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Spores in Situ and Problems of the Classification of Mesozoic Tree Ferns

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Abstract—Although tree ferns dominated the Mesozoic flora, their taxonomic relationships are poorly understood at the generic level, and next to nothing can be said of evolutionary trends within the group. At least five genera are recognized based on the remains of spore-bearing structures. However, the dispersed spores belong to the same generalized morphotype, and cannot be assigned to genera based on macroscopic remains of fertile leaves. Electron microscopy of spores in situ may partly resolve these problems providing additional criteria for classification of spore-bearing structures and disperse spores. We studied in situ spores of the Early Cretaceous *Alsophilites nipponensis* (Oishi) Krassilov, which are comparable to dispersed spores *Cyathidites minor* Coup. Spore wall micromorphology and ultrastructure indicate their affinities with the modern genus *Alsophila* R. Brown. Only occasional poorly preserved striate sculptures survive the standard treatment of maceration of the perispore. Our data confirm the primitive status of the species with a great number of spores per sporangium, thick unsculptured exospore consisting of two ultrastructural layers, and the possibility that whole sporangia with unshed spores can function as dispersal units.

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Key words: Mesozoic tree ferns, in situ spores, sporoderm ultrastructure, electron microscopy, Primorye Region.

INTRODUCTION

Tree ferns are among the most numerous groups of Mesozoic plants recorded both as macrofossils and as dispersed spores. However, in spite of their paleofloristic and phytostratigraphical importance, they are rather poorly studied: the taxonomic diversification of the group is poorly understood and its evolutionary trends have not been revealed. The situation might have been related to technical and conceptual problems of fossil spore studies rather than to a lack of material.

Although macrofossils of tree ferns are abundant, spores of these plants are relatively poorly represented in palynological assemblages. Spores of the Cyatheaceae are attributed to the formal genus *Cyathidites* R.A. Couper, which includes psilate trilete forms that possibly belong to different families. Such spores occur in the Gleicheniaceae, Dicksoniaceae, Matoniaceae, and some other families of living ferns. The family Weichseliaceae (and, possibly, some other extinct families) is characterized by the same type of spores. Spinate, verrucose, and striate forms predominate in modern tree ferns; however, perispore sculptural elements are not always preserved in the fossil state or are indistinguishable in transmitted light. The apparent uniformity of fossil spore morphology may be related to these factors; a more detailed morphological study of fossil spores would require electron microscopy.

It should be noted that dispersed striate spores that are conventionally assigned to the Schizaeaceae in some cases resemble spores of *Cibotium* Kaulfuss, *Alsophila* R. Brown, *Nephelea* R. Tryon, and some other modern cyatheaceous genera. The possibility exists that such spores belong to unknown Mesozoic members of tree-fern families.

To solve these problems, palynological studies of both modern and fossil material should be significantly elaborated; electron microscopy, along with light microscopy, should be broadly applied. Of particular importance in this context are detailed investigations of spores extracted from sporangia of Mesozoic ferns. Until now, in situ Mesozoic spores have mainly been studied by light microscopy. The present work deals with in situ spores of a member of the Cyatheaceae, *Alsophilites* Hirmer, compares them with dispersed spores, and discusses the results obtained in the context of the taxonomic and evolutionary problems of tree ferns.

PROBLEMS OF THE TAXONOMY AND PHYLOGENY OF TREE FERNS

The present unsatisfactory state of paleopteridology adversely affects the taxonomy of the modern tree ferns, numbering about 700 species. The conceptual basis of their classification was not clearly enough defined; hence, it is difficult to select between alternative variants of familial and generic systems. The traditional classification was largely based on the position of the sori and the morphology of the indusium. These characters differentiate several related families: the Cyatheaceae (sori superficial, indusium basal, cap-shaped, meniscus-like, or lacking), Dicksoniaceae (sori marginal, indusium bivalved, the outer is formed by a more or less modified margin of the leaf blade), and the Lophosoriaceae and Metaxyaceae, which are occasionally united into the "Protocyatheaceae" (sori superficial and without indusia).

At different times, up to nine genera were recognized within the Cyatheaceae (*Cyathea* J.E. Smith, *Sphaeropteris* Bernardi, *Alsophila* R. Brown, *Hemitelia* R. Brown, *Trichipteris* Presl, *Gymnosphaera* Blume, *Cnemidaria* Presl, *Schisocaena* Hooker, and *Nephelea* R. Tryon), some of which were later treated as suprageneric taxa. Since on the basis of vegetative characters and, in particular, trichomes, tree ferns are divisible into scaly and hairy groups, some researchers distinguished only two genera, *Cyathea* and *Cnemidaria*, or, taking into consideration their karyological similarity and intergeneric hybridization, united them into one broadly understood genus *Cyathea* (Kramer, 1990). The largest genus of the family, *Alsophila* (350 species), is often united with *Cyathea* and/or *Nephelea*. However, intergeneric hybrids with mixed characters are only formed with the latter genus, not with the typical *Cyathea* (Conant, 1983). The spore morphology shows that the genera *Sphaeropteris, Alsophila, Cyathea, Cnemidaria*, and *Nephelea*, as well as *Lophosoria* C. Presl and *Metaxya* C. Presl, assigned to separate families, usually differ in sculpture (Gastony and Tryon, 1976), although *Alsophila* occasionally shows characters of the relatively primitive *Sphaeropteris* (spinate perispore) and the specialized *Cnemidaria* (three equatorial pores). Dispersed spores of *Lophosoria*, which nowadays grows only in America, were reported from the Tertiary of Australia (Gastony and Tryon, 1976; Hill et al., 2001).

Recently, a system has been widely used in which petiole scale morphology plays a leading role. It differentiates six genera of the Cyatheaceae and unites them into three groups: (1) *Sphaeropteris* with matching scales (identical in color to the petioles); (2) *Alsophila* and *Nephelea* with bristly marginal scales; and (3) *Trichipteris, Cyathea*, and *Cnemidaria* with bristleless, fan-shaped scales (Tryon, 1970). According to Tryon, two phylogenetic lineages are traceable: from *Sphaeropteris* (or similar ancestral forms) to *Nephelea* in one lineage and to *Cnemidaria* in the other.

Liew and Wang (1976) attempted to reconstruct an analogous phylogeny on the basis of spore morphology: the former lineage runs from predominantly echinate spores in *Sphaeropteris* to striate in *Nephelea* with several transitional variants having mixed sculpture in *Alsophila*; and the latter lineage is directed towards perforated spores of *Cnemidaria*, with transitional types in *Trichipteris* and *Cyathea*. In this direction, the number of spores per sporangium decreases from 64 to 16, and the perispore layers are also reduced.

Paleobotanical data have scarcely been used in phylogenetic reconstructions. Characters such as scaly or hairy petioles have not been observed in fossil material, and spore-bearing structures have been insufficiently studied.

Among the Mesozoic ferns, only *Coniopteris* Brongn. is an acknowledged member of the tree-fern family Dicksoniaceae. This genus is related to the modern *Thyrsopteris* Kunze, which has marginal sori with a cup-shaped indusium. However, the Siberian *Coniopteris burejensis* (Zal.) Sew. has a distinctly bivalved indusium with a thicker outer valve. Krassilov (1978) placed *C. burejensis* and some allied species into the modern genus *Dicksonia* L'Heritier, which, therefore, is traced back up to the Jurassic time. Bivalved indusia are described in the common Cretaceous genus *Onychiopsis* Yokoyama, which has spores of the *Coniopteris* type (Krassilov, 1967). Later, the assignment of *Onychiopsis* to the Dicksoniaceae was confirmed on European material (Friis and Pedersen, 1990).

Remains of Mesozoic Cyatheaceae were long assigned to other families. Thus, leaves with superficial sori of the Cyatheaceae type were reported as *Gleichenites* Goeppert, *Polypodites* Goeppert, *Aspidistes* Harris, implying an affinity to the Gleicheniaceae, Polypodiaceae and Dryopteridaceae, respectively. Morphological study of sori and sporangia showed that at least some species of these genera are closer to the Cyatheaceae or related families.

Some of these species were assigned to the fossil genus *Alsophilites* (Krassilov, 1967), and the others were placed into the modern *Cyathea* (Krassilov, 1978).

Thus, micromorphological studies of spore-bearing organs revealed five Mesozoic genera, *Coniopteris, Onychiopsis, Dicksonia, Alsophilites*, and *Cyathea*, the composition of which needs to be refined, yet the diversity of Mesozoic tree ferns might have been much more extensive.

MATERIAL AND METHODS

The material comes from the Lipovetsk open-cast coal mine, southwestern Primorye Region, 140 km north of Vladivostok (Fig. 1). The Lipovetsk coalfield is one of the six large coalfields of the Razdol'nenskii basin. Cretaceous deposits are represented by the Nikanskaya Series (with the Ussuriisk, Lipovetsk, and Galenkovskaya formations). They are overlain by the Albian red beds of the Korkinskaya Series (Krassilov, 1967). The Aptian deposits of the Lipovetsk Formation are exposed in an open-cast coal mine.

The Early Cretaceous flora of Primorye is quite diverse in fern remains with well-preserved spore-bearing structures accompanied by rich palynological

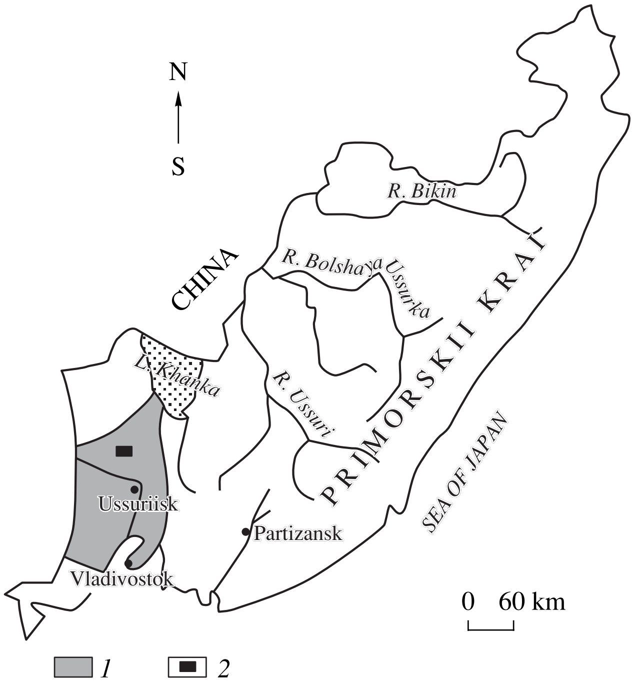


Fig. 1. Geographical position of the Lipovetsk coalfield in the Primorye Region: (*1*) Razdol'nenskaya Depression; (*2*) Lipovetsk coalfield.

assemblages. Krassilov (1967) studied sporangia and spores of several fern species using light microscopy; the comparison with dispersed spores was not achieved. The dominant fern species of the Lipovetsk coalfield was referred to as *Gleichenites nipponensis* Oishi, which was established from the Lower Cretaceous of Japan, and for which a new combination, *Alsophilites nipponensis* (Oishi) Krassilov, was proposed by Krassilov (1967). Spores of this species were compared with those of *Cyathea* and the fossil genus *Onychiopsis*.

New specimens of *Alsophilites nipponensis* were studied by means of transferring the compression onto varnish film. The compression was studied with a light microscope and in a CAMSCAN scanning electron microscope. Organic residue for palynological analysis was obtained from a portion of the rock containing the impression of *Alsophilites nipponensis* by the conventional maceration technique (Pokrovskaya, 1966). Apart from other miospores, the palynological assemblage contained psilate trilete spores of several morphotypes, including *Cyathidites*. Spore masses from several sporangia were embedded into a mixture of epoxy resins (Telnova and Meyer-Melikian, 2002). Ultrathin sections were obtained using an ultramicrotome. Some sections were stained with lead citrate after Reynolds (Gayer, 1973), the others were observed non-stained in a JEOL-100 transmission electron microscope.

The collection IBPS-R1 is housed in the Institute of Biology and Soil Science, Vladivostok.

TERMINOLOGY

The ultrastructural layers of the sporoderm of ferns are often identified with the exine and perine of pollen grains of seed plants; however, as their homology is not proved, we have adopted the recommendation of Lugardon (1974) and refer to the thin external layers as perispore, and to the underlying thicker layer that constitutes most of the sporoderm as exospore. The perispore is destroyed by sodium hydroxide (and is sometimes identifiable by this property). It is formed in a late phase of sporogenesis, first as granular deposits on the exospore surface on which external layers are accumulated.

The perispore (or only its inner granular layer) may fuse with the exospore forming the spore surface. In other cases, the perispore (or its outer layer) is separated, and sculptural elements of the surface belong to the inner perispore or to the exospore. The inner and outer layers of the exospore are discernable, although not always distinctly, by their difference in electron density.

An advantage of scanning electron microscopy over light microscopy is that it allows more profound micromorphological studies. It is possible to observe three-dimensionally preserved spores in proximal, distal, and equatorial view. The main topographical elements of the proximal face are the contact area surrounded by a peripheral zone (curvature) and the tetrad scar with an elevated suture in the form of a commissural ridge suture and its border (if developed). The curvature is observed in both distal and equatorial (lateral) views, where its configuration has a certain taxonomic value.

RESULTS OF ELECTRON-MICROSCOPICAL STUDY OF SPORES

Family Cyatheaceae Kaulfuss, 1827

Genus *Alsophilites* Hirmer, 1927

Alsophilites nipponensis (Oishi) Krassilov, 1967

Plate 10, figs. 1–3

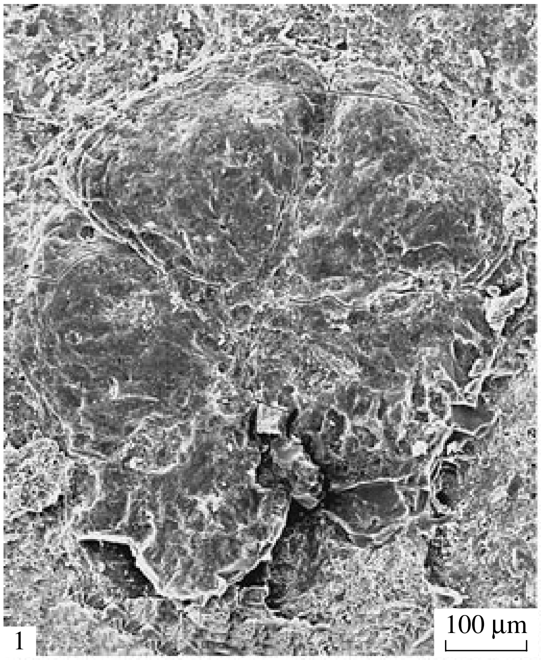
Alsophilites nipponensis: Krassilov, 1967, p. 113.

The spores were extracted from sporangia of fertile fronds of *Alsophilites nipponensis* (Oishi) Krassilov (Krassilov, 1967), in which the pinnules bear seven sori in two rows along the midrib (Fig. 2). The sori are attached at the branching point of a lateral vein. They are superficial, rounded, flattened, and without indu-

Explanation of Plate 10

Figs. 1–3. Fern *Alsophilites nipponensis* (Oishi) Krassilov, IBPS-R1 no. 14/1, SEM: (1) sorus with six sporangia; (2) spore mass extracted from a sporangium; (3) spores in proximal and distal (arrow) view. Primorye, Lipovetsk coalfield, Lipovetsk Formation, Aptian.

Plate 10



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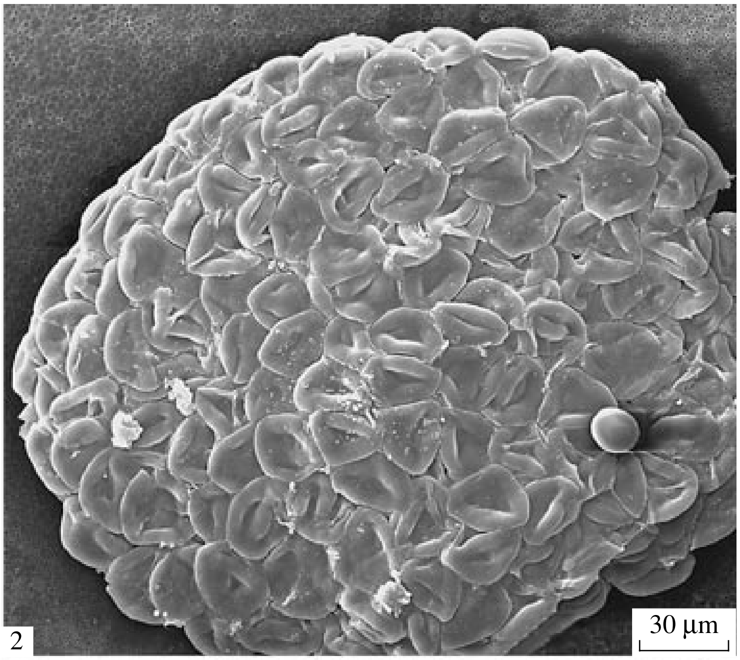

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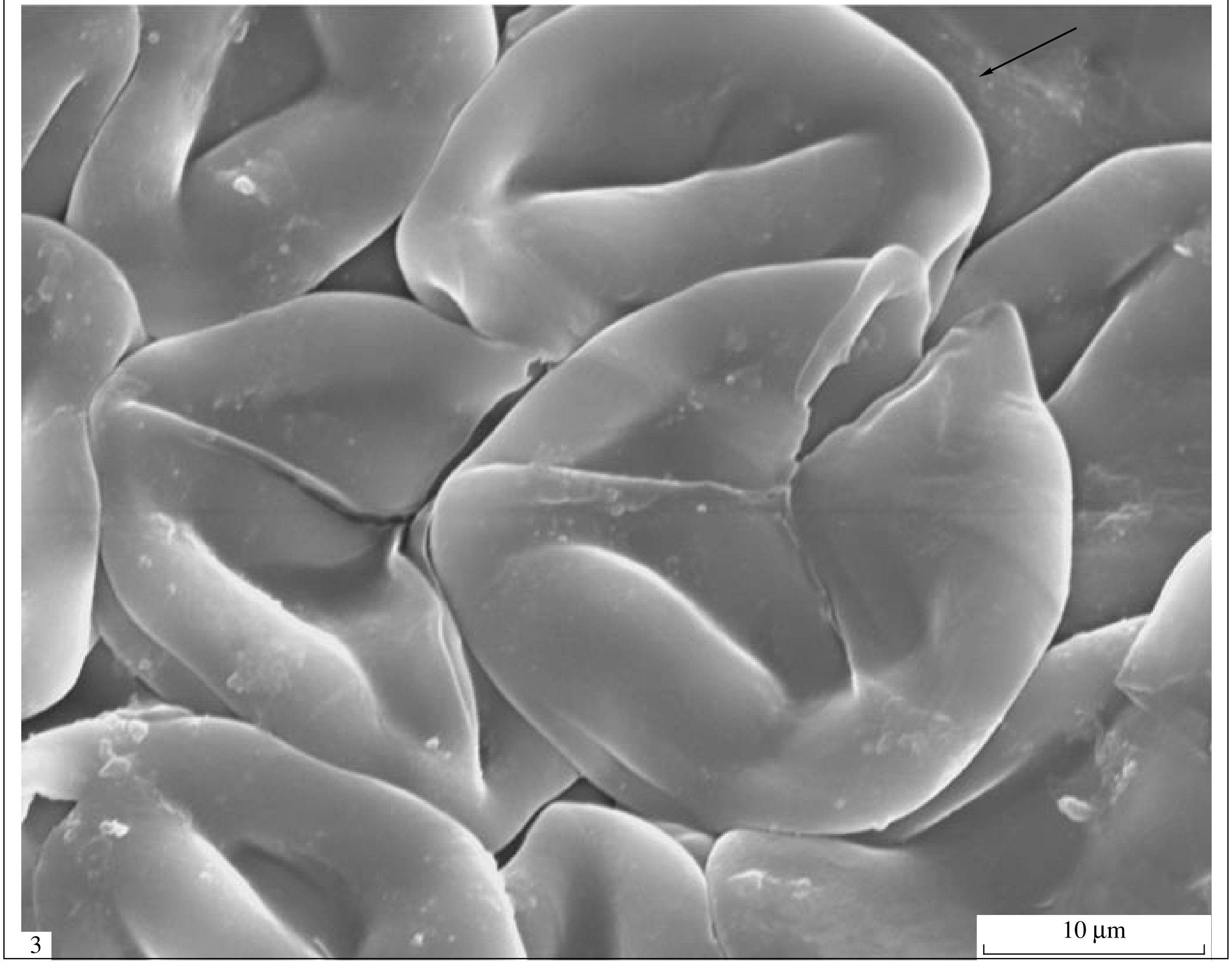

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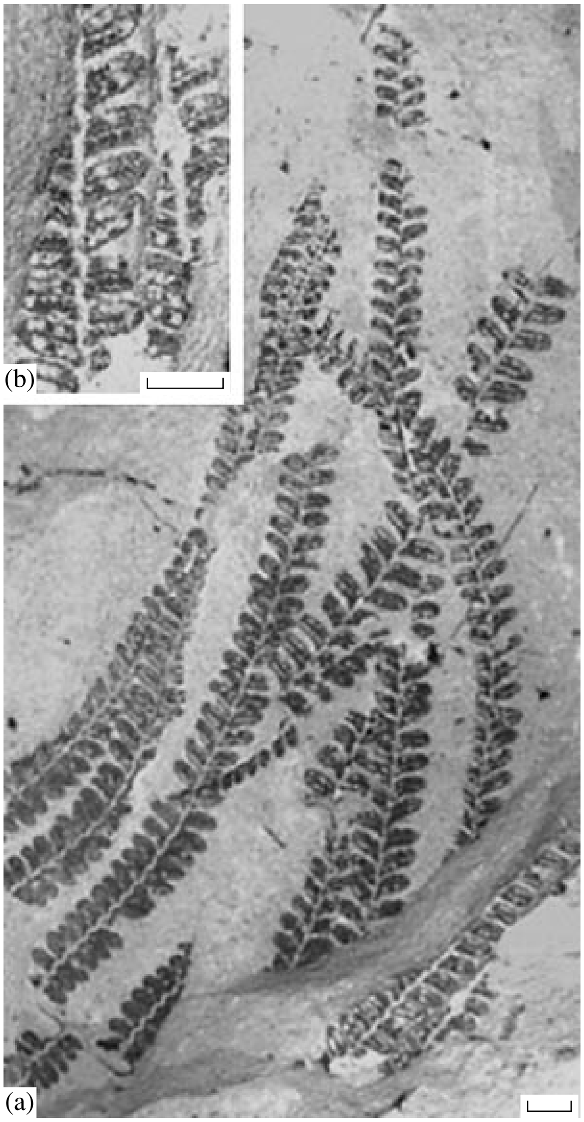

Fig. 2. Fern *Alsophilites nipponensis* (Oishi) Krassilov, IBPS-R1 no. 14/1: (a) fertile and sterile leaves and (b) a fragment of a leaf. Primorye Region, Lipovetsk coalfield, Lipovetsk Formation, Aptian. Scale bar 6 mm.

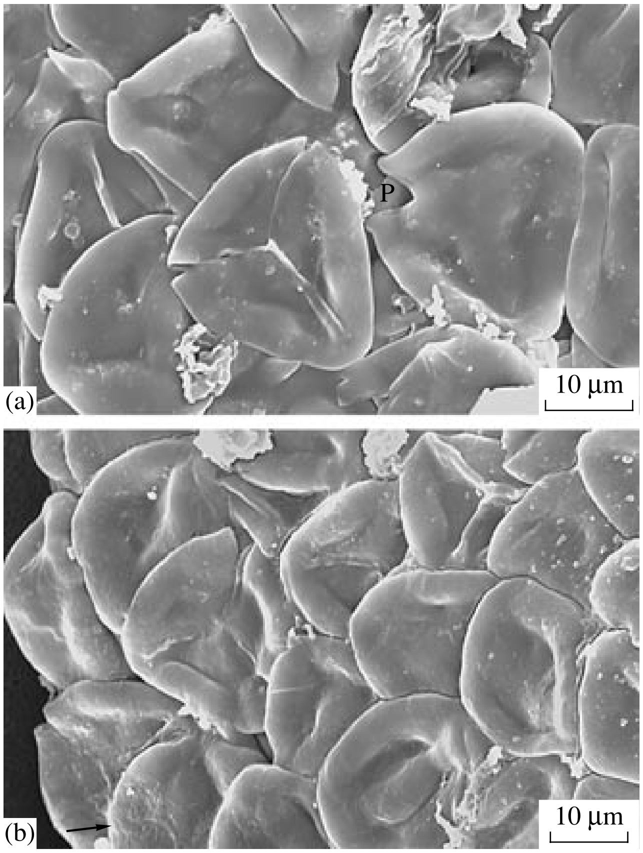

Fig. 3. *Alsophilites nipponensis* (Oishi) Krassilov, IBPS-R1 no. 14/1, SEM: (a) spores in proximal and distal view, a large equatorial pore (P) is visible; (b) variability of commissural ribs of the tetrad scar, the arrow indicates fragments of striate sculpture of the perispore. Primorye Region, Lipovetsk coalfield, Lipovetsk Formation, Aptian.

sium. There are four to six sporangia, which are imbricate, pear-shaped, about 1mm in diameter, and with a nearly vertical continuous ring of thickened cells (Pl. 10, fig. 1).

Each sporangium contains 128 spores in tetrahedral tetrads forming a solid mass of rounded–elliptical outline, about 300 μm in diameter, inseparable by maceration (Pl. 10, fig. 2). All spores are of similar dimensions, about 22–25 μm in diameter, tetrahedral–spherical, the equatorial outline is rounded–triangular with rounded, occasionally elevated or split corners. The contact area of the proximal face is triangular, distinctly delineated, and flat or concave. The curvatures appear as wide convex rims. The rays of the trilete scar are simple (without bordering). The commissural ridges are thin, distinct, straight or weakly arching, occasionally split (Pl. 10, fig. 3), occasionally interrupted, thickened at the extremities, and reaching the equator or terminating before the curvatural rim. One of the commissural ribs is often traceable up to the equator, and transects the curvatural rim, whereas two other ribs are observed only within the curvature.

The distal face is moderately convex, with a more or less distinct curvature. On the inside of the rim, pitted, elongate or irregular pits are developed. They delineate the convex central area, which approximately corresponds to the proximal contact area. A few porous depressions are also present within the convex central area. As a rare anomaly, some spores show a large subequatorial pore on the distal face (Fig. 3a). The equatorial (lateral) surface is elliptical with a thick straight or more or less curved, proximally convex curvatural rim, which is bordered by two deep parallel grooves.

The surface of the spore is formed by the exospore with scattered grains of various sizes, which are possible remnants of an earlier phase of perispore deposition. Apparent perispore structures are only occasionally preserved. These are a fragment of a thin membranous striate layer with parallel striae (Fig. 3b) and a reticulum of small pits and sinuous interlacing striate elements that cover a region of the exospore surface (Fig. 4). The latter might have been formed by sclerification and fusion of the exospore and the inner perispore layer.

The ultrathin sections in TEM (Fig. 5) show an exospore with unsculptured psilate external and undulated internal surfaces. In equatorial sections, the thickness of the exospore varies from 1 μm between the rays to 2 μm over the ends of the rays. Two layers are discernable: the outer one is thick and homogeneous, and the inner one is much thinner, of constant thickness (about 0.2 μm) throughout the perimeter of the section, fine-grained, with traces of lamellation expressed in parallel rows of pits. These layers are only slightly different in electron density; the boundary between them may be distinct or gradual.

DISPERSED SPORES

Psilate trilete spores from the palynological assemblages from the Lower Cretaceous of the Razdol'nenskii basin include *Cyathidites, Leiotriletes* (Naumova) Potonié et Kremp, and several species of *Gleicheniidites* Ross. Among them, two species of *Cyathidites*, *C. australis* Coup. and *C. minor* Coup., most closely resemble the in situ spores of *Alsophylites nipponensis* in their morphological characteristics. In the lower portion of the Lipovetsk Formation, each of these species constitutes up to 10% of the palynological assemblage, whereas in the upper part of the formation, where thick coal measures are concentrated, they reach up to 24%.

Spores of *Cyathidites australis* are triangular, with straight or concave sides, broad and rounded angles, and a relatively thin sporoderm, which is occasionally folded. The spore diameter is 50–76 μm.

Spores of *Cyathidites minor* are triangular, with straight, slightly concave or convex sides and a thin psilate sporoderm, which occasionally forms characteristic folds. The rays of the trilete scar are long, more than three-quarters of the spore radius; the arms of the trilete scar are close or open and simple. The spore diameter varies from 23 to 29 μm. These spores are slightly larger than in situ spores of *Alsophylites nipponensis*, but no remains of the perispore were found. We can conclude that the absence of a perispore in these three species is more likely to be caused by oxidizing agents rather than underdevelopment of spores in sporangia.

DISCUSSION

The number of spores per sporangium is of some taxonomic and phylogenetic value in the Cyatheaceae. The high number of spores per sporangium found in the species under study fits the supposed evolutionary trend from species with 64 spores per sporangium to those with 16 spores. Species with 64 spores are characteristic of the relatively primitive genus *Sphaeropteris*, in

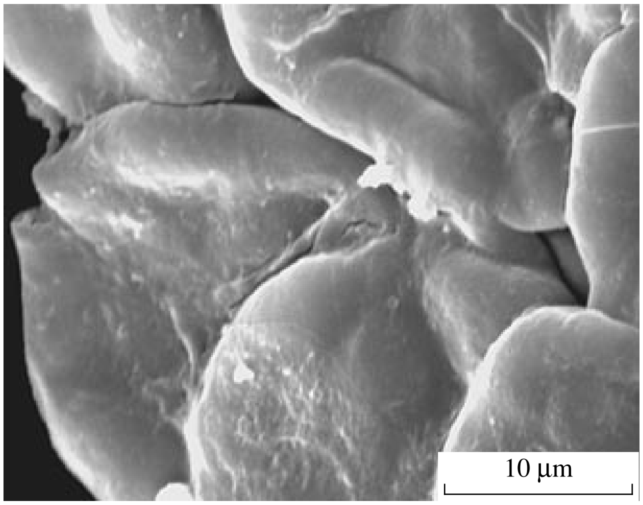

Fig. 4. Spores of *Alsophilites nipponensis* (Oishi) Krassilov, IBPS-R1 no. 14/1, SEM, traces of striate perispore sculpture are visible on the psilate surface of the exospore. Primorye Region, Lipovetsk coalfield, Lipovetsk Formation, Aptian.

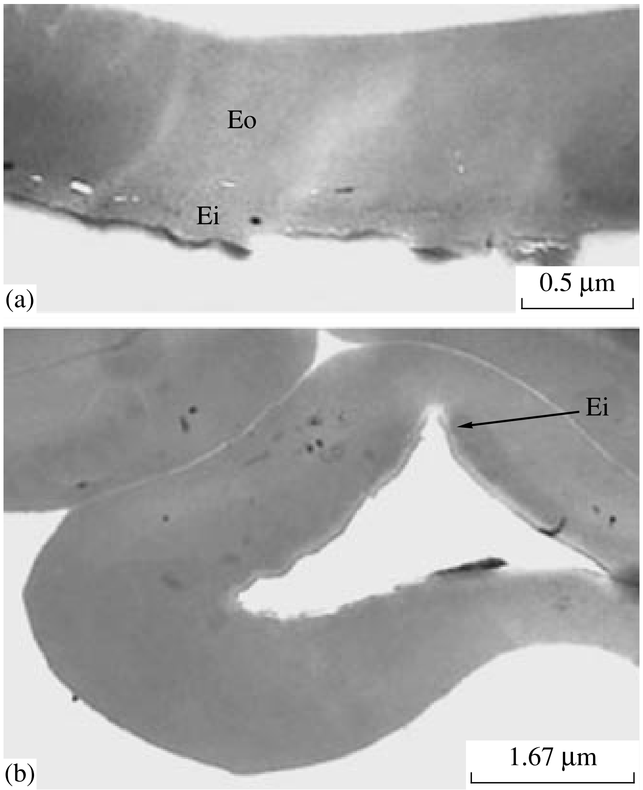

Fig. 5. Spores of *Alsophilites nipponensis* (Oishi) Krassilov, IBPS-R1 no. 14/1, TEM: (a) ultrastructure of the outer (Eo) and inner (Ei) layers of the exospore, note perforations in the layered inner layer; (b) configuration of the outer and inner (arrow) layers of the exospore, subequatorial section. Primorye Region, Lipovetsk coalfield, Lipovetsk Formation, Aptian.

which forms with 32 spores also occur (Gastony and Tryon, 1976). *Alsophila* and *Nephelea* typically have 16 spores, although in the former genus species with 64 spores are also known.

Incipient heterospory, when spores of two size categories develop in the same sporangium, can be considered an evolutionary advanced feature of modern Cyatheaceae relative to the fossil form with spores of one size category.

The cohesion of spores (they are very difficult to separate from the mass) may indicate dispersion by whole sporangia, a mechanism also known in modern ferns of the Cyatheaceae (Gastony, 1974). This is a possible explanation of the relative rarity of such spores in palynological assemblages contrasting with the dominant position of this fern species in the respective macrofossil assemblage and its high spore production.

In the Cyatheaceae, the perispore sculpture is of high taxonomic value, supposedly developed from echinate in *Sphaeropteris* to striate in *Alsophila* and *Nephelea*. A full-developed perispore has a two- or three-layered ultrastructure (Lugardon, 1974), but only the inner granulate layer may be present because of delayed development of the upper layers. The exospore is smooth or, in its turn, ornamented; and *Sphaeropteris* has the most prominent heteromorphic verrucate sculpture of larger and smaller verrucae, bordered pits or perforations. In the majority of species in *Alsophila* the perispore is smooth, but in the forms with a reduced perispore it can be finely verrucate and variously pitted, occasionally with three equatorial pits, as in *Cnemidaria*. An exospore with compound sculpture is reported in *Lophosoria* (Gastony and Tryon, 1976), whereas in *Metaxya* a psilate exospore with scattered granules is exposed under the easily detached echinate perispore. Psilate spores of *M. rostrata* lacking a perispore show long thin commissural ridges of the tetrad scar and greatly resemble Cretaceous *Cyathidites*.

Unfortunately, the conventionally used technique of extraction of in situ spores from sporangia of fossil ferns inevitably leads to the loss of the perispore, which is destroyed by oxidation. It must be noted, however, that in the Cyatheaceae the perispore is formed late in sporogenesis and may be underdeveloped even in mature spores. Consequently, perispore characters are of limited use in the classification of fossil Cyatheaceae. Nevertheless, although our material has been strongly oxidized in the course of technical treatment, it still testifies to at least fragmentary preservation of the perispore. If our interpretation of the structures (Fig. 4) indicated by the arrow in Fig. 3b as fragments of the inner layer of a striate perispore is correct, then this feature justifies a comparison with *Alsophila* and, in part, with *Nephelea*, with their regular thin striation along the rays of the tetrad scar. It is noteworthy that *Nephelea* is considered among the most evolutionary advanced genera of the Cyatheaceae.

In the bilayered exospore with a very fine-grained and indistinctly lamellate inner layer, the fossil form resembles modern species of *Cyathea* (Lugardon, 1974).

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