A new species of *Todites* (Pteridophyta) with *in situ* spores from the Upper Permian of Pechora Cis-Urals (Russia)

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Todites lobulatus sp. nov. is described from the lowermost Upper Permian (Ufimian) of the Pechora basin. The fossil remains preserved as compressions and impressions, were collected from near-shore lake deposits of the Intinskian Formation. The species belongs to protoleptosporangiate ferns (Pteridophyta) of the Osmundaceae, and is characterized by tripinnate fertile fronds with deeply dissected lobate pinnules with round apexes. Sporangia are round or ovoid, free, and located on the abaxial leaf surface. A group of specialized thick-walled cells is located on the top or side part of the sporangia. The species is the most ancient representative of Osmundaceae. Spores of *Osmundacidites*-type, preserved *in situ,* are characterized.

Key words: Pteridophyta, Osmundaceae, spores, ferns, Permian, Russia.

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Introduction

Very little data have been published concerning the Permian ferns of the Osmundaceae with spores preserved *in situ*. At the same time, such data, as well as new evidence on taxonomic diversity among these plants are important for the reconstruction of the phylogeny of ferns. Such studies allow us to move towards a whole plant concept taxonomy, which is necessary for an understanding of vegetation of the geological past.

Osmundalean ferns of the genus *Todites* (Seward, 1900) from the uppermost Upper Permian and early Mesozoic of Angaraland were studied in detail during the last several decades (e.g., Radczenko 1955; Fefilova 1973; Mogutcheva 1973, 1984; Esaulova 1996), but only scarce information is available on *in situ* spores of these ferns. Besides leaves of osmundaceous affinity preserved as compressions/impressions, there are stems of this group known from the Upper Permian of Angaraland. Zalessky (1927) described trunks of *Eichwaldia* and related forms, which are characteristic of the Upper Permian, especially the Kazanian of the Cis-Urals and Russian platform. These remains occur together with similar forms initially reported by Kutorga (1838) and Eichwald (1854), who described the stems *Sphallopteris schlechtendalii* Eichwald, 1854, *Chelepteris gracilis* Eichwald, 1854, *Bathypteris rhomboidalis* Eichwald, 1854, and *Anomorrhoea fischerii* Eichwald, 1854. Some of them were later refigured by Zalessky (1927).

Representatives of *Todites* are more typical elements of Mesozoic floras rather than Palaeozoic ones. Therefore, the presence of these ferns characterized both by sterile, and fertile pinnae attributed to *Todites* lets us more precisely reconstruct the history of early development of Mesozoic vegetation. New material described in this paper gives additional information about *Todites* spores preserved *in situ*. Moreover, the material studied is the most ancient (Ufimian; lowermost Upper Permian) finding of a fern belonging to the Osmundaceae.

Material and methods

The specimens studied originated from the sequence of Permian deposits (Fig. 1) located along the left bank of Kozhim River, Pechora Cis-Urals (Russia). All specimens came from the Intinskian Formation of Upper Permian (Ufimian) (Fig. 2). The floristic assemblage also includes the moss *Vorcutannularia* sp., predominant "cordaite-like" leaves *Rufloria* (*Alatorufloria*) *derzavinii* (Neuburg, 1936) Meyen, 1966, scale-like leaves *Nephropsis* (*Sulcinephropsis*) spp., *Lepeophyllum* sp., probably belonging to the Vojnovskyales, ferns *Orthotheca semilibera* Naugolnykh, 1998b, *Prynadaeopteris* sp., sphenophytes *Paracalamitina striata* (Schmalhausen, 1879) Zalessky, 1934, *Paracalamites* sp., and dispersed isolated seeds *Samaropsis vorcutana* Tschirkova, 1938 (in Zalessky and Tschirkova, 1938), and *Samaropsis* sp. (Naugolnykh, 1998a).

The standard procedure of maceration in Schultze reagent was used for spore exploration. The macerated sporangia and extracted spores were studied under SEM (Stereoscan 600, Cambridge, UK).

The collection studied is kept at the Geological Institute of the Russian Academy of Sciences, Moscow (GIN) under the number 4846.

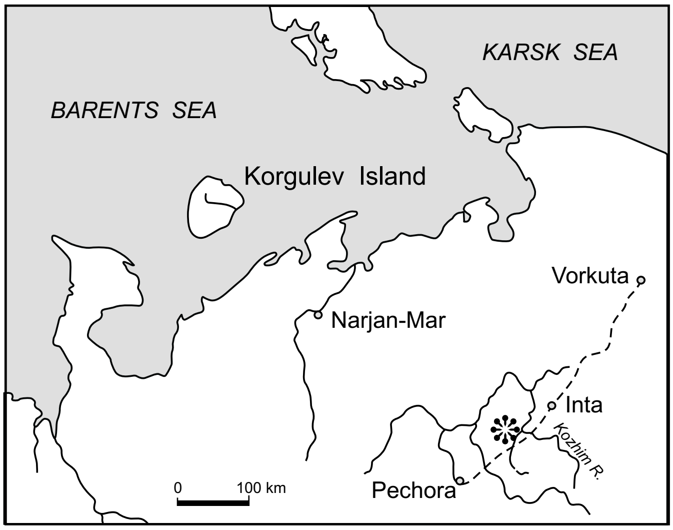

Fig. 1. Geographical position of the locality (✻) studied.

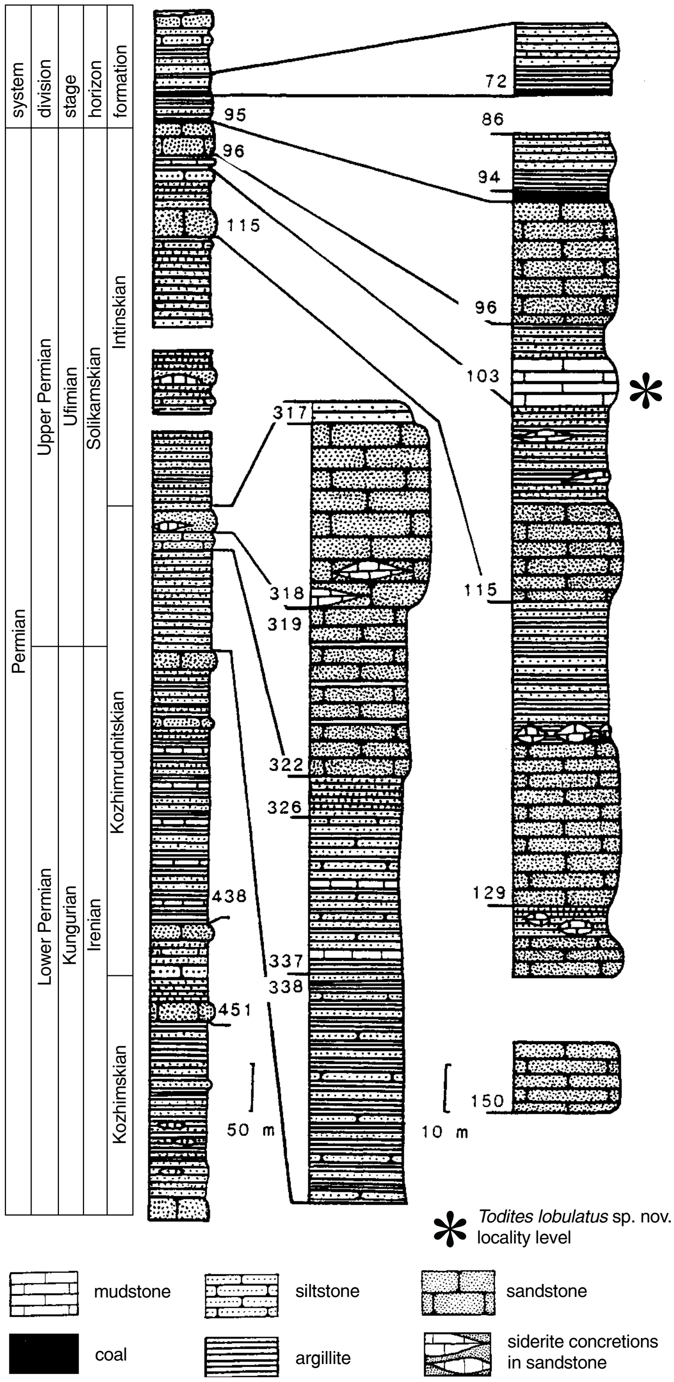

Fig. 2. Stratigraphical column of the locality studied.

Description

Order Osmundales
Family Osmundaceae
Genus *Todites* Seward, 1900
Todites lobulatus sp. nov.

Figs. 3–7.

Holotype: GIN 4846/102.

Type horizon: Bed 103, Intinskian Formation, Upper Permian (Ufimian).

Type locality: Left bank of Kozhim River, 4 km downstream from the bridge near Kozhim-Rudnik station, the Pechora Cis-Urals, Russia.

Derivation of the name: From Latin *lobulatus*, lobed.

Diagnosis.—Ferns with tripinnate fronds. Pinnules deeply dissected with well developed lobes. Pinnule apex round. Sporangia free, located on abaxial leaf surface. Sporangia round or ovoid, small (0.5 mm in diameter), with group of thick-walled cells on sporangia top or side. Spores circular, laesura trilete, radii simple, straight, spore surface sculptured by granulate scabrae. Size of the spores ranges from 20 to 45 µm.

Material.—Two representative pinnae of last order belonging to one individual plant.

Description.—The single representative fragment of a tripinnate frond with two preserved pinnae of the last order is shown on Fig. 3A–D and Fig. 4. The preserved part of the most complete pinna is 31.5 mm long and 2.8 mm wide. The pinna rachis is straight in the apical part, but slightly curved (undulating) in its proximal part. The rachis width is 1.5 mm. The narrow wing is present in the apical part of the pinna. One can see eight pinnules with lobed margins. The pinnules are attached to the pinna rachis in regularly alternate order. Pinnule length varies from 13.3 up to 15.8 mm. Maximal width of the pinnules is 8 mm. Pinnule outlines are subtriangular.

The frond surface is exposed on its adaxial side without sporangia. Since the leaf lamina is considerably eroded, the numerous sporangia attached to abaxial frond surface are clearly seen (Fig. 3B, C).

The pinnules are dissected into well developed lobes in 1/2 of pinnule width in their proximal parts. The apical parts of the pinnules are not so deeply dissected. The pinnate venation is simple. One well developed robust midvein enters each pinnule. Lateral veins enter each pinnule lobe. Lateral veins in the apical part of the pinnule are simple; those of the

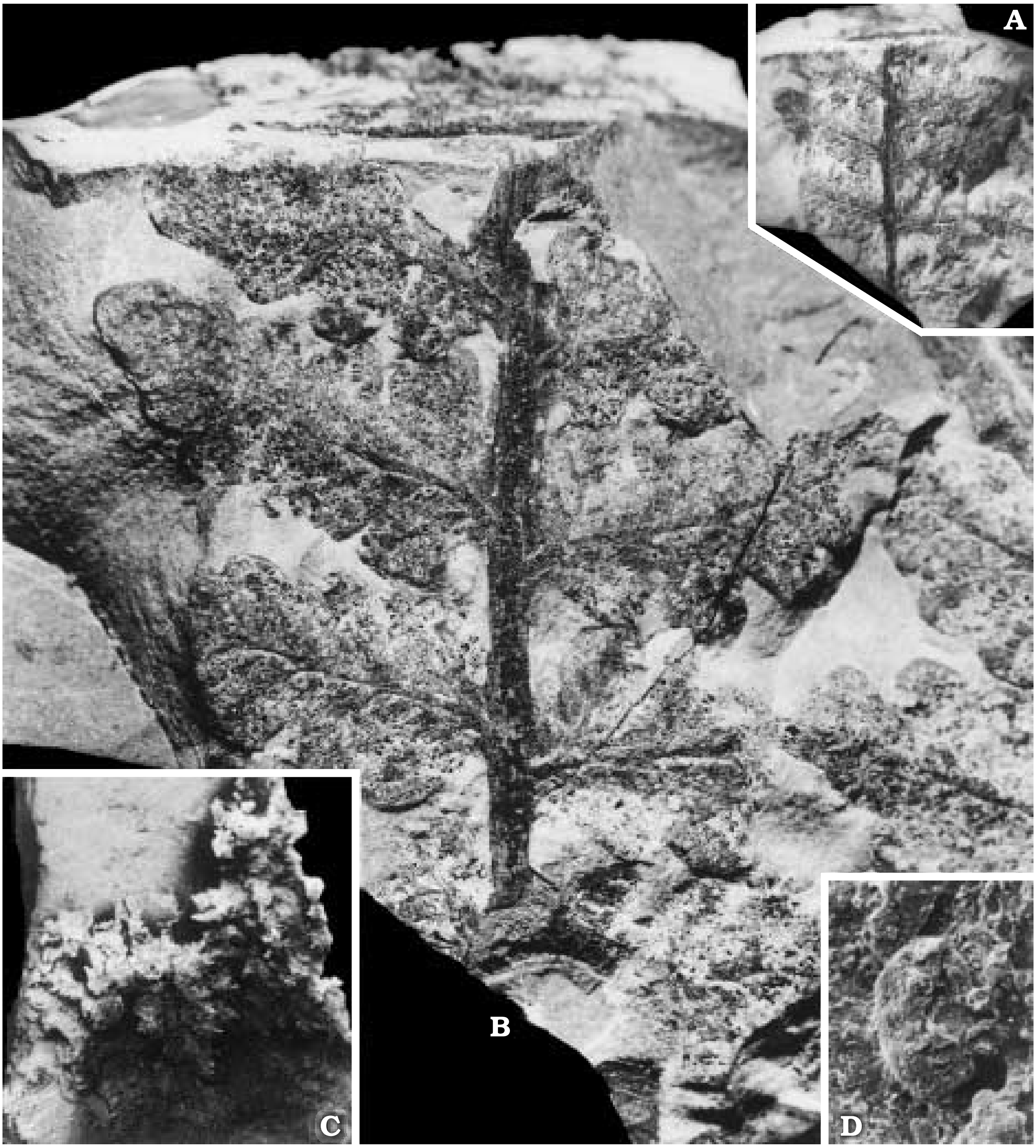

Fig. 3. *Todites lobulatus* sp. nov. Intinskian Formation, Ufimian, Upper Permian. Holotype GIN 4846/102. **A**, **B**. General morphology of fertile pinna, before (**A**) and after (**B**) preparation; **A**, × 1; **B**, × 4. **C**. Two prepared sporangia; left sporangium shows a group of thick-walled cells near the stomium (dark depression); × 18. **D**. The spore of *Osmundacidites* type, preserved *in situ*, under SEM, × 800.

proximal parts of the pinnules are rarely pinnately branched. Lateral veins originate from the midvein in alternating order, but sometimes almost opposite. The pinnule apex is round, the pinnule base is narrow, sphenopteroid.

The abaxial surface of the leaf lamina is covered by sporangia and one pinnule bears up to three hundred sporangia. Sporangia are so closely spaced, that they appear to form a mass, in which single sporangia are very difficult to observe. Individual sporangia are small (about 0.5 mm in diameter), round or ovoid, and bear small stalks basally (sporangiophore), by which they are attached to the leaf lamina.

One can see several well preserved sporangia, each showing a group of specialized cells with thicker walls located near the sporangial stomium (Figs. 3C, 5), which represents the opening mechanism of maturity. This structure is characteristic of recent osmundalean ferns, and fossil ones.

Fig. 4. *Todites lobulatus* sp. nov. Intinskian Formation, Ufimian, Upper Permian. Holotype GIN 4846/102. General morphology of a fertile pinna. Scale bar 0.5 cm.

The uppermost fertile pinnule figured in Fig. 3A and Fig. 4, right, was macerated. Numerous spores were extracted from the sporangia. During the maceration the sporangium walls were completely dissolved, but all spores were preserved *in situ* as a round or spherical mass (Figs. 6F, G, 7A–F). This mass of spores has outlines corresponding to the original form of the sporangium. Separate spores are clearly seen at the periferal zone of the spore mass (Fig. 7B, C). The spores have a well developed tetrad scar (trilete mark or laesura), and the rays of the trilete mark almost reach the spore margin (Figs. 6E–G, 7D). The spore surface is sculptured by very fine granulate microstructure (Figs. 6D, 7B, D). Very similar, but slightly more developed and larger, spores were extracted from the matrix housing the *Todites lobulatus* fertile pinnae (Figs. 8, 9). Most probably they belonged to the same species, but dispersed spores have a larger size because they are mature as opposed to those still in the sporangia. The dispersed spores of the same type, which can be attributed to *Osmundacidites* Couper, 1953, are known from the Upper Permian of other regions of the Urals and the Russian platform.

Comparison and remarks.—The new species differs from the type-species *Todites williamsonii* (Brongniart, 1828) Seward, 1900 in having deeply dissected pinnules and round pinnule apices; from *T. crenatus* Barnard, 1965 in considerably shorter and wider pinnules; from *T. sibiricus* (Schmalhausen, 1879) Radczenko, 1955 and *T. evenkensis* Radczenko, 1955 in having well developed pinnule lobes, but shares with them the general structure of the fertile pinnules, e.g., form and position of sporangia; from *T. sibiricus*—in larger size of the pinnules (15 mm instead 8–10 mm) and slightly curved pinnule (straight pinnules of *T. sibiricus* are disposed almost perpendicularly to the pinna rachis), from *T. evenkensis*—in round pinnule apex and wider angle of pinnule orientation on the last order pinna; *Todites lobulatus* has narrow wings on the rachis. In contrast, *T. sibiricus* and *T. evenkensis* have no wings.

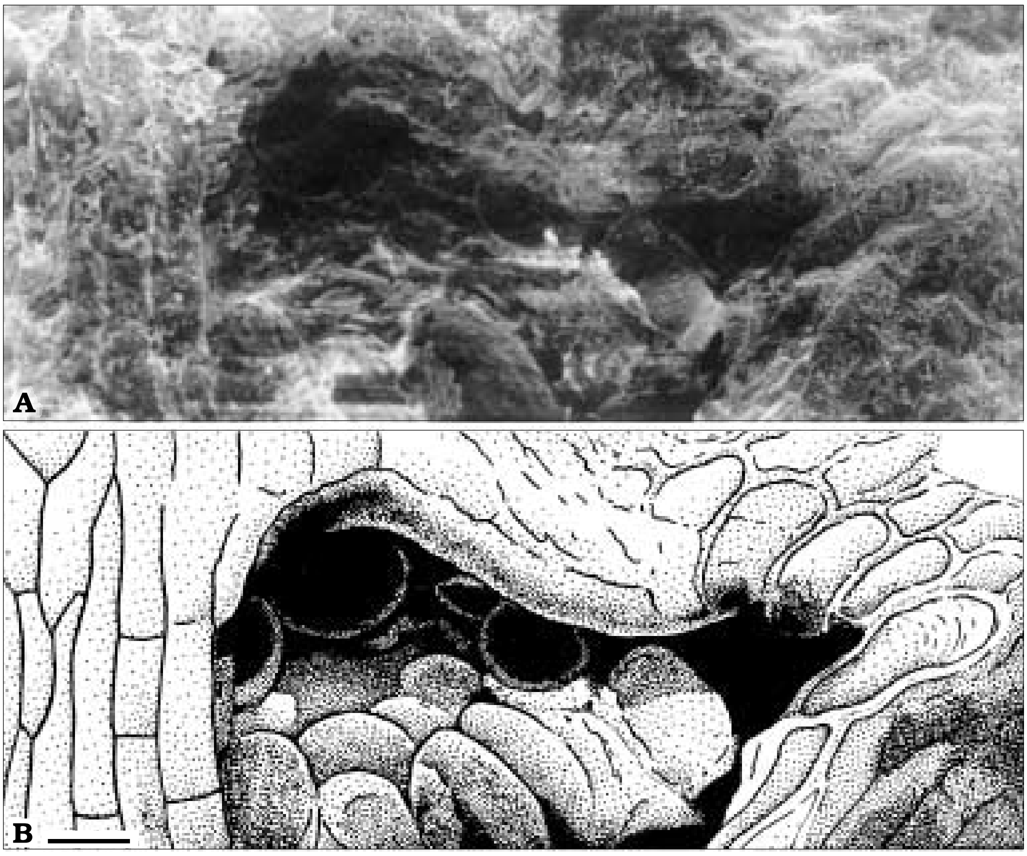

Fig. 5. *Todites lobulatus* sp. nov. Intinskian Formation, Ufimian, Upper Permian. Holotype GIN 4846/102. Sporangium with open stomium and thick-walled cells located near its right side, photograph (**A**) and line drawing of the same sporangium portion (**B**). Scale bar 20 mm.

Fefilova (1973) described several sterile and fertile pinnae from the Upper Permian (Ufimian and Kazanian) deposits of Kosju, Big Synja and Perebor river basins (Pechora Cis-Urals). These pinnae were attributed to *Todites* sp. in open nomenclature. Some spores of *Lophotriletes* Potonie and Kremp, 1954 were extracted from the sporangia. Later very similar fertile fronds of *Todites* sp. were reported from the Seidinskian and Talbeiskian Formations (presumably Kazanian in age, at least partly) of the Pechora coal district, in the Heyaha and Adzva rivers basin (Pukhonto, Fefilova 1983).

Mogutcheva (1984) established the species *Todites orulganensis* from the Lower Triassic Surbeljakhskian Formation of North Verkhoyanie (Siberia). This species is similar to *T. lobulatus* described above, but differs by entire margined pinnules. There is no information on the *in situ* spores of *T. orulganensis*.

In general, the new species *T. lobulatus* differs considerably from other species of *Todites* known from the Upper Permian and Lower Triassic deposits of Angaraland by wider pinnules and extremely well developed pinnule lobes.

Discussion

The presence of "Mesozoic" plants in Permian floras of Western Angaraland and the Subangaran ecotonous belt was discussed by many palaeobotanists (see Zalessky 1937; Meyen 1982; for general review of the Late Paleozoic floras, for the Mesozoic elements see DiMichele et al. 2001). For example, the sterile leaves of ferns assigned to the genus *Cladophlebis* Brongniart, 1828 are present in the Upper Permian of this region. *Cladophlebis* is often regarded as a typical Mesozoic genus and considered as a representative of the Osmundaceae (see, for example, Shorokhova 1975; Litwin 1985; Schweitzer et al. 1997). Leaves of this genus are known from the Upper Permian of the Pechora basin (Pukhonto, Fefilova 1982) and Mongolia (Durante 1976), i.e., from Angaraland in a wide sense. At least some of the ferns with *Cladophlebis*-like leaves bear sporangiophores of the *Todites*-type (Shorokhova 1975; Schweitzer et al. 1997) but any data about *in situ* preserved spores of Permian representatives of *Todites* were absent for a long time.

Spores preserved *in situ* were extracted from some Mesozoic representatives of *Todites* (Barnard 1965; van Konijnenburg-van Cittert 1978; Litwin 1985; Schweitzer et al. 1997; general review see in Balme 1995). Most of them were attributed to *Osmundacidites*: *Todites crenatus*, Jurassic of Iran; *Cladophlebis* (al. *Todites*) *denticulata* Brongniart, 1828, Jurassic of England and Greenland; *T. recurvatus* Harris, 1931, Triassic and Jurassic of Greenland. Some *Todites* species have been associated with the spore *Todisporites* Couper, 1958: *T. princeps* (Presl, 1961) Gothan, 1914, Triassic and Jurassic of England and Greenland; *T. thomasii* Harris, 1961, Jurassic of England; *T. nebbensis* (Brongniart, 1828) Kilpper, 1964, Upper Triassic of Iran; *Leiotriletes* Potonie and Kremp, 1954:

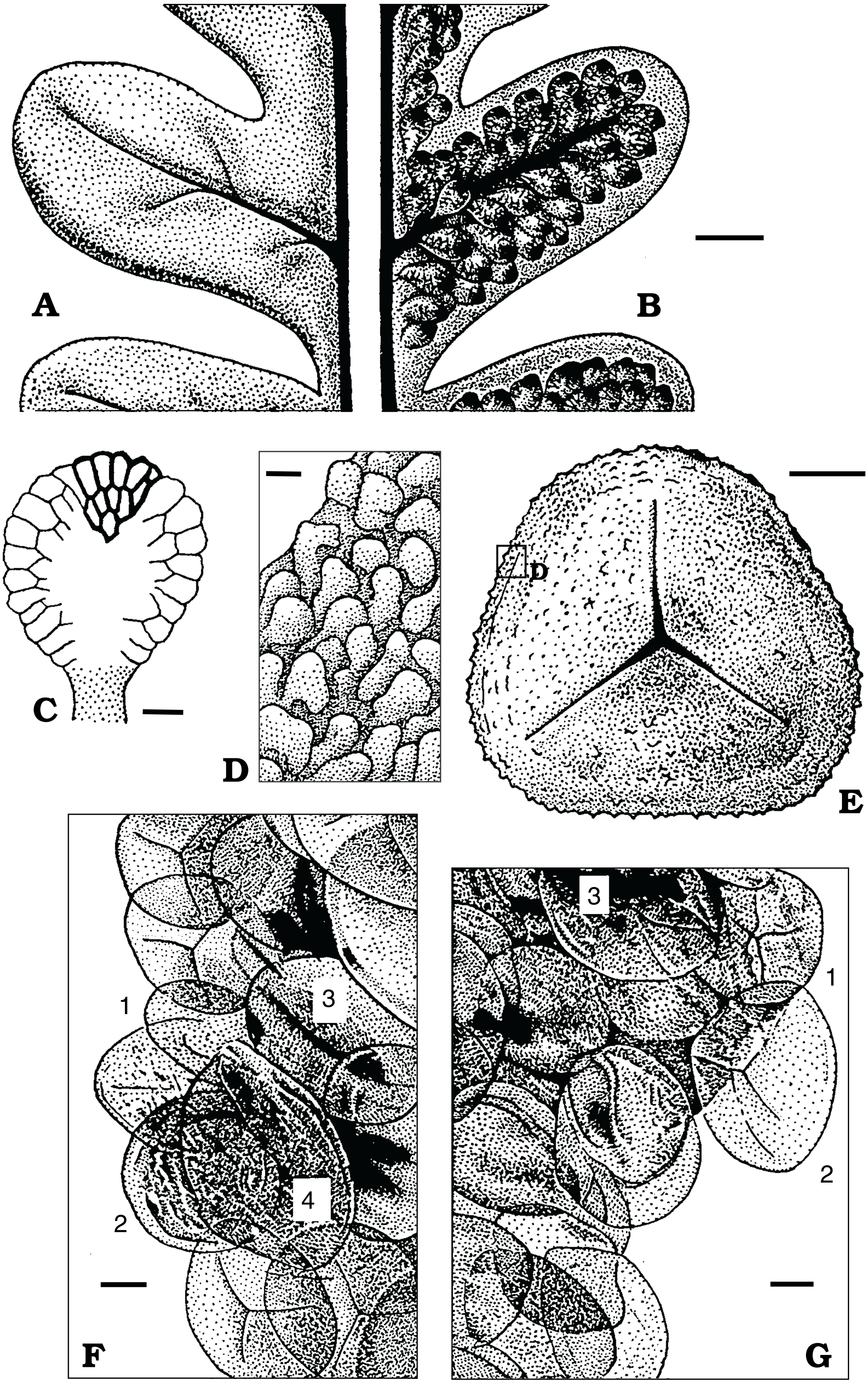

Fig. 6. *Todites lobulatus* sp. nov. Intinskian Formation, Ufimian, Upper Permian. Macromorphology and *in situ* spores, based on holotype GIN 4846/102. **A**, **B**. Fertile pinnule reconstruction, upper (adaxial, **A**) and lower (abaxial, **B**) view, numerous sporangia attached to lower side of the pinnule surface (**B**). **C**. Individual sporangium with thick-walled cells on the top area. **D**. Granulate microstructure of the spore surface. **E**. General view on the isolated spore. **F**, **G**. Spore mass extracted from the sporangia, note different sizes (relatively small spores 1 and 2 and big spores 3 and 4 of F) and different outlines of the spores (round spores 2 and ovoid 1, 3 and 4 of F; round spore 1, rounded subtriangular spore 2 and ovoid spore 3 of G). Scale bars: **A**, **B**, 5 mm; **C**, 0.1 mm; **E**, **F**, **G**, 50 μm; **D**, 5 μm.

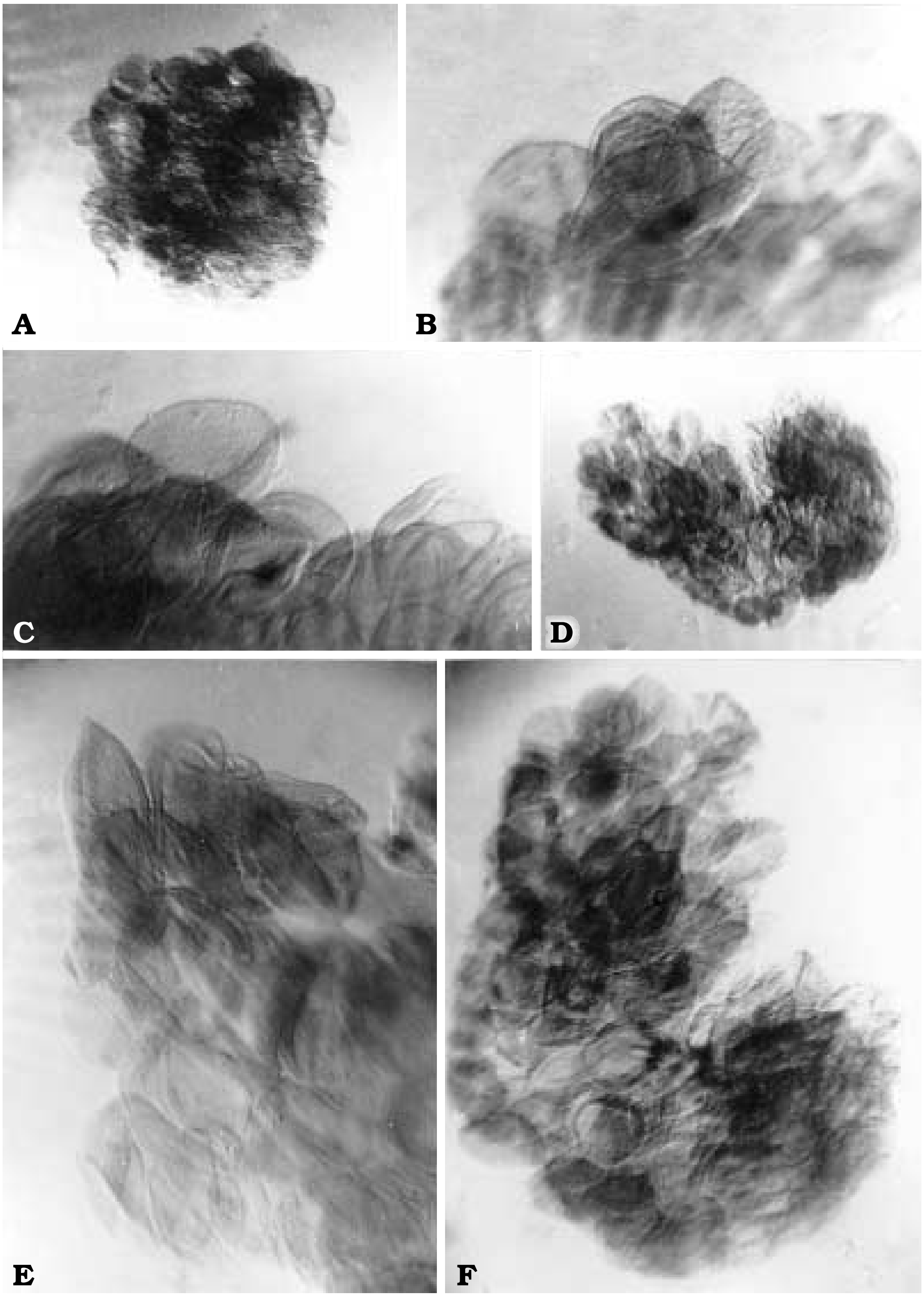

Fig. 7. *Todites lobulatus* sp. nov. Intinskian Formation, Ufimian, Upper Permian. *In situ* spores extracted from the holotype GIN 4846/102. **A**. Spore mass repeating the initial round form of sporangium, × 50. **B**. Several spores of different size and form, × 200. **C**. Spore with clearly seen laesura (left part of the photograph), × 200. **D**. Spore mass of ovoid form from relatively elongated sporangium, × 50. **E**. Spore mass in detail, × 200. **F**. Detail of D, × 100.

T. pseudoraciborskii Schorochova, 1975, Triassic of Siberia, and *Punctatisporites* Potonie and Kremp, 1954/*Todisporites*: *Todites williamsonii* (Brongniart, 1828) Seward, 1900, Triassic of China and Jurassic of England.

Todisporites and *Osmundacidites* differ mainly in the type of the spore surface sculpturing. Commonly, spores with granulate and reticulate exine are attributed to *Osmundacidites*, and similar forms with a relatively smooth surface

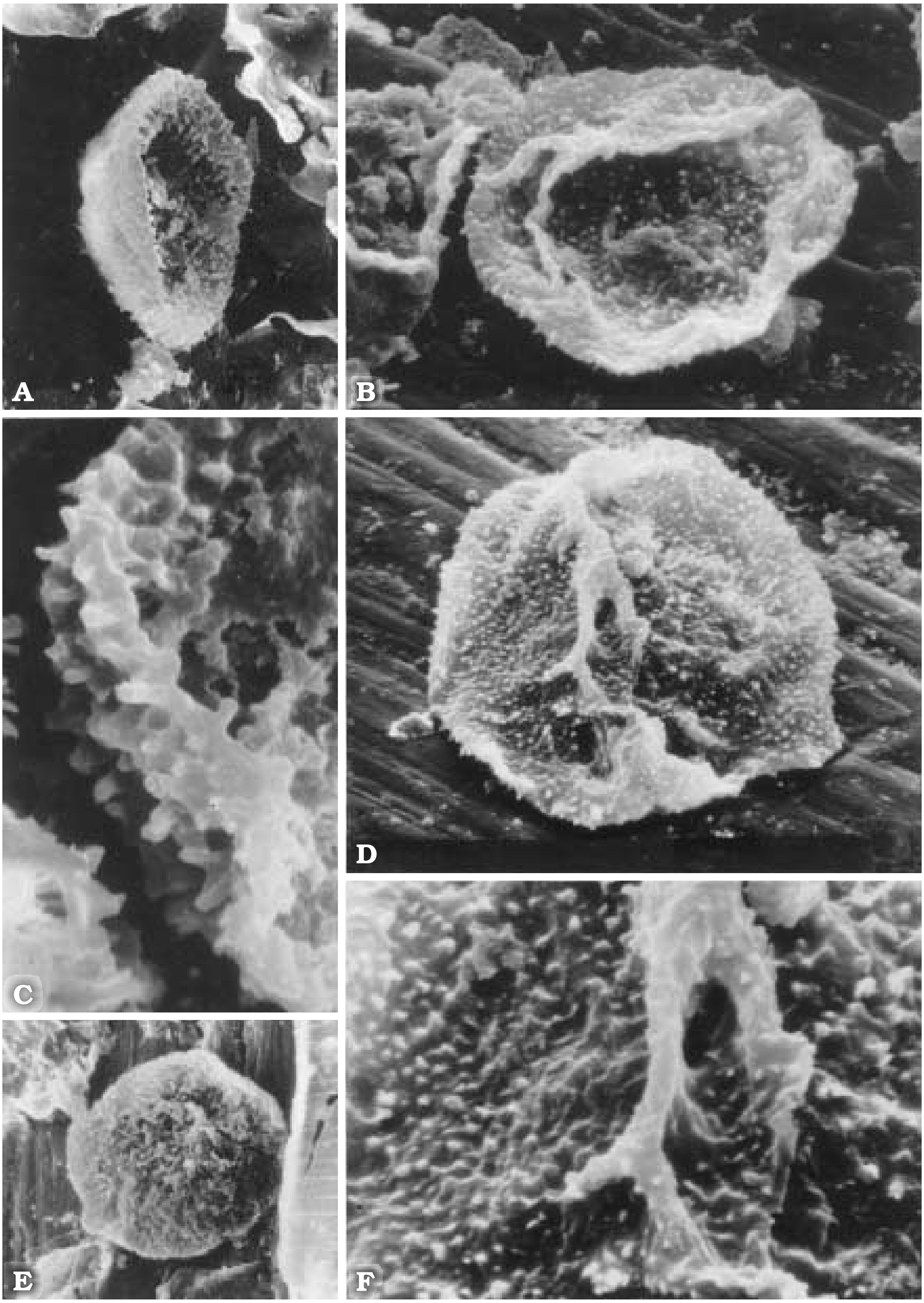

Fig. 8. Spores of *Osmundacidites* type, extracted from the matrix containing the holotype of *Todites lobulatus* sp. nov.,GIN 4846/102. **A**, **B**, **D**, **E**. Different individual spores; **A**, **B**, **D**, × 1500; **E**, × 750. **C**, **F**. Granulate sculpture of spore surface, × 3000.

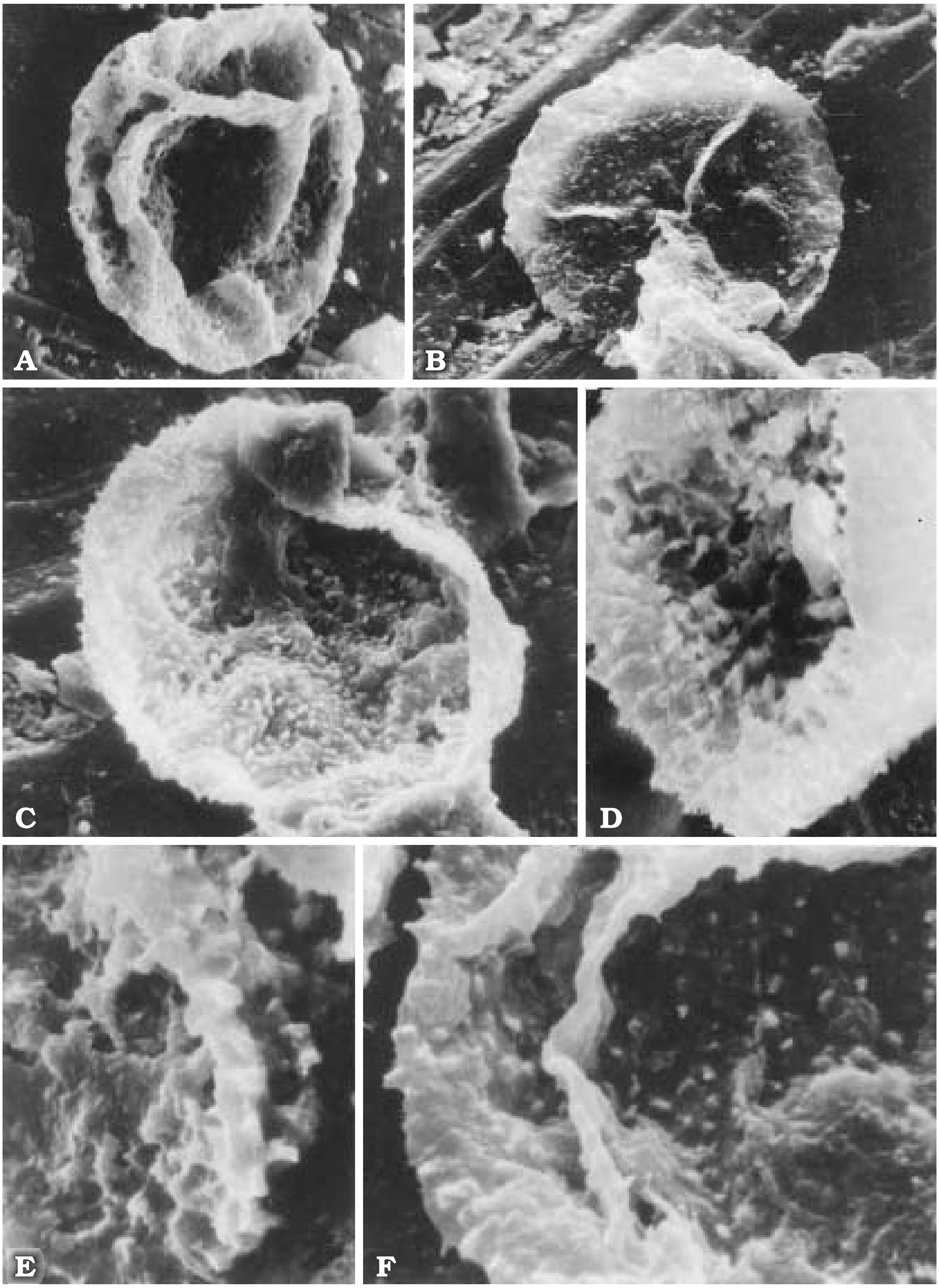

Fig. 9. Spores of *Osmundacidites* type, extracted from the matrix containing the holotype of *Todites lobulatus* sp. nov.,GIN 4846/102. **A**–**C**. Different individual spores, × 1500. **D**–**F**. Granulate sculpture of spore surface, × 3000.

with rare granulae and/or spines to *Todisporites*. Hence, sometimes the granulate and almost smooth spores do occur in sporangia of one and the same fertile frond of *Todites* (Schweitzer et al. 1997). The *T. lobulatus* spores certainly belong to the same morphological group as Mesozoic ones and can be classified into *Osmundacidites* according to its formal status and diagnosis (Balme 1995).

Regarding Permian dispersed spores of proposed osmundalean affinity, similar to *Osmundacidites*, it should be noted that there are some other form-genera like *Cyclogranispo-*

rites Potonie et Kremp, 1954 of quite similar morphology: (for additional comments and comparison see Hart 1965). At least some of them can belong to ferns of the Osmundaceae, too. Spores of this kind appeared in the Urals and Russian platform region in the Kungurian. Therefore, it is possible that predecessors of *Todites* or other Osmundacean ferns, existed in Early Permian according to palynological data.

Acknowledgements

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