

Morphological Diversity of the Exine Sculpture of Some Frasnian Spores from the Northern Timan: Applications for Taxonomy and Significance for Spore Dispersal

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Abstract—Microspores and megaspores from micro- and megasporangia of a Late Frasnian plant from the northern Timan are identified as the genus *Cristatisporites* and *Ancyrospora*, respectively. The exine sculpture is studied in in situ spores, as well as in dispersed microspores of *Cristatisporites*, *Ancyrospora*, and *Hystri-cosporites*, found in the rock enclosing the plant. The use of exine appendages as a generic level character is proposed. The shape of appendage extremities and the presence of irregular holes in the exine that are considered to be probable insect feeding damage, allowing us to consider wingless insects as main dispersal agents of the spores.

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INTRODUCTION

The Late Devonian flora is characterized by a highly diverse systematic composition: nearly all groups of spore-bearing plants, early seed plants, and many plants of uncertain systematic position are present. Major changes of the plant cover, related to forest formation, took place in that time. Forests covered vast areas, as shown by numerous finds of *Archaeopteris* Dawson and *Callixylon* Zalesky. In the northern Timan, on the eastern coast of the Cheshskaya Guba Bay of the Barents Sea, a new and still undescribed plant has been uncovered from Upper Devonian deposits. It is represented by impressions of smooth stems of various sizes up to 80 cm long, with attached reproductive organs. Lateral branches of the middle parts of the fossil bear adaxial sporangia on sporophylls that are slightly curved towards the axes (up to 10 sporangia per sporophyll). The sporangia are ovaly elongate, erect, attached to its entire base, tightly contacting with each other. Each sporophyll bears either microsporangia, or megasporangia, or both. The plant has been studied by a large team of scientists: A.L. Jurina, N.R. Meyer-Melikian (Moscow State University, Moscow, MGU), N.V. Gordenko and N.E. Zavalova (Paleontological Institute of the Russian Academy of Sciences, Moscow, PIN), M.G. Raskatova (Voronezh State University, Voronezh, VSU), and S.M. Snigirevsky (St. Petersburg State University, St. Petersburg, SPSU).

Jurina and Raskatova (2005) discussed in detail the stratigraphic position of this find and its assignment to the Ustbezmoshitsa Formation. Originally, the only information about the Late Devonian age of the enclosing deposits was available from a label written by G.A. Chernov, who found this plant in the northern Timan (Jurina et al., 2002). Palynological samples were taken from several parts of the rock with impressions of the plant. This palynological assemblage allowed Jurina and Raskatova (2005) to date the enclosing rocks to the Late Frasnian portion of the Ustbezmoshitsa Formation and to assign them to the *Membrabaculisporites radiatus* Subzone of the Voronezh horizon of the Russian Platform.

MATERIALS AND METHODS (IN SITU AND DISPERSED SPORES)

The rock sample with numerous remains of fertile axes bearing sporangia was treated with hydrofluoric acid for three or four days. Then, the material was treated with hydrochloric acid for 24 hours, and neutralized using water with several drops of Kodak Photo-flo, a chemical with a high pH, enhancing neutralization and diminishing the surface tension of the liquid, thus preserving the integrity of fossil plant parts. As a rule, undamaged sporangia were selected for the study. Detached sporangia were placed on slides with a median depression and covered with Schultze solution

($\text{HNO}_3 + \text{KClO}_3$). Then, slides were placed in a thermostat for 10 min at a temperature of 70°C for the oxidation of the organic matter. After that, each sporangium was placed on an individual slide and washed several times with distilled water to remove the Schultze solution. The sporangia were opened with a dissecting needle under a stereomicroscope. Micro- and megaspores were taken off with glass micropipettes and placed in a drop of glycerin for photographing in transmitted light.

Dispersed miospores were extracted from rocks using modern physical-chemical methods (*Guidelines...*, 1986). Since megaspores could be mechanically damaged, some samples were treated without preliminary fragmentation (Oshurkova, 2001). When miospores occur sporadically in organic residues, which mostly contain various fragments of plant tissues, enrichment of samples was used based on the difference between the specific gravity of the organic matter and miospore coats (Tetryuk and Filippov, 1986).

Miospores were studied with a POLAM-312 light microscope and photographed with a NIKON camera at the Laboratory of Historical Geology and Paleontology (VSU). The study and photographing of the spore surface were accomplished with a CAMSCAN scanning electron microscope at PIN.

Studied *in situ* spores are kept at SPSU, collection PM SPSU, no. 21. Light slides of dispersed miospores macerated from the rock with the impression of the Late Frasnian plant are kept at the Laboratory of Paleobotany, PIN (PIN NTd). One slide is kept at the Geological Museum of VSU, collection, no. 351. The slide number VSU no. 351 NTd is deciphered as follows: collection no. 351 of the Voronezh State University, NT is the northern Timan, and d is a dispersed miospore.

MICROSPORES AND MEGASPORES

It was revealed that only microspores were contained in some sporangia and only megaspores were contained in others. The diameter of microspores is two or three times smaller than the diameter of megaspores. Both types of spores vary slightly in size and characteristic sculptural elements within one sporangium. The differences in microspores include the size and density of sculptural elements of the exoexine; those of megaspores include the height, width, and length of the rays of the proximal scar, the peculiarities of the contact between the bases and tips of spines covering the distal surface and forming an equatorial zone.

In detail, we have studied three megaspores and one microspore *in situ* showing various types of appendages and their contacts. Dependent on the contact between sculptural elements, a zone of a given width is formed, additionally ornamented with smaller spines and verrucae.

General characterization of megaspores. Megaspores are larger than microspores, about 300–400 μm in size including appendages, and have dark (brown or

reddish brown) intense color in transmitted light. Megaspores are radial, trilete, zonate, rounded, with a wide equatorial zone, formed by the exoexine. The width of the equatorial zone is 50–70 μm . The distal surface and equatorial area are covered with large appendages of varying shape and length, which are continuations of the exoexine. The length of the appendages is from 3–15 to 20 μm , rarely up to 22–23 μm . The width is from 8–10 to 12 μm . The appendages are conical to elongate with curved tips. Occasionally, the appendage tips are needle-shaped (Figs. 1, 3c, c'). Some appendages (two, three, or more) are connected base to base and form high ridges. The total number of appendages around the equator is 50–65 (Pl. 22, fig. 5). Distally, appendages are more widely spaced and have narrower bases. The scar is lipped, its rays are straight or slightly sinuous; their length varies from one-third of the spore radius up to the total radius. The height of the lips of the trilete scar is up to 30–40 μm (Pl. 22, fig. 7), the width of rays near the pole is up to 20–25 μm . According to the system used for dispersed Devonian miospores, the megaspores under description are assigned to *Ancyrospora* (Richardson) Richardson.

Megaspore (Figs. 1, 1a, 1a'). The length of appendages does not exceed 15 μm . The height of the elements was measured from their base, disregarding the width of the zone. In its upper part, the element rapidly narrows, to 2–3 μm . However, it does not usually transform into a needle, retaining the inner space and having a triangular tip. In some cases, two or three appendages are connected, widening the zone by 3–6 μm . On average, two connected appendages make the zone wider by 2–3 μm , and three appendages, by 5–6 μm . In the specimen under consideration, three connected appendages form a ridge with three triangularly widened apices.

Megaspore (Figs. 1, 2b, 2b'). The length of appendages is within 15 μm . In some, the apices are broken. The majority of appendages are curved in the upper region. Three appendages form an uneven ridge 8.5 μm high and 9 μm wide (basally). The appendages become wider in the middle area of the axis. Undamaged appendages have rounded or indistinctly triangular tips, 1.2 μm in diameter.

Megaspore (Figs. 1, 3c, 3c', 3c''). Appendages are 3–15 μm in length and of variable morphology: from conical, gradually widening toward the base up to sharply conical with wide bases (5–8 μm). Needle-shaped tips (1.8–3 μm) may be curved and bifurcated. The other type of appendages irregularly covering the zone includes conical appendages with rounded, triangular, or triangular-widened apices. The volume of conical appendages enlarges gradually, sharply changing at the base because of several fused appendages.

Microspore (Pl. 22, fig. 1; Figs. 1a, 1a', 2). The microspore is light-colored and well-preserved, radial, trilete, cavate, zonate, rounded-triangular, 120 μm in size. The size of the central body is 70–75 μm . The layers of the exine are split in the equatorial and distal

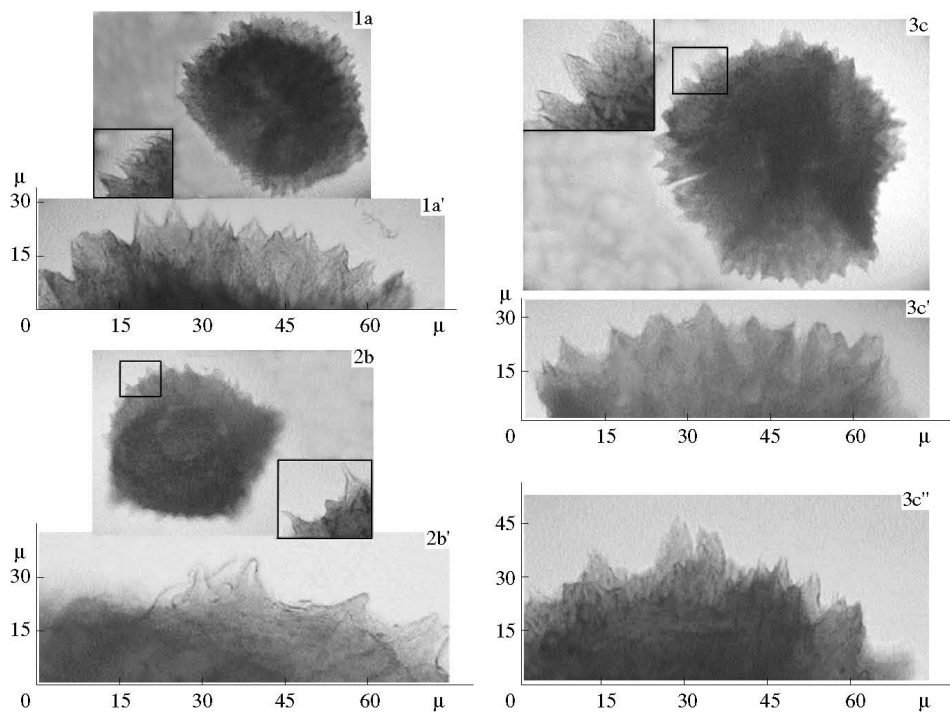


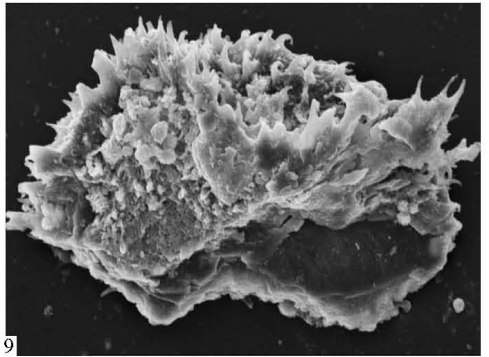
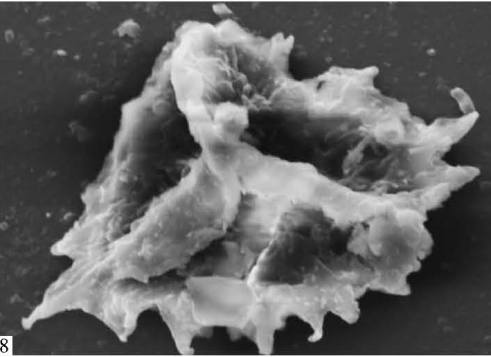
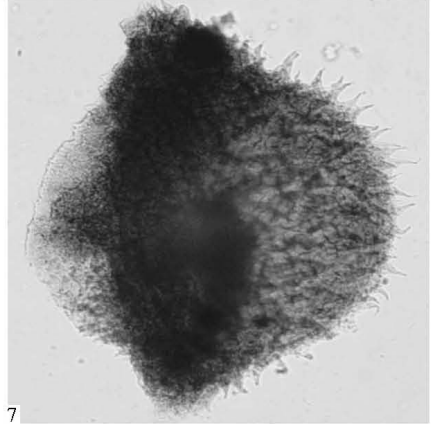
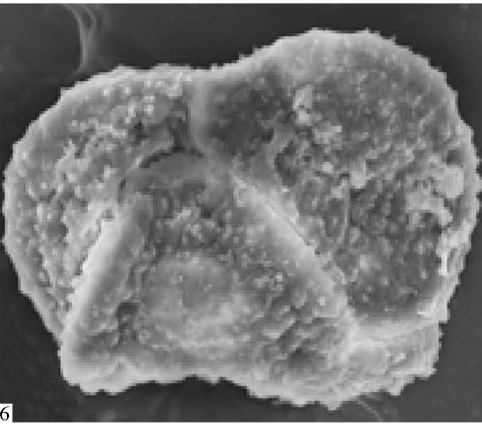
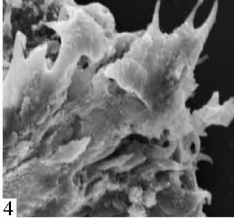
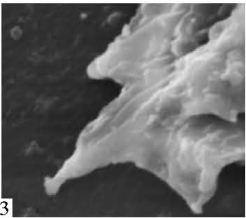
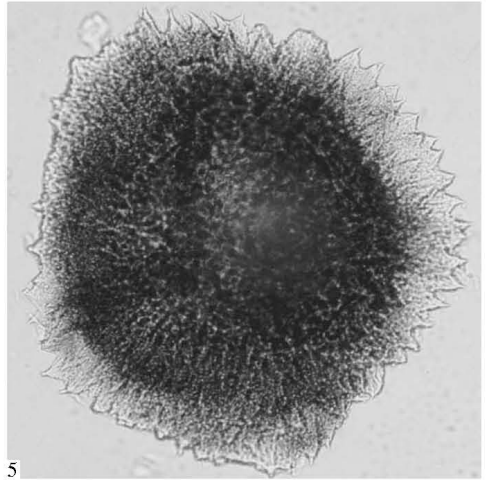
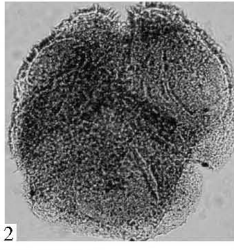
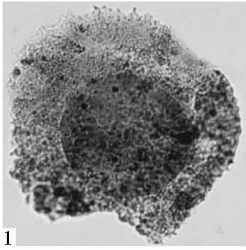
Fig. 1. Morphology of appendages in Upper Frasnian megaspores of *Ancyrospora* extracted from megasporangia, PM SPSU, no. 21/10, LM: (1a) first megaspore, general view from the proximal side, $\times 380$; (1a') equatorial appendages forming a zone, $\times 950$; (2b) second megaspore, equatorial zone, $\times 380$; (2b') equatorial appendages, $\times 950$; (3c) third megaspore, general view from the proximal side, $\times 450$; (3c', 3c'') equatorial appendages, $\times 1000$.

regions, forming a small cavity, distinctive as a narrow double contour around the central body. The intexine is thin. The exoexine is thin, without ornamentation, forms a zone. The sculpture of the zone is represented by small pointed cones with basal elevations 1.2–3.5 μm in size. Occasionally, the apices of the cones are needle-shaped, bifurcated, or rounded. The cones are widely spaced and occasionally form fused pairs. The distal and equatorial sculpture is represented by small pointed cones with basal elevations of 1.2–1.5 μm . In other microspores of the same tetrad, the sculpture of the marginal area of the zone is reduced. The contour of the microspore is uneven because of elevated sculptural elements (Pl. 22, fig. 1). The proximal sculpture of the central body is reduced to low variously orientated cones. The scar is simple or with a low margin formed by an elevation of the exine. The rays of the scar are straight or slightly sinuous; their length is equal to the spore radius. Microspores are preserved as tetrads (Pl. 22, fig. 2) or monads (Pl. 22, fig. 1). The microspores described resemble dispersed microspores

of the genus *Cristatisporites* (Potonié et Kremp) Butterworth, Staplin et Jansonius.

EXINE SCULPTURE

The morphology and arrangement of exinal appendages are analyzed in three genera: in situ microspores of the genus *Cristatisporites*, megaspores of *Ancyrospora* (both in situ and dispersed), and microspores of *Hystricosporites* McGregor (dispersed). Earlier, Jurina and Raskatova (2005) revealed a rich assemblage of dispersed microspores (up to 20 genera) from the rock enclosing the plant. The assemblage contains numerous spores of *Cristatisporites* and *Ancyrospora*, similar to micro- and megaspores, respectively, extracted from sporangia, and spores of *Hystricosporites*, which were not found in sporangia. The latter genus is given less attention here, since the main objects of our study were large spores with appendages, both in situ and dispersed.



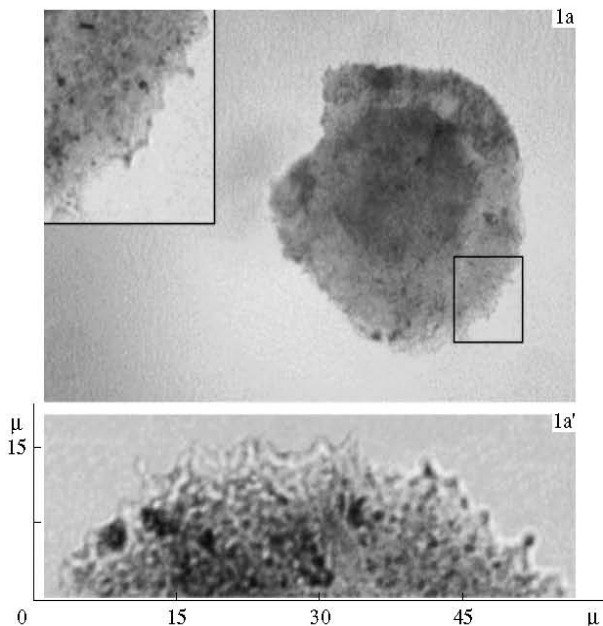


Fig. 2. Morphology of appendages in Upper Frasnian microspore of *Cristatisporites* sp. extracted from a microsporangium, PM SPSU, no. 21/11, LM: (1a) general view of the spore from the proximal side, $\times 800$; (1a') fragment of the zone with appendages, $\times 2400$.

Owens (1971) made diagrams of appendages for five Middle–Late Devonian species of *Ancyrospora*: *A. furcula* Owens, *A. melvillensis* Owens, *A. ampulla* Owens, *A. involucra* Owens, and *A. pulchra* Owens. He characterized each species by the presence of a narrow, broad, or false flange. Only *A. ampulla* showed short appendages with widening and bulbous bases (Owens, 1971, p. 91, text-fig. 13). Other species of this genus were characterized by large appendages with conically widening bases, fused by two or more appendages into large ridges. The appendages bore repeatedly branch-

ing starlike tips (Owens, 1971, p. 90, text-fig. 12; p. 90, text-figs. 14, 15).

Spores of the genus *Ancyrospora*, including in situ megaspores under study, are trilete, acavate, and zonate with a broad equatorial zone. The exine sculpture is characterized by large appendages of the distal and equatorial regions. Usually, the bases of appendages are widened to form an equatorial zone. Appendages are ended in bi-, tri-, or multifurcate tips. The dispersed megaspore of *A. incisa* (Naumova) M. Raskatova et Obukhovskaja (Avkhimovich et al., 1993) is character-

Explanation of Plate 22

Fig. 1. *Cristatisporites* sp., microspore from a microsporangium, PM SPSU, no. 21/11, general view showing a distinct central body and zone, LM, $\times 400$.

Fig. 2. Tetrad of microspores extracted from a microsporangium, PM SPSU, no. 21/12, LM, $\times 400$.

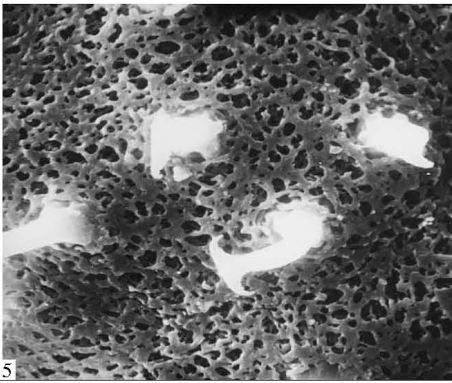
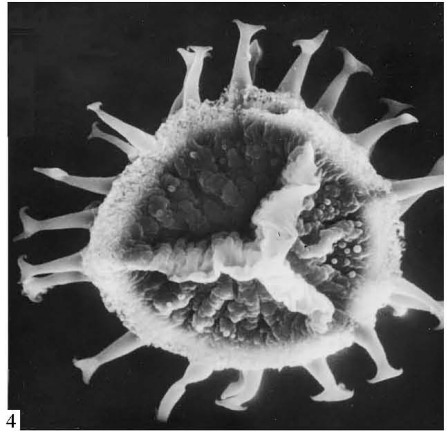
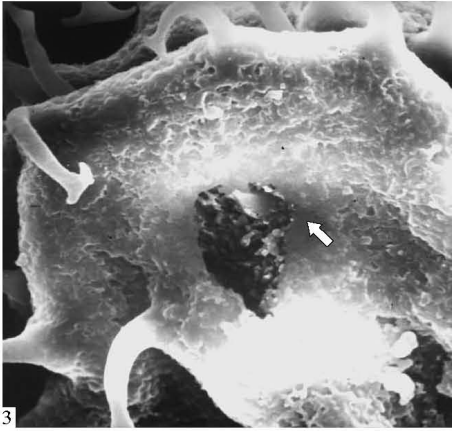
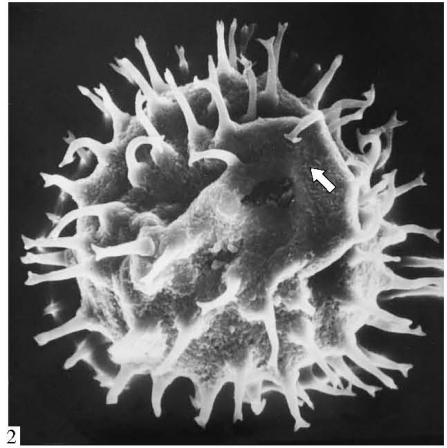
Figs. 3 and 8. *Ancyrospora incisa* (Naumova) M. Raskatova et Obukhovskaja, a dispersed microspore macerated from the rock with an impression of the Late Frasnian plant, slide collection PIN NTd, specimen no. 1, SEM: (3) exinal appendage, enlargement of fig. 8, $\times 750$; (8) general view of the proximal surface with an elevated trilete scar and large conical appendages forming a zone, $\times 500$.

Figs. 4 and 9. *Ancyrospora* sp., dispersed microspore macerated from the rock with an impression of the Late Frasnian plant, slide collection PIN NTd, specimen no. 2, SEM: (4) exinal appendages, enlargement of fig. 9, $\times 700$; (9) distal surface with large appendages fused base to base in groups of three or more, $\times 450$.

Figs. 5 and 7. Megaspore of *Ancyrospora* sp. extracted from a sporangium, PM SPSU, no. 21/10, LM: (5) general view of the proximal surface, zone is formed by bases of numerous appendages, $\times 450$; (7) equatorial zone, note a high ridgelike trilete scar and convex distal side bearing numerous appendages, $\times 450$.

Fig. 6. Microspore tetrad macerated from the rock with an impression of the Late Frasnian plant, slide collection PIN NTd, specimen no. 3, SEM, $\times 450$.

Figs. 1–9. Eastern coast of the Cheshskaya Guba Bay of the Barents Sea, northern Timan; Ustbezhmshitsa Formation, Upper Frasnian.



under study: *Cristatisporites* and *Ancyrospora*. Spores of these genera found as spores dispersae and in situ are morphologically close. The former genus is represented by large microspores, and the latter, by megaspores. They vary in total sizes as well as in the sizes of sculptural elements.

The detailed study of the shape of exinal appendages of dispersed and in situ spores belonging to the genera under consideration has shown that the shape of exinal appendages should be used as a generic character. For *Ancyrospora*, these are spinelike appendages with widening axes, often fused by their basal conical parts and with anchor-shaped or repeatedly branching tips; for *Hystricosporites*, widely spaced appendages with bulbous bases, nearly equilateral axes and anchor-shaped tips; and for *Cristatisporites*, acute small cones with widened bases, occasionally forming polyconic ridges.

The shape of exinal appendages, consisting of rather long axes and peculiar tips (repeatedly branching, starlike, mushroom-shaped, forked, and anchor-shaped), the morphology of appendage bases (in case of fusion and formation of flanges), as well as the hole in the exine between appendages interpreted as a probable insect feeding damage, allow us to suppose that the main dispersal agents of spores belonging to the genera *Ancyrospora* and *Hystricosporites* were wingless insects. It is not excluded that some mature spores were shed off from sporangia.

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ized by wide conical appendages and starlike, rounded, and triangular tips (Pl. 22, figs. 3, 8; Fig. 3). One more dispersed megaspore of this genus has narrower bases of appendages and narrow needle-shaped terminations (Pl. 22, figs. 4, 9).

Thus, species of *Ancyrospora* are characterized by exinal appendages varying in size (Figs. 1, 3), typically conical in shape with a remarkably widened basal part and anchor-shaped and repeatedly branching (starlike) tips (Raskatova, 1989). The accomplished analysis of morphological variability in the exinal sculpture of spores of *Ancyrospora* allows us to supplement the diagnosis of this genus with the information about the shape of exinal appendages.

SYSTEMATIC PALEOBOTANY

Genus *Ancyrospora* (Richardson, 1960) Richardson, 1962, emend. M. Raskatova

Emended diagnosis. Radial trilete acavate zonate spores, rounded or triangularly rounded, with wide thick equatorial zone. Scar lipped; rays straight, from one-third to total radius of central body in length. Exoexine moderately thick, form wide equatorial zone; intexine moderately thick. Structure punctuate. Exine sculpture in form of conical appendages, significantly widening basally and often fused with bases, with anchor-shaped and repeatedly branching endings. Spore contour uneven with strongly projecting sculptural appendages. Sizes of spores 72–200 μm .

Spores of the genus *Hystricosporites* also have equatorial and distal appendages of the exine. The appendages are situated at different distances from each other. Usually, they are rather widely spaced (Fig. 3). One specimen of *H. reflexus* Owens (Pl. 23, figs. 1, 2) has varying shape of the bases of the appendages (from bulbous to slightly widened) and terminations (from forked to triangular and anchor-shaped). The axes of the appendages are straight and virtually parallel-sided. One more specimen of this species shows a virtually uniform bulbous appendage base and anchor-shape terminations (Pl. 23, figs. 4–6). The axes are thicker and slightly widened toward the base. We believe that this variability is related to fossilization, maturity of spores, and, possibly, intraspecific variability. The variability is expressed in a double equatorial rim (compression along the polar axis, Pl. 23, fig. 1), number, length, and thickness of appendages with bifurcated tips (Pl. 23,

figs. 1, 4), which occasionally form elevated bulbous bases, and number of ridges covering contact areas (Pl. 23, figs. 1, 4, 6).

Owens (1971) made diagrams showing appendages that allow one to differentiate between Givetian–Frasnian species of *Hystricosporites*: *H. delectabilis* McGregor, *H. furcatus* Owens, *H. reflexus*, *H. grandis* Owens, *H. gravis* Owens, and *H. harpagonis* Owens. In our opinion, transitional forms exist between the species depicted by Owens that preclude the specific differentiation on the basis of the exine sculpture. Thus, identical appendages with horizontally elongated and curved terminations are shown in *H. reflexus* (Owens, 1971, text-fig. 7, p. 88) and *H. grandis* (Owens, 1971, text-fig. 8, p. 89). *H. grandis* (Owens, 1971, text-fig. 8, p. 89) shows the same mushroom-shaped tips of appendages as *H. reflexus*. Owens noticed morphological peculiarities of appendage bases: occasionally, bulbous bases of appendages can be situated separately, as revealed in *H. reflexus* (Owens, 1971, text-fig. 7, p. 88) and *H. furcatus* (Owens, 1971, text-fig. 7, p. 88).

Allen and Robson (1981) reviewed the exine morphology in five more species of *Hystricosporites*: *H. multifurcatus* (Winslow) Mortimer et Chaloner, *H. bedfordi* (Winslow) Allen et Robson, *H. cf. delectabilis* McGregor, *H. pyramidalis* Allen et Robson, and *H. proximo-tuberculatus* Allen et Robson. Unlike Owens, these authors described the equatorial exine. In their characterization of *H. bedfordi* (Allen and Robson, 1981, pl. 1, figs. 5–7) and *H. proximo-tuberculatus* (Allen and Robson, pl. 3, figs. 3–7), they mentioned the presence of a zone, a character that does not agree with the generic diagnosis of *Hystricosporites*. In *H. multifurcatus* (Allen and Robson, 1981, pl. 1, figs. 1–4) and *H. pyramidalis* (Allen and Robson, 1981, pl. 2, figs. 3–7), they described appendages with widening bases and tips varying from horizontally widening (mushroom-shaped) and repeatedly branching to triangular elongated (with a concave upper surface) and anchor-shaped. *H. cf. delectabilis* (Allen and Robson, pl. 2, figs. 1, 2) is characterized by widening and, occasionally, bulbous bases of appendages and anchor-shaped tips with two or a few deviations. Therefore, one species can show a combination of morphological characters of two other species (morphology of appendage bases) or broad variations in appendage tips, described in several species of the genus under consideration (Allen and Robson, text-fig. 1, p. 395). Allen and Robson, who discussed the morphology of Upper Devo-

Explanation of Plate 23

Figs. 1–6. *Hystricosporites reflexus* Owens, dispersed miospores from the rock with an impression of the Late Frasnian plant, SEM: (1–3) VSU, no. 351; (1) general view of the proximal surface with a ridgelike trilete scar, radiating ribs, and various appendages, $\times 500$; (2) deformed distal surface with a hole between appendages (arrow), $\times 500$; (3) fragment of the distal surface with a hole, $\times 7000$; (4–6) VGU, no. 351 NTd; (4) general view of the proximal surface with a ridge like trilete scar, radiating ribs, and appendages, $\times 500$; (5) fragment of the distal surface bearing appendages, $\times 2000$; (6) equatorial and distal surfaces with rare appendages, $\times 500$.

Figs. 1–6. Eastern coast of the Cheshskaya Guba Bay of the Barents Sea, northern Timan; Ustbeznoshitsa Formation, Upper Frasnian.






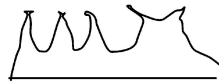
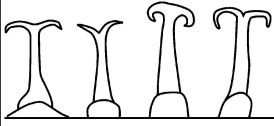

Species	Structure of equatorial area	Appendage shape	Average length of appendages and range of its variations, μm
<i>Ancyrospora fucula</i> Owens (Owens, 1971)	False flange		25 (10–38)
<i>A. involucra</i> Owens (Owens, 1971)	False flange		30 (18–46)
<i>A. pulchra</i> Owens (Owens, 1971)	Flange		45 (15–70)
<i>A. cambrica</i> Allen et Robson (Allen, Robson, 1981)	False flange		155– (132–185)
<i>A. incisa</i> (Naumova) M. Raskatova et Obukhovskaya (Avkhimovich et al., 1993)	Zone		13 (9–18)
<i>Ancyrospora</i> sp. (present paper)	Zone		15 (10–25)
<i>Hystricosporites reflexus</i> Owens (Owens, 1971)	Zone and flanges lacking		20 (9–35)
<i>H. reflexus</i> Owens (present paper)	Zone and flanges lacking		30 (20–40)

Fig. 3. Morphology of exinal appendages in spores of some species of *Hystricosporites* and *Ancyrospora*.

nian–Lower Carboniferous spores with appendages, believed that spores from older (Givetian–Frasnian) and younger deposits differ: more ancient spores have shorter vertically orientated axes of appendages. This statement, however, needs to be confirmed based on additional material.

In *Hystricosporites*, appendages consist of a bulbous or slightly widened base, a straight axis parallel-sided or slightly widening toward the base, and tips varying in shape from widening (mushroom-shaped) to

anchor-shaped. Owens (1971) proposed definitions describing terminations of appendages and revealed nine variants. The present paper partially uses these names, with some changes. Thus, we replace “expanded” (Owens, 1971, text-fig. 4a, p. 89) with “mushroom-shaped,” which better fits the appendage tip depicted, “extended” (Owens, 1971, text-fig. 4e, p. 87) with “forked” (Pl. 23, figs. 1, 2), and the overly long “laterally extended, expanded and reflexed” (Owens, 1971, text-fig. 4i), with “anchor-shaped” (Pl. 23, fig. 4).

The analysis of the diagnoses of species of *Hystri-
cosporites* along with the study of available specimens
of the genus leads us to the conclusion that description
of the shape of exinal appendages should be added to
the generic diagnosis. The inclusion of characteristics
of exinal appendages makes the generic diagnosis more
precise than the application of a rather general term
“anchor-shaped appendages” both for *Hystri-
cosporites* and *Ancyrospora* (Oshurkova, 2003). The differentiation
between species of *Hystri-
cosporites* by the shape
of appendage tips, as made in many papers, does not
seem completely correct, since tips vary even in one
specimen.

Genus *Hystri- cosporites*

McGregor, 1960, emend. M. Raskatova

Emended diagnosis. Spores radial, trilete,
acavate, azonate, rounded, or triangular-rounded. Scar
lipped, occasionally gulate; rays of scar straight, two-
thirds of spore radius. Area distinct, margined by curva-
ture. Exine thick and punctuate. Sculpture of area in
form of short radially orientated ridges; rest of proximal
side and distal side sculptured by long appendages.
Appendages with bulbous base and parallel-sided or
weakly widening axis. Tips of appendages from mush-
room-shaped to forked, to anchor-shaped. Spore sizes
82–175 µm.

SUPPOSED MODES OF SPORE DISPERSAL

The correlation between modes of spore dispersal
and exinal sculpture has so far been poorly studied.
A paper by Nikitin (1934) was among the first works,
where transportation of spores was discussed in Late
Devonian plants. The heterosporous plant *Krysh-
tofovichia africanii* Nikitin was described from the Lower
Frasnian deposits of the Voronezh Region (Petino), pre-
served as isolated micro- and megasporangia, dispersed
large megaspores (500 µm on average) and tetrads of
microspores in microsporangia, as well as solitary
microspores stuck onto megaspores.

It is pertinent to discuss in more detail nomencla-
tural questions related to this plant, since they are not
covered adequately. The spherical trilete megaspores
that were described by Nikitin bear numerous long
(up 720 µm, 250–350 µm on average) appendages
(=glochidia in the terminology of Nikitin). The tips of
the appendages are in the form of a small anchor, or
rounded (apparently broken). Nikitin assigned *Krysh-
tofovichia africanii* to Pteridophyta because of the pres-
ence of mega- and microspores and the absence of
seeds. A hypothesis was formulated about a possible
lycopsid affinity based on the morphological similarity
between megaspores of *Krysh-
tofovichia africanii* and
spores of *Lagenicula* Potonié et Kremp, extracted from
sporangia of *Lepidodendron* Sternberg.

Later, some nomenclatural changes were made con-
cerning the name *Krysh-
tofovichia africanii*. Chaloner
(1959) believed that as the name is based on micro- and

megasporangia and micro- and megaspores, this name
cannot be used for isolated megaspores described by
Nikitin. Chaloner proposed to assign the isolated
megaspores to the genus *Nikitinsporites* Chaloner, bas-
ing his diagnosis on the diagnosis of megaspores made
by Nikitin. Later scientists shared the opinion of Chal-
oner and started using the name *Nikitinsporites*.

McGregor (1969) showed that microspores of *Kry-
sh-
tofovichia africanii* are identical to dispersed
microspores of the genus *Archaeoperisaccus* Naumova,
particularly to *A. concinnus* Naumova. He agreed with
Chaloner about the nomenclature of *Nikitinsporites*,
developed the ideas about lycopsid affinity of the
genus, expressed by Nikitin (1934), Chaloner (1959),
and Taugourdeau-Lanz (1967), and supposed that this
genus is a possible ancestor of the Triassic–Jurassic lycop-
sid group *Lycostrobus* Nathorst–*Cyclostrobus* Helby et
Martin–*Pleuromeia* Corda and modern *Isoetes* L.

Nikitin (1934) analyzed possible modes of dispersal
of megaspores of *Krysh-
tofovichia africanii* (currently,
Nikitinsporites) and noticed the double function of
exine appendages, particularly, their anchor-shaped
tips. He did not support the possibility of transportation
of megaspores by hooking onto “woolly animals,” or
other moving terrestrial organisms with a smooth skin,
with their anchor-shaped appendages. He considered
that resistance of spores to remote transportation by
water, far away from original habitats of the parent
plants, to be a more probable function of the anchor-
shaped appendages of the exine. Krassilov (2000) dis-
cussed these megaspores and the ideas of Nikitin, and sug-
gested that arthropods might have served as agents of
spore dispersal in Devonian thallose and telome mats.

Rather recently, a discussion about the interactions
between pteridophytes and arthropods has begun in
papers on the Devonian and Upper Paleozoic. Such
interactions are supported by finds of plant tissues dam-
aged by borings and oviposition, spores in the guts of
arthropods, and arthropod coprolites with spores (Scott
et al., 1985). The first examples were related to the
famous Early Devonian flora of Rhynie. Some axes of
Rhynia were damaged by animals that fed on plant sap.
In a sporangium, trigonotarbid were found, which
either fed on spores or used the sporangium as a protec-
tive shell, or fed on microarthropods that lived in the
sporangium (Scott et al., 1985).

A collaborative paper by paleobotanists and paleo-
ontologists discussed relationships between the
morphology of plant spores and arthropods (Kevan
et al., 1975). Particular attention was paid to the scul-
pture of dispersed Devonian spores of *Ancyrospora*,
*Hystri-
cosporites*, *Nikitinsporites*, and *Densosporites*
(Berry) Butterworth, Staplin et Jansonius, with specific
anchor-shaped tips of exinal appendages. Earlier,
Taugourdeau-Lanz (1967) also noticed this group of
megaspores, but did not analyze it in detail. Kevan et al.
(1975) paid attention to morphological features of
spores (size, ornamentation, and exinal appendages)
that, in their opinion, confirmed the existence of inter-
relationships between terrestrial arthropods and plants.

Spores of the mentioned group of genera bore hook- and anchor-shaped exinal appendages facilitating spore dispersal: the appendages attached to the chaetae of arthropods, and the arthropods dispersed the spores. In addition, these authors discussed the simultaneous appearance of some characters in terrestrial plants and arthropods, implying a coevolutionary process. Spores with small conical, long, needle-shaped, or anchor-shaped appendages of the exine are associated with the existence of myriapods, mites, and collembolans, which could have dispersed such spores. The appearance of arborescence and the development of winged insects were related: the long trip to the terminal sporangia, on which they most probably fed, was accompanied by rapidly changing conditions, dehydration due to the elevation was destructive to the soft bodies of the insects; therefore, wings appeared and the exploitation of the air environment took place (Kevan et al., 1975).

Tryon (1986) tried to reveal the correlation between the sculptural type of the exine and the mode of dispersal of spores. She noticed the morphological similarity between numerous spiny exinal appendages of modern *Selaginella kunzeana* A. Brongniart and Devonian *Ancyrospora*; Taugourdeau-Lanz (1967) noted the similarity between spores of *Ancyrospora* and the modern *Selaginella spinosa* L. Having observed modern plants, Tryon revealed that small-spined appendages of exine have two functions. In *Selaginella kunzeana*, microspores attach with such appendages to megaspores and disperse together; in ferns-myrmecophytes, spiny spores attach to ants for transportation.

Meyen (1987) briefly described the mode of dispersal of megaspores of *Lagenicula*, which were extracted from sporangia of an Early Carboniferous lycopsid of the Lepidodendraceae. The megaspores are 850–1175 µm in size, large appendages of their exine are 225–500 µm long (Oshurkova, 2001). Meyen supposed that such megaspores floated in water due to these appendages retaining air bubbles. Spermatozoids reached the archegonium in the floating megaspore. In his opinion, this reproductive process resembled that of water ferns. Tryon (1986) noted that spores of modern ferns have a very high percentage of dry weight, exceeding 95% of the total weight of fresh spores, that hampering their free floating. Megaspores of *Lagenicula* were apparently too heavy for free floating, but were passively transported not far from the habitats of the parent plant with help of the air that was retained by exinal appendages.

Our review of published data revealed that only a limited number of papers, from Russia or abroad, are devoted to modes of spore dispersal. The transportation of spores by arthropods is the most common hypothesis (Kevan et al., 1975; Tryon, 1986; Krassilov, 2000). We do not completely abandon Nikitin's theory of dissemination of spores from mature sporangia near habitats of the parent plants, and the attachment of spores to an immobile substrate by means of exinal appendages. It is most probable that the majority of spores were dis-

persed by arthropods, but some spores fell on the substrate nearby the parent plant, and the anchor-shaped appendages of the exine prevented a remote transportation by water.

Previous scientists have shown that Devonian arthropods and plants were syngenetically related. The visiting of sporangia and feeding on spores were profitable for both arthropods (nutrition and development of wings) and plants (dispersal of spores and obtaining of nitrogen). It is believed that feeding on generative organs of plants was ancestral for insects; they require proteins, which are abundant in embryonic tissue of the generative sphere (*Historical...*, 1980; *History...*, 2002). No reliable remains of insects or insectlike organisms were found in the Upper Devonian deposits in question. One of the oldest sites with remains of myriapods, mites, and supposed insects is the Lower Devonian Rhynie locality (Scotland). A gap exists in the geological record until the Early Carboniferous, where unequivocal insect remains were found. Paleontologists believe that the absence of insect remains in the Middle and Late Devonian is not evidence of the appearance of the group as late as the Early Carboniferous. Ancient, wingless insects had a cryptic lifestyle with few opportunities for fossilization (*Historical...*, 1980), but they definitely existed throughout the Devonian. Plate 23, figs. 2 and 3 shows a dispersed miospore of *Hystricosporites reflexus* from the Upper Frasnian of the northern Timan with an irregular hole between the appendages of the exine. Discussion with paleontologists led us to the idea that such holes are most probably traces of feeding by insectlike arthropods. Spores of this species are characterized by peculiar exinal appendages (Pl. 23, figs. 1–6), identical to those in *Hystricosporites* sp. studied from the Upper Devonian of England (Kevan et al., 1975, pl. 55, fig. 7). It is probable that spores with mushroom- and anchor-shaped appendages of exine used them as hooks by attaching to arthropods and being dispersed by these agents (Kevan et al., 1975). So far, we suppose that dispersed spores of the genus *Hystricosporites* were spread by insectlike organisms. No direct evidence has been found of interactions between in situ spores of *Ancyrospora* and *Cristatisporites* and insects or insectlike organisms. However, these genera belong to the same group as *Hystricosporites*, *Densosporites*, and *Nikitinsporites*, which are united by the same type of appendages facilitating the dispersal of spores by means of arthropods. We believe that wingless insects were most probably the main dispersal agents of spores from the sporangia of the Late Frasnian plant under study. Some mature spores probably fell on the substrate.

CONCLUSIONS

Only two members of a rich (about 20 genera) palynological assemblage from the upper part of the Ustbezmoshitsa Formation of northern Timan were discovered in situ, in sporangia of the Late Frasnian plant