposits of the underlying Timan horizon, the *Ancyrodella binodosa* local zone is recognized and this is correlated with the Lowermost *asymmetricus* zone of standard conodont zonal scheme of Ziegler (1971).

The detailed faunal analysis of material from Givetian-Frasnian boundary interval in the Ukhta area has shown that the Timan Formation deposits are characterised by the remains of spineless, basically endemic forms of brachiopods and ostracods. The lower Timan Formation corresponds to the *Uchtospirifer nalivkini* brachiopod zone and the *Ornatella multiplex* ostracod zone. The Upper Timan Formation is assigned to the *Uchtospirifer timanicus* local brachiopod zone and the *Cavellina devoniana* ostracod zone (Frasnian Field Guide, 1997).

The individual fragments of rugose coral colonies with a wide stratigraphic range have been described from this interval.

Investigations of conodont assemblages from the stratotype sections of the Timan (being also stratotype of Timan regional horizon) and Ust'yarega (equivalent to the Sargaevo horizon) formations in southern Timan has shown that *Ancyrodella binodosa* occurs rarely, and its distribution covers not only Lowermost *asymmetricus* zone but also the Lower *asymmetricus* zone. At the same time in the Sargaevo horizon sections, *Ancyrodella rotundiloba* occurs only in the middle and upper parts. Conodont complexes from the top part of the Timan and lower part of the Ust'yarega formations are similar on their composition and can be correlated with the Lower *asymmetricus* zone (Kuz'min, 1995).

The stratigraphic interval covering the upper part of the Timan and the lower part of the Ust'yarega horizons has however been correlated with the *Polygnathus pennatus – P. lanei* conodont zone. This implies that the correlation of conodont complexes from shallow water facies to the standard chronostratigraphical sequence remains unclear and consequently the lower boundary of the Frasnian in southern Timan is also not established (Ovnatanova, Kononova, Menner, 2005).

In this connection data recovered from miospore assemblages have special value. The rich and diverse Devonian miospore assemblages recovered from southern Timan provide the opportunity to utilise them as the standard in undertaking reconstructions of palaeo-vegetation and for regional and inter-regional correlations. The analysis of taxonomic composition of miospore assemblages from Middle-Upper Devonian deposits in southern Timan has allowed the succession in the *C. optivus – S. krestovnikovii* palynozone sequence to be subdivided into eight independent palynozones (fig. 4) and prove phytostratigraphic boundary corresponding

to the Givetian-Frasnian boundary (Telnova, 2007). The stratigraphical distribution of some of the species of *Ancyrospora* encountered in the Givetian – Frasnian sequence of southern Timan are plotted on Fig 5. from which the following conclusions can be drawn.

The youngest records of *Hymenozonotriletes tichonovitschi* in southern Timan are in the Vorobiev Horizon which is assigned to the *varcus* conodont zone and the upper part of the *G. extensa* palynozone. It is replaced in the Ardatov and Mullin horizons by the appearance of *Ancyrospora polyacantha* which extends through the uppermost parts of the *G. extensa* palynozone into the basal part of the C. *optivus – S. krestovnikovii* zone in the lowest part of the Pashiya Horizon. The youngest records of A. *polyacantha* occur close to the top of the C. *optivus – H. tichomirovii* local palynozone in southern Timan. The oldest record of *Ancyrospora incisa* in southern Timan occurs at the base of the Pashiya horizon which also marks the base of the *C. optivus – S krestovnikovii* palynozone.

This species appears to occur throughout all of the Givetian and a significant part of the Frasnian with a range that extends from the base of the *hermanni – cristatus* conodont zone to the Late *rhena* zone at the top of the Evlanovo Horizon.

The base of the Timan Horizon, at the base of the local *S. bellus – D. meyeriae* palynozone, marks the appearance of *Ancyrospora melvillensis* and *A. ampulla*. Both species occur throughout the Timan and Sargaevo horizons and disappear at the upper boundary of the *C. optivus - S. krestovnikovii* palynozone. Throughout this interval, they occur in close association with representatives of A. *incisa*. They are joined in the uppermost parts of the Timan Horizon, at approximately the position of the lower boundary of the *D. sorokinii* local palynozone, by *Ancyrospora laciniosa*. The range of this latter species extends through the Sargaevo Horizon to the upper boundary of the Domanik Horizon.

Records of the distribution of *Ancyrospora arguta* suggest that it may not appear until the base of the Domanik Horizon.

Data from the Canadian Arctic is drawn from a number of well-documented sections on Bathurst, Melville and Prince Patrick Islands. These sections which are separated by up to approximately 450 kilometres, are located at the western end of the Franklinian Miogeosyncline. Tozer and Thorsteinsson (1964) carried out the first regional survey of these Middle and Upper Devonian clastic sediments in the region and established a comprehensive lithostratigraphical nomenclature for the sequence. Detailed sedimentological analyses of the sequences in the Queen Elizabeth Islands by Embry and Klovan (1976) resulted in significant revisions to stratigraphic nomenclature and the suggested correlations to standard stage boundaries (see text fig. 6).

Correlation of the clastic Middle and Upper Devonian sequences in the Arctic Islands is difficult because of the paucity or total absence of diagnostic faunas. McGregor (1981) and McGregor and Camfield (1982) have highlighted the potential of miospore assemblages for both local and regional correlations in the area. The predominantly clastic nature of the sequences makes placement of the Givetian – Frasnian stage boundary in the region difficult. Various interpretations have been made but all lack definitive independent biostratigraphical controls.

The Weatherall Formation of probable Givetian age consists of coarsening upward cycles of shale, siltstone and sandstone with thicker white sandstones commoner in the upper part. Conodonts have been reported from close to the base of the formation which indicate an *australis* to Lower *varcus* Subzone age and suggest an early Eifelian to early Givetian age.

The overlying Hecla Bay Formation consists predominantly of white-grey, cross-bedded sandstones with infrequent to rare siltstone and shale intercalations. No independent faunal evidence is available from the formation.

The Beverley Inlet Formation, formally the Griper Bay Formation, is more varied in composition. Greenish grey to white sandstones and siltstones predominate but are accompanied at various horizons by shale and thin coal interbeds. Exposures probably from this formation on Prince Patrick Island have yielded conodont faunas assigned to the *triangularis* Zone suggesting a middle Frasnian age.

Well preserved and diverse miospore assemblages have been reported by numerous authors (Kerr *et al,* 1965; McGregor, 1960, 1981; McGregor and Camfield, 1982; McGregor and Uyeno, 1972; Owens, 1971; Richardson and McGregor, 1986 and Whiteley, 1980; from these formations at several key sections throughout the region. McGregor (1981) has commented that many of the taxa might potentially serve as palynological proxies to define the Givetian – Frasnian boundary in the region. His review of the potential role of miospores in the definition of the Middle – Upper Devonian in the Canadian Arctic also identifies the difficulties of correlating sections in which facies changes often account for significant thickness variations in the sections and the common widely spaced nature of the sample database. These criteria make direct comparisons of stratigraphic ranges of miospores from one section to another difficult with ranges being expressed in relative terms to formational boundaries.

A synopsis of published occurrences of selected species of *Ancyrospora* from the Canadian Arctic region is illustrated in Fig. 6. The oldest occurrences of *Ancyrospora ampulla* made by Owens, 1971 and McGregor and Camfield, 1982 are in the upper part of the Hecla Bay Formation whilst Owens, 1971 and McGregor and Uyeno, 1972 indicate that the

appearance of A. *melvillensis* is probably in the lowermost part of the overlying Beverley Inlet Formation. Whiteley (1980) listed both of these species as typical components of his "upper assemblage" which had its base in the upper part of the Hecla Bay Formation and extended through all of the Beverley Inlet Formation into the Parry Islands Formation. Although no distribution data was documented for individual taxa within this assemblage, Whiteley did comment that *Ancyrospora (Hymenozonotriletes) incisa* occurred with a frequency of up to 40% in the younger Parry Islands Formation part of its range. This record constitutes the only known record of this species in the Canadian Arctic but no data was supplied to confirm its presence in either the Hecla Bay or Beverley Inlet Formations.

The appearances of *A. ampulla* in the upper part of the Hecla Bay Formation and A. *melvillensis* in the basal part of the Beverley Inlet Formation appear to coincide with the appearances of *Contagisporites optivus* (Chibrikova) Owens and several species of *Archaeoperisaccus including A. scabratus* Owens*, A. timanicus* Pashkevich and *A. opiparus* Owens. McGregor, 1981 suggested that these range data together with the disappearance of characteristic Givetian taxa such as *Rhabdosporites langi* (Eisenack) Richardson might serve as palynological criteria to define the Givetian-Frasnian boundary

Richardson and McGregor 1986 utilised the appearance of *Contagisporites optivus* to define the base of their *Contagisporites optivus – Cristatisporites triangularis* Assemblage Zone to which they assigned a late Givetian – early Frasnian age and correlated to the upper part of the *varcus* to Lower *asymetricus* conodont zones.

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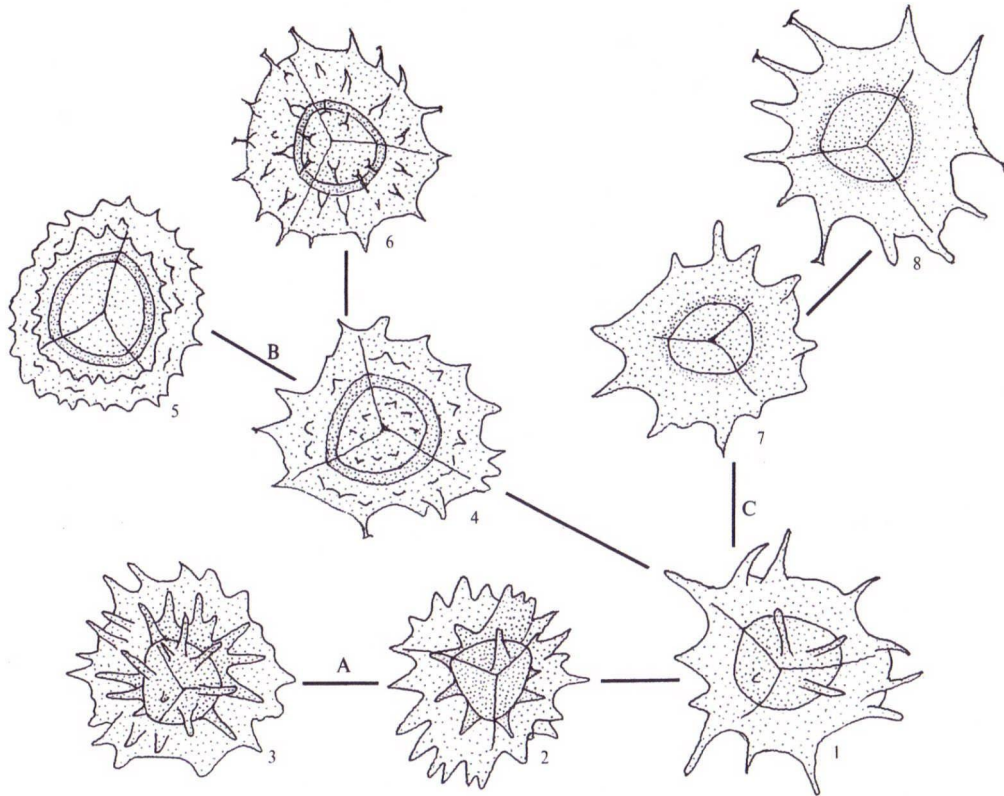
Text Fig. 1. Location of the outcrop samples studied from the Timan-Pechora, Komi Republic, Russia
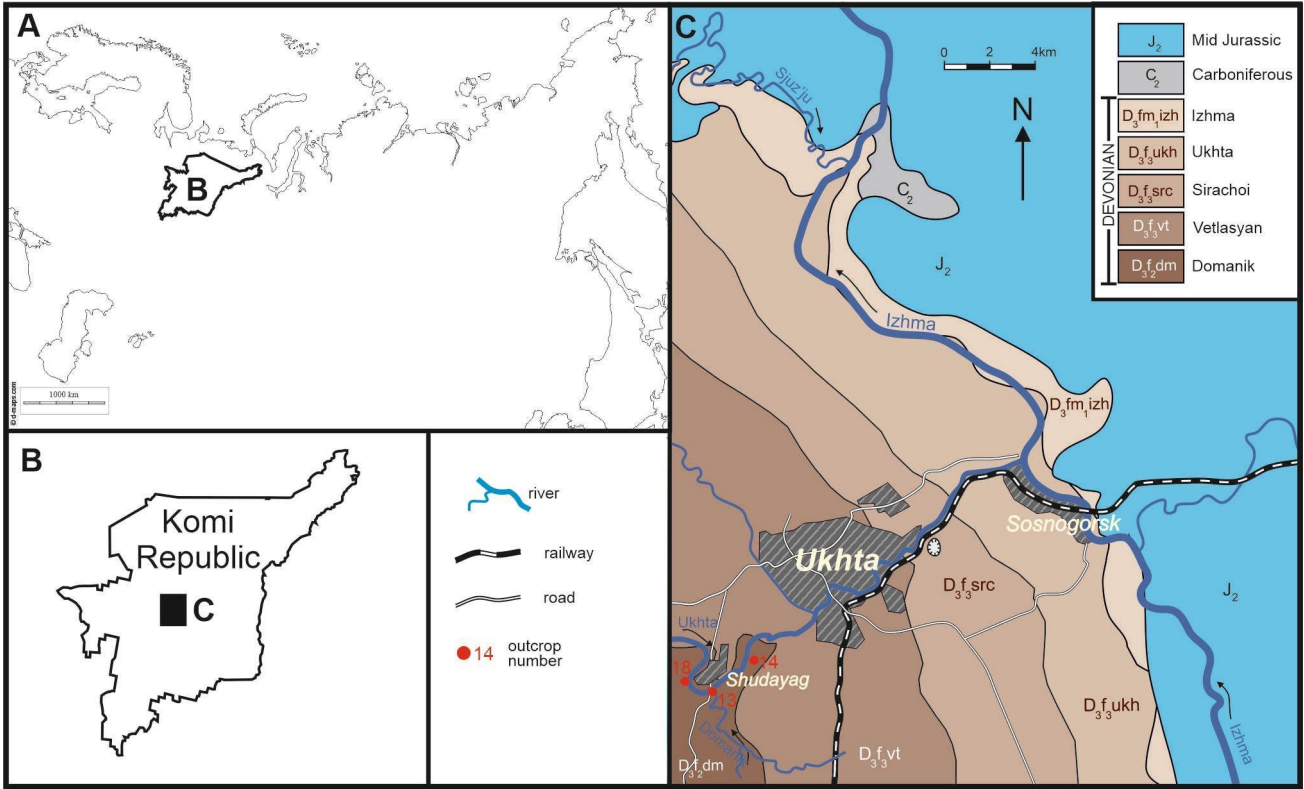
Text Fig. 2. Diagrammatic profiles of sculptural elements of selected *Ancyrospora* species.

A. melvillensis

A. ampulla

A. incisa

A. lacinosa

A. simplex
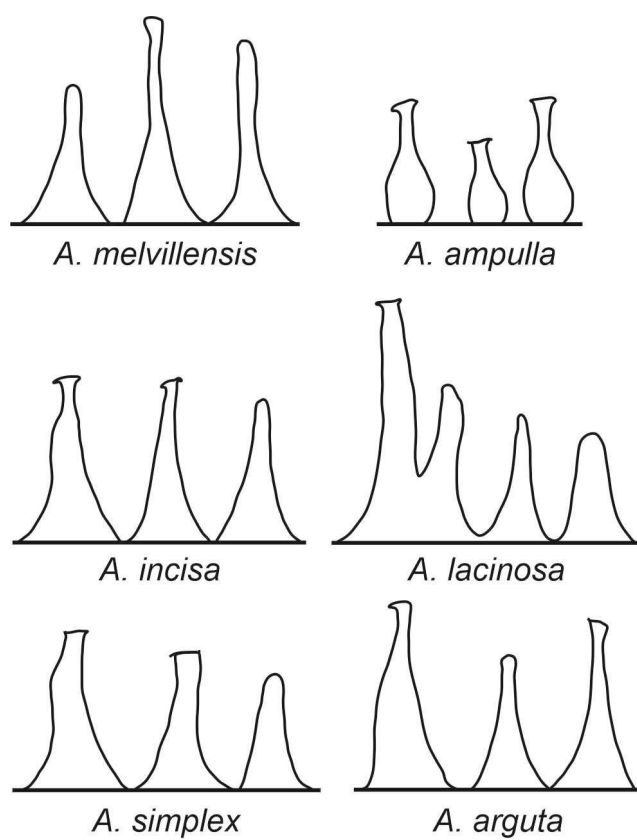
A. arguta

Text Fig. 3. Diagrammatic representation of potential lineages in the *Ancyrospora melvillensis* Morphon.

Lineage A. *Ancyrospora melvillensis* (1) - *A. incisa* (2) – *A. laciniosa* (3)

Lineage B. *Ancyrospora melvillensis* (1) – *A. arguta* (4) – *A. arguta sensu* Kedo 1955 (5) – *A. ampulla* (6)

Lineage C. *Ancyrospora melvillensis* (1) – *A. simplex* (7) – *A.* sp. cf., *A. simplex sensu* McGregor & Playford 1992

Text Fig. 4. Comparison of the *C. optivus – S. krestovnikovii* palynozone in eastern and western sections of Europe and Canada

Western Europe & Canada Richardson, McGregor 1986			Eastern Europe Avkhimovitch et al. 1993			Timan-Pechora Province	
			palynozone	subzone	horizon	palynozone	
D₃	Frasnian	*ovalis - bulliferus*	*A. ovalis - V. grumosus*				Frasnian
				S. bellus	Semilouky		
			G. semilucensa - P. donensis				
					Sargaevo	*C. pseudodeliquescens*	
D₂	Givetian	*optivus - triangulatus*	*C. optivus - S. krestovnikovii*	*A. bucerus - A. variabilis insignis*	Timan	*D. sorokinii*	Givetian
						S. vermiculatus - S. domanicus	
						S. bellus - D. meyeriae	
				A. incisa - G. micromanifesta	Pashiya	*A. bucerus - A. variabilis insignis*	
						A. accretus	
						A. incisa - S. krestovnikovii	
						C. optivus - H. tichomirovii	
	Eifelian	*lemurata - magnificus*	*G. extensa*		Starooskol		

Text Fig. 5. Stratigraphical distribution of *Ancyrospora* spp. in Southern Timan

	Conodont Zonation		Southern Timan	*Ancyrospora* species
			Regional Stage	
	Ziegler, 1962; 1971	Ziegler,Sandberg 1990	Ovnatanova *et al.* 2017	
Famennian	middle triangularis		Volgograd	
	lower triangularis			
Frasnian	uppermost gigas	linguiformis	Livny	
	upper gigas	late rhenana	Evlanova	
	lower gigas	early rhenana	Sirachoi	
	Ancyrognathus triangularis	jamieae	Vetlasyan	
		late hassi		
	unzoned	early hassi	Domanik	
	upper asymmetricus			
	middle asymmetricus	punctata		
	lower asymmetricus	transitans	Sargaevo	
		late falsiovalis		
	lowermost asymmetricus	early falsiovalis	Timan	
Givetian		disparilis	Pashiya	
		hermanni-cristatus		
		varcus	Mullin Ardatov Vorobiev	

Text Fig. 6. Stratigraphical distribution of *Ancyrospora* spp. and associated taxa in the Canadian Arctic Archipelago.
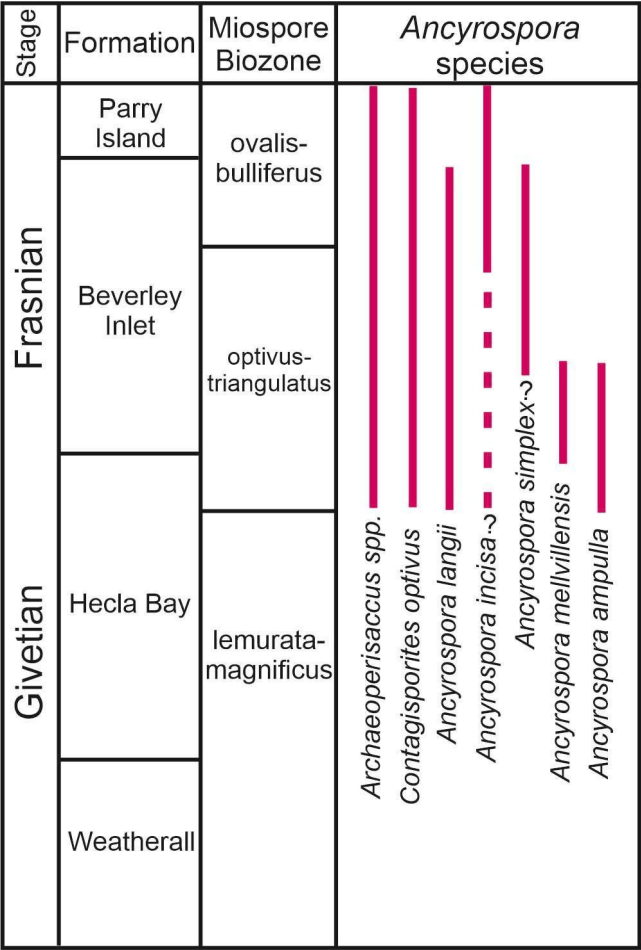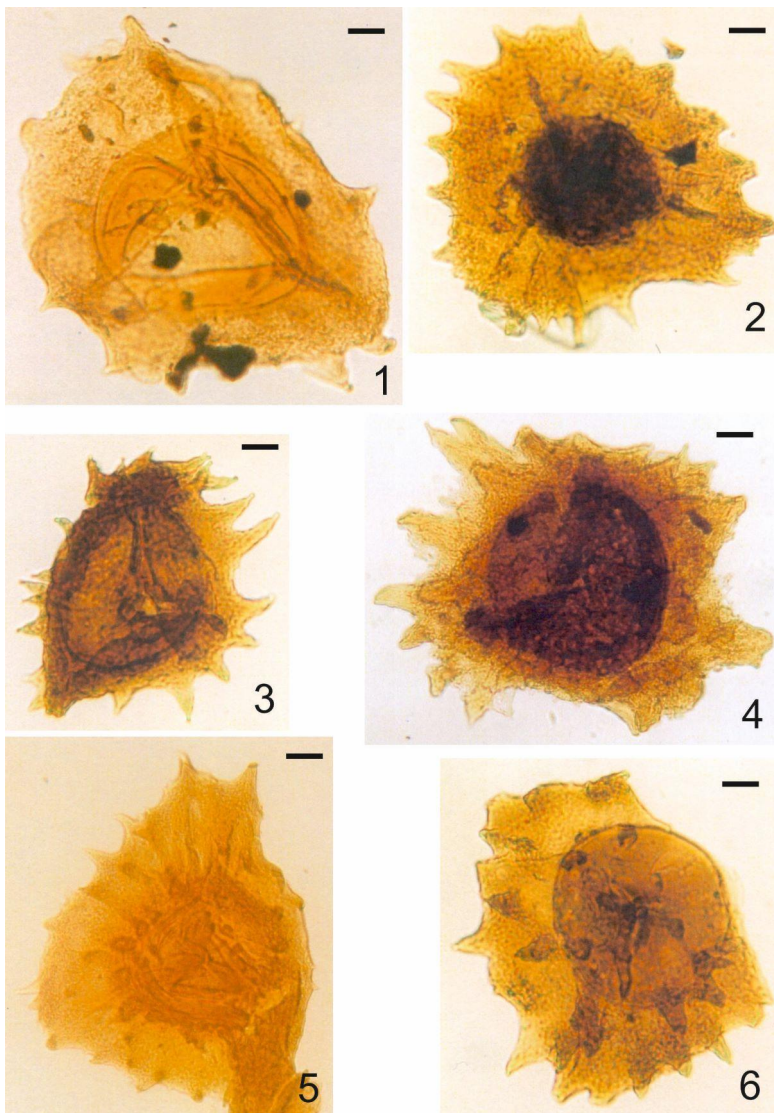
Plate 1 (scale bar is 10 μm)

1   *Ancyrospora* cf. *simplex* Guennel, 1963. Sample 54-3-8, Slide 54-3-8 / 31.

2   *Ancyrospora* ?*melvillensis* Owens, 1971. Sample 13, Slide 13 / 08/10

3   *Ancyrospora arguta* (Naumova) nov. comb. Sample 13, Slide 13 / 08 / 4.

4   *Ancyrospora laciniosa* (Naumova) Mantsurova 1993, Sample 14, Slide 14 / 08 / 94,.

5   *Ancyrospora melvillensis* Owens, 1971. Sample 83A, Slide 83a / 75.

6   *Ancyrospora laciniosa* (Naumova) Mantsurova, 1993. Sample 13, Slide 13 /08 / 17.

Plate 2. (scale bar is 10 μm)
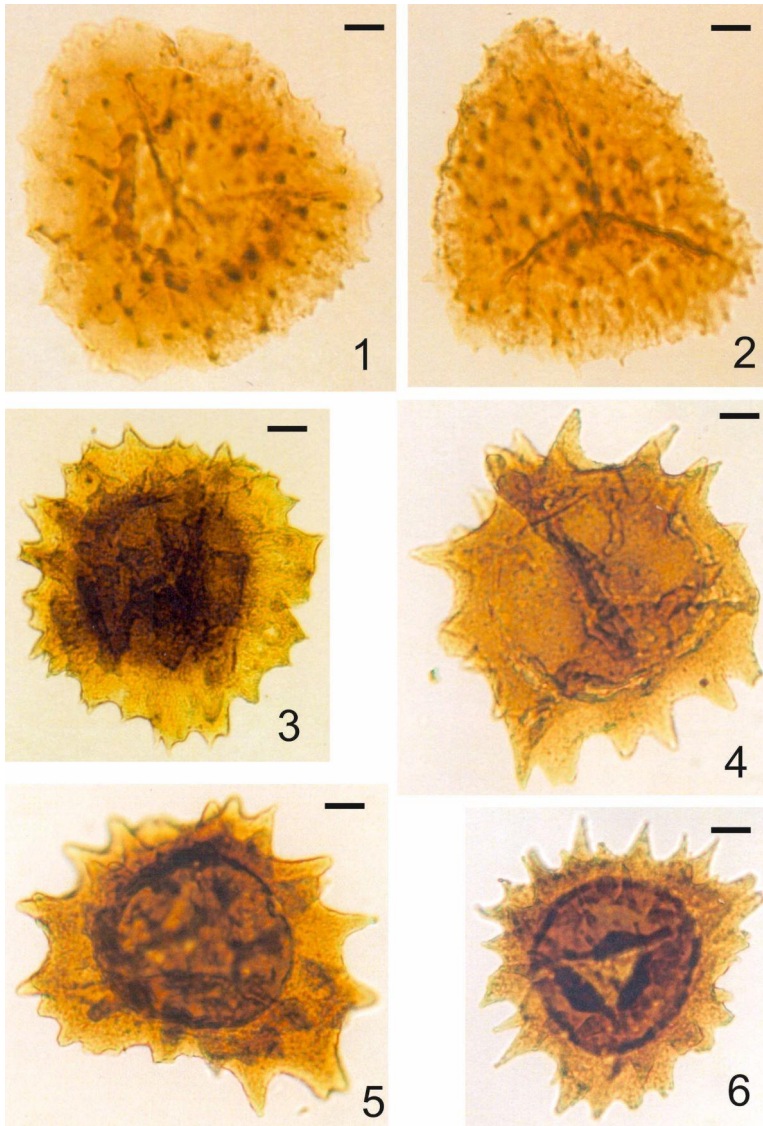
1   *Ancyrospora ampulla* Owens, 1971. Sample KP 1460, Slide KP 1460/29.

2   *Ancyrospora ampulla* Owens, 1971. Sample KP 1460, Slide KP 1460/21.

3   *Ancyrospora ampulla* Owens, 1971. Sample 13, Slide 13 / 08/14.

4   *Ancyrospora ?incisa* (Naumova) Raskatova & Obukhovskaya , 1993. Sample 14, Slide 14 /08/66.

5   *Ancyrospora ?incisa* (Naumova) Raskatova & Obukhovskaya, 1993. Sample 13, Slide 13 / 08/1.

6   *Ancyrospora ?incisa* (Naumova) Raskatova & Obukhovskaya, 1993. Sample 13, Slide 13 /08/7

Plate 3. (scale bar is 10 μm)
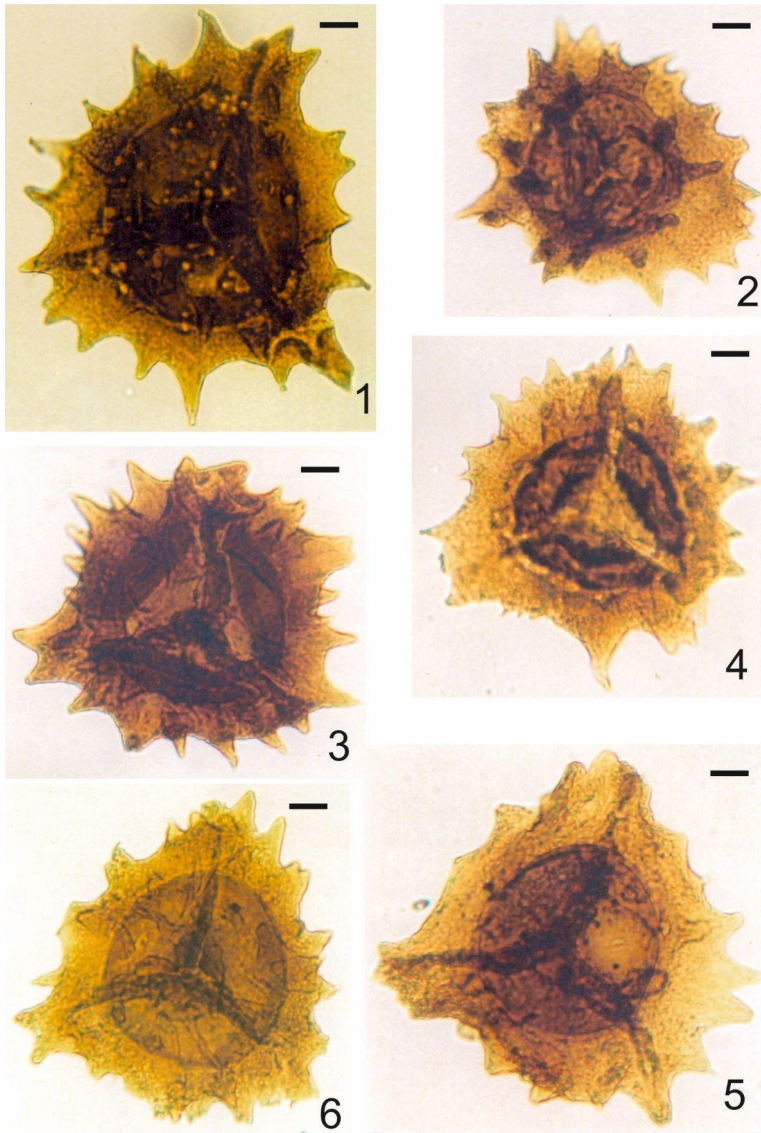
1 *Ancyrospora* cf. *incisa* (Naumova) Raskatova & Obukhovskaya, 1993, Sample 13, Slide 13 / 8/ 16.

2 *Ancyrospora incisa* (Naumova) Raskatova & Obukhovskaya, 1993, Sample 13, Slide 13 / 08 / 9.

3 *Ancyrospora* cf. *argutus* (Naumova) Mantsurova 1993, Sample 14, Slide 14 / 08/ 63.

4 *Ancyrospora argutus* (Naumova) Mantsurova, 1993, Sample 13, Slide 13/ 08 / 35

5 *Ancyrospora* cf. *argutus* (Naumova) Raskatova & Obukhovskaya, 1993. Sample 13, Slide 13 / 08 / 27.

6 *Ancyrospora* cf. *melvillensis* Owens, 1971. Sample 13, Slide 13 / 08 / 44.