ISSN 0031-0301, Paleontological Journal, 2006, Vol. 40, No. 2, pp. 215–223. © Pleiades Publishing, Inc., 2006.
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A New Lycopod, *Novgorodendron conophorum* gen. et sp. nov., from the Lower Carboniferous of the Moscow Syneclise

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Received February 2, 2005

Abstract—A new lycopod, *Novgorodendron conophorum* gen. et sp. nov., is described from the Upper Visean deposits of the Kamenka River, near the town of Borovichi (Novgorod Region). The morphology of the leaf cushions of the new plant implies its intermediate position between the families Sublepidodendraceae Chaloner et Boureau and Lepidodendraceae Endlicher. The bases of the leaf cushions have peculiar conical appendages, a previously unknown morphological feature not recorded from other lycopods. We propose the term basal conical appendages for them. The interpretation of some epidermal elements in the leaf cushions of the Lepidodendraceae is revised. The structures of the leaf cushions that were previously treated as either stomata or cells with cystoliths are shown to be sunken multicellular trichomes.

DOI: 10.1134/S0031030106020134

Key words: lycopods, Visean, leaf cushions, epidermal elements.

INTRODUCTION

Lycopod remains from the Lower Carboniferous of central Russia were studied by, among others, Eichwald (1840, 1841, 1854, 1860), Auerbach and Trautschold (1860), Zalessky (1905a, 1905b, 1915, 1948), and Bode (1929). Recent studies have shown that in this region the taxonomic composition of lycopods is unusual (Orlova, 2001, 2003; Snigirevsky and Orlova, 2001). Apart from the common members of the Euramerian Lepidodendrales, new taxa that have leaf cushions with a peculiar morphology have been established. *Novgorodendron conophorum* gen. et sp. nov. is one of these taxa. The unique preservation of the material made it possible to study both morphological and epidermal structures of this plant and, thus, to reveal previously unknown details of the epidermal structure of leaf cushions in Lepidodendraceae.

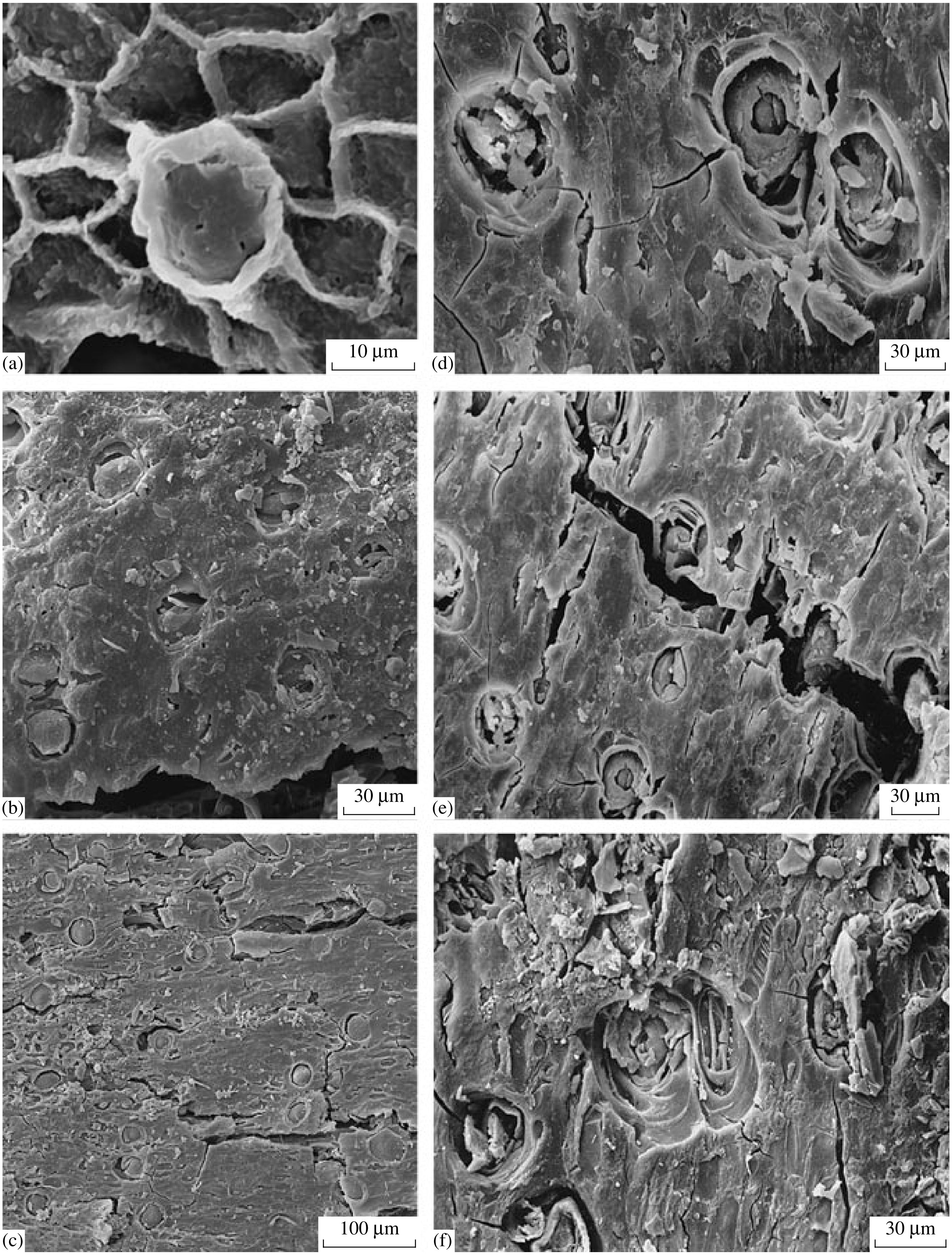
To date, more than 30 genera of the Lepidodendrales (or of supposed lepidodendralean affinity) have been established from the Lower Carboniferous throughout the world based on the morphology of the stem surface. The anatomy (Boureau, 1967) and epidermal morphology (Thomas, 1970; Thomas and Masarati, 1982) are known for only a small proportion.

The epidermal morphology is conventionally interpreted on the basis of cuticular studies that occasionally lead to erroneous conclusions. The material under description has both epidermal cells and cuticle. The cells of the leaf cushions were not distorted by the pressure of the surrounding rocks during fossilization, as is the case with the majority of plant remains. This allowed us to study the three-dimensional structure of the epidermis and to prove that cuticular characteristics do not always adequately show the morphology of the epidermis. The cuticles of Lepidodendrales that were earlier described by different authors are indistinguishable from the cuticle of the plant under consideration. The lack of information about non-cutinized parts of the epidermis gave rise to misinterpretation of closely spaced depressions on the cuticle: they were misinterpreted either as cystoliths (Snigirevskaya, 1964) or as stomata (Thomas, 1970; Thomas and Masarati, 1982). The unique degree of preservation of the leaf cushions of *N. conophorum* gen. et sp. nov. makes it possible to reject these interpretations.

MATERIAL AND METHODS

The material comes from an Upper Visean locality, Kamenka River, which is situated in the Msta River Basin, 3 km from the town of Borovichi of the Novgorod Region. The specimen under description was found in a band of pyritized coaly rocks (paper-coals) that is situated within the limestone beds of the Msta Formation. The specimen consists of a part and its counterpart with the phytoleim and the cuticle of leaf cushions. Although the rock is significantly pyritized, some elements of the leaf cushions are exceptionally well preserved.

The phytoleims of the leaf cushions were macerated by conventional methods: first with nitric acid and then



10 μm
(a)
30 μm
(d)
30 μm
(b)
30 μm
(e)
100 μm
(c)
30 μm
(f)

with potassium hydroxide (KOH). The prepared specimens were studied with a light microscope (AXIOPLAN) and a scanning electron microscope (CAMSCAN). Some fragments of leaf cushions were placed on stubs for scanning electron microscopy without maceration. The photographs were made with a scanning electron microscope (CAMSCAN) and light microscopes (Laboval) and (Olympus SZ-6045).

MATERIAL

The material (collection, no. 297) is housed in the Department of Paleontology, Geological Faculty, Moscow State University (MGU).

SYSTEMATIC PALEOBOTANY

DIVISION LYCOPODIOPHYTA

CLASS ISOËTOPSIDA

Order Lepidodendrales

Family ?Lepidodendraceae Endlicher, 1836

Genus *Novgorodendron* Gordenko, O. Orlova et S. Snigirevsky, gen. nov.

Etymology. From the Novgorod Region and the Greek δενδρον(tree).

Type species. *Novgorodendron conophorum* sp. nov.

Diagnosis. Leaf cushions rounded-rhomboidal, inversely tear-shaped, basally abruptly converging, 10–11 mm wide and 10 mm high. Leaf scar in upper part of leaf cushion, transversely elongate, 4–5 mm wide and 2.5 mm high. Leaf trace scar in central region of leaf scar. Slender keel in lower part of leaf cushion. Infrafoliar bladder rounded or, rarely, rounded-triangular in middle part of leaf cushion. Ligule and parichnos not observed. Basally, leaf cushion with basal conical appendages; axial appendage most prominent. Epidermal cells polygonal with straight anticlinal walls. Cuticle of leaf cushion below leaf scar and basal conical appendages bears numerous rounded multicellular trichomes.

Species composition. Type species.

Comparison. *Novgorodendron* gen. nov. resembles the Carboniferous genus *Lepidodendron* in the position of the leaf scar (upper region of the leaf cushion), presence of a keel, and such epidermal characteristics as epidermis topography, shape of epidermal cells, and the morphology of trichomes of the lower region of the leaf cushion. However, the new genus differs from *Lepidodendron* in the shape of leaf cushions, presence of basal conical appendages (BCAs), and the absence of a ligule and parichnos. In addition, unlike *Lepidodendron*, the leaf cushion in *Novgorodendron* gen. nov. bears a solitary leaf trace scar, whereas *Lepidodendron* has a leaf trace scar and a pair of parichnos. The genus under study is close to the Early Carboniferous genus *Valmeyenodendron* Jennings from the Illinois Basin of North America (Jennings, 1972) in the position of the leaf scar (in the uppermost part of the leaf cushion), presence of a solitary central scar, and the absence of a ligule pit and parichnos. However, the latter genus has a leaf cushion with its length exceeding its width that distinguishes *Valmeyenodendron* from the new genus, in which the length of the leaf cushion is equal to or shorter than the width, and the upper part of the leaf cushion is rounded and does not form an angle. Moreover, *Novgorodendron* gen. nov. differs from *Valmeyenodendron* in having trichomes.

The shape of the leaf cushions in the new genus resembles that of the Early Carboniferous genus *Lepidofloyos* Sternberg (from here on we use the valid spelling of this generic name, since exactly this spelling was used in the first description of this genus and therefore follows the principle of priority; Kvaček and Straková, 1997). However, the leaf scar is situated in the upper region of the leaf cushion in *Novgorodendron* gen. nov. and in the lower part in *Lepidofloyos*.

Novgorodendron gen. nov. differs from all genera mentioned above in having an infrafoliar bladder and BCAs.

Remarks. We faced a problem assigning *Novgorodendron* gen. nov. to a particular family, since, on the one hand, the remains of the new genus lack reproductive structures, and, on the other hand, the morphology of the leaf cushions (presence of BCAs) is very peculiar. We hope that further study of this locality may discover more remains of the genus, and the taxonomic position will be determined with more certainty. The morphological and micromorphological characters of the leaf cushion detected in the plant under study most closely resemble those of the Lepidodendraceae. Thus, the genus *Novgorodendron* gen. nov. is tentatively assigned to this family.

Let us consider characters that relate the plant under study to members of the Lepidodendraceae. The position of the leaf scar in the upper third of the leaf cushion and the presence of a trace on the leaf scar (this peculiarity proves that the leaf scar is not false; Meyen, 1990) relate *Novgorodendron* gen. nov. to *Lepidodendron*. We compared the plant under study and those members of *Lepidodendron* that most closely resemble this plant in morphology. Rounded-rhomboidal (inversely tear-shaped) leaf cushions, the pattern of relative

Fig. 1. *Novgorodendron conoforum* gen. et sp. nov., holotype, no. 297/1: (a) cutinized base of a trichome, inner surface of the cuticle, SEM; (b) trichomes covered with caps (middle part of a leaf cushion), SEM; (c) trichomes in the upper part of a leaf cushion, under the leaf scar, SEM; (d) partially destroyed trichomes in the middle part of a leaf cushion, SEM; (e) partially destroyed trichomes in the middle part of a leaf cushion, multicellular morphology is visible, SEM; and (f) depressions that mark the position of destroyed trichomes, SEM.

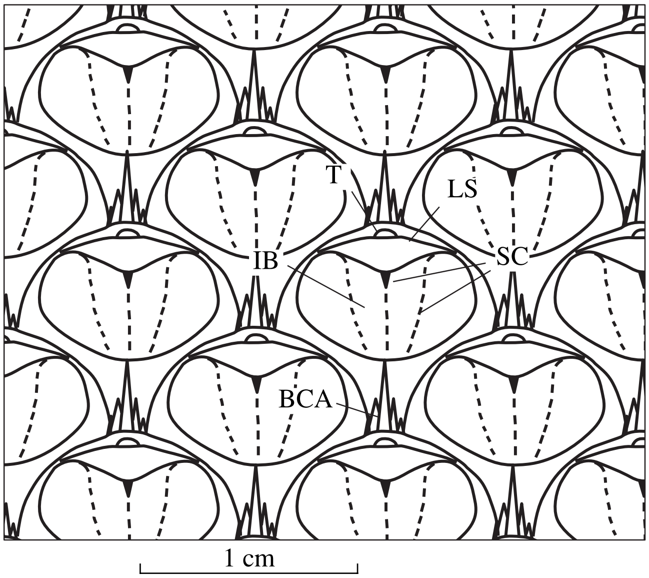


Fig. 2. Scheme of the surface of the outer bark of *Novgorodendron conophorum* gen. et sp. nov.: (BCA) basal conical appendages; (IB) infrafoliar bladder; (SC) secretory canal; (LS) leaf scar; and (T) trace.

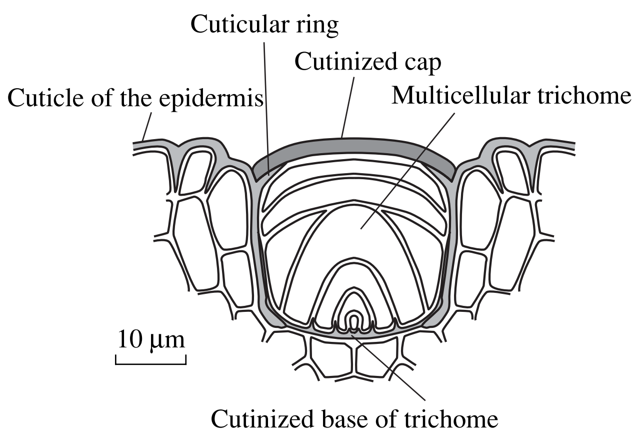


Fig. 3. Scheme of the trichome of *Novgorodendron conophorum* gen. et sp. nov. Cutinized regions are in black.

arrangement of the leaf cushions, and the position of the leaf scar in the very upper third of the leaf cushion are characters of *Novgorodendron* gen. nov. that most closely resemble the Euramerian primitive Carboniferous *Lepidodendron volkmannianum* Sternb. However, unlike *L. volkmannianum* Sternb., *Novgorodendron* gen. nov. lacks infrafoliar and leaf parichnos, and its keel is less prominent.

L. peariforme Liu et Zhao (Liu and Zhao, 2000) from the Carboniferous of China is similar to the plant under description in the shape and size of the leaf cushions and the leaf scar position, but differs in having distinct imprints of parichnos on the leaf scar. The plant studied superficially resembles imprints of "juvenile shoots of *Lepidodendron olivieri* Eichw." that were shown by Zalessky (1915, pl. 1, figs. 3, 3a, 3a^1, pl. 2, figs. 6a, 7, 7a). Indeed, the shapes of the leaf cushion and scar are similar to those in *Novgorodendron* gen. nov., but they are one-tenth of the size of those in our specimen. Moreover, the leaf scar of "juvenile shoots of *Lepidodendron olivieri* Eichw." is false, in contrast to *Novgorodendron* gen. nov., in which the leaf scar bears a definite trace that supports its true nature.

The presence of BCAs (their cuticular characteristics are identical to those of the central region of the leaf cushion), a new structural element that is unknown in any other Carboniferous lycopods, sharply differentiates *Novgorodendron* gen. nov. from all known Carboniferous lycopods. These structures probably enlarged the surface area of the leaf cushion.

The plant under study has several characters in common with the relatively primitive family Sublepidodendraceae Chaloner et Boureau (Boureau, 1967). Thus, the genus *Sublepidodendron* Hirmer is also characterized by the absence of a ligule and parichnos, but differs in the shape of the leaf cushion and position of the leaf scar. One more genus of this family, *Lepidodendropsis* Lutz (Lutz, 1933), is close to *Novgorodendron* gen. nov. in the position of the leaf scar that is situated in the very upper third of the leaf cushion. However, it differs in the epidermal structure (lacking trichomes) and the shape of the leaf cushions. Of interest is the fact that primitive Angarian lepidophytes *Tomiodendron* Radczenko, emend. S. Meyen, 1972; *Lophiodendron* Zalessky, emend. S. Meyen, 1976; and *Angarodendron* Zalessky, emend. S. Meyen, 1976, which are similar to the plant under study, have an infrafoliar bladder. However, unlike *Novgorodendron* gen. nov., they usually have a false leaf scar and ligule.

There are relatively few publications on the epidermal and cuticular structure of Carboniferous lepidophytes. Thomas devoted much attention to this question (Thomas 1970; Thomas and Masarati; 1982). In particular, he revealed that lepidophytes have the same type of epidermal morphology of leaf cushions and no distinguishing features of the generic rank (Thomas and Masarati; 1982). We fully share this view.

***Novgorodendron conophorum* Gordenko, O. Orlova et S. Snigirevsky, sp. nov.**

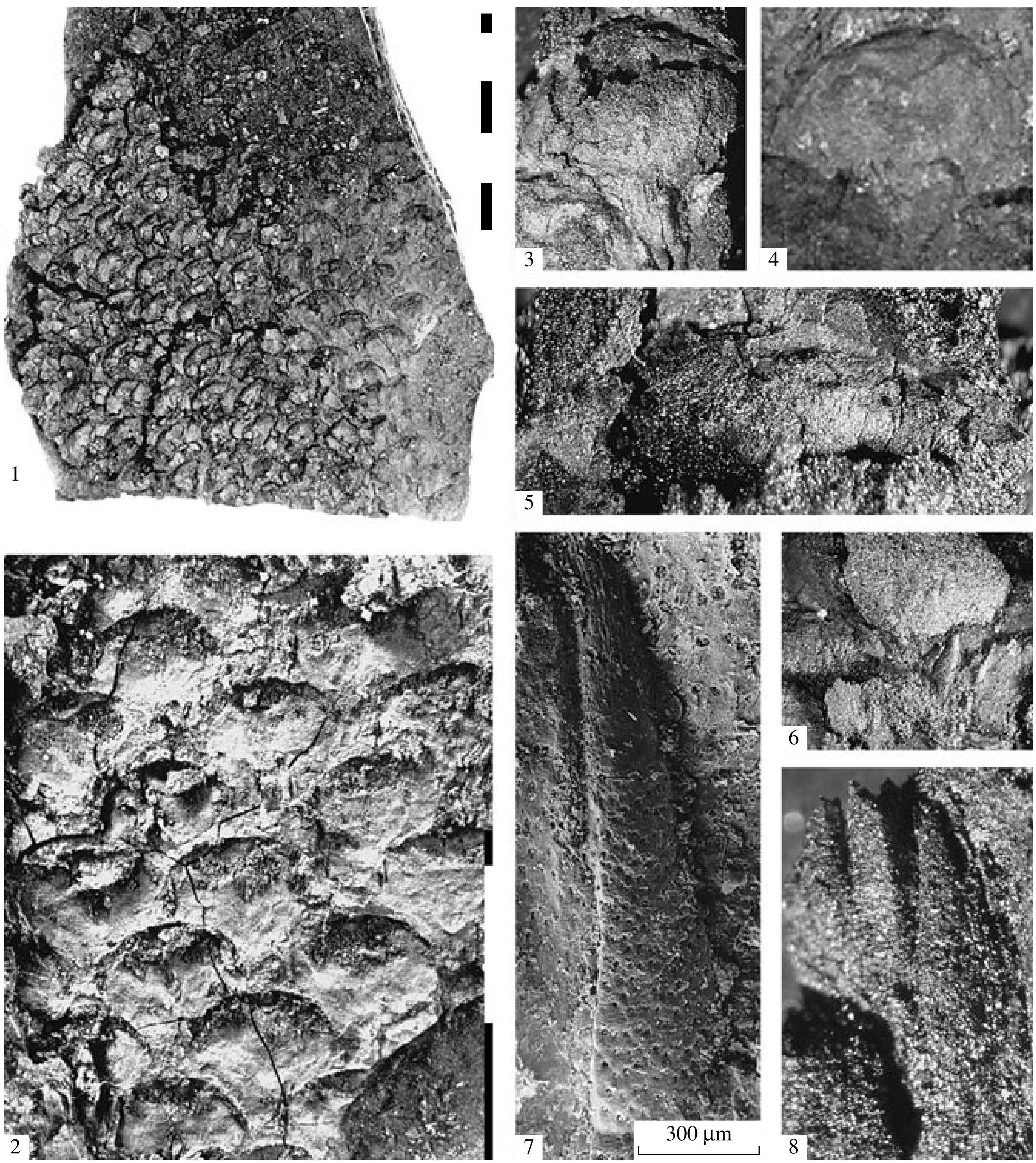
Plate 12, figs. 1–8; Plate 13, figs. 1–7

E t y m o l o g y. From the Greek χῶνος (cone) and φορά (to bear).

H o l o t y p e. Moscow State University (MGU), Geological Faculty, no. 297/1; Russia, Novgorod Region, vicinity of the town of Borovichi, Kamenka River locality, Lower Carboniferous, Upper Visean.

D e s c r i p t i o n (Figs. 1–3). The stem fragment reaches 100 mm long and 75 mm wide. It bears rounded, rhomboidal leaf cushions, which are abruptly constricted in the lower third and are arranged in paras-

Plate 12

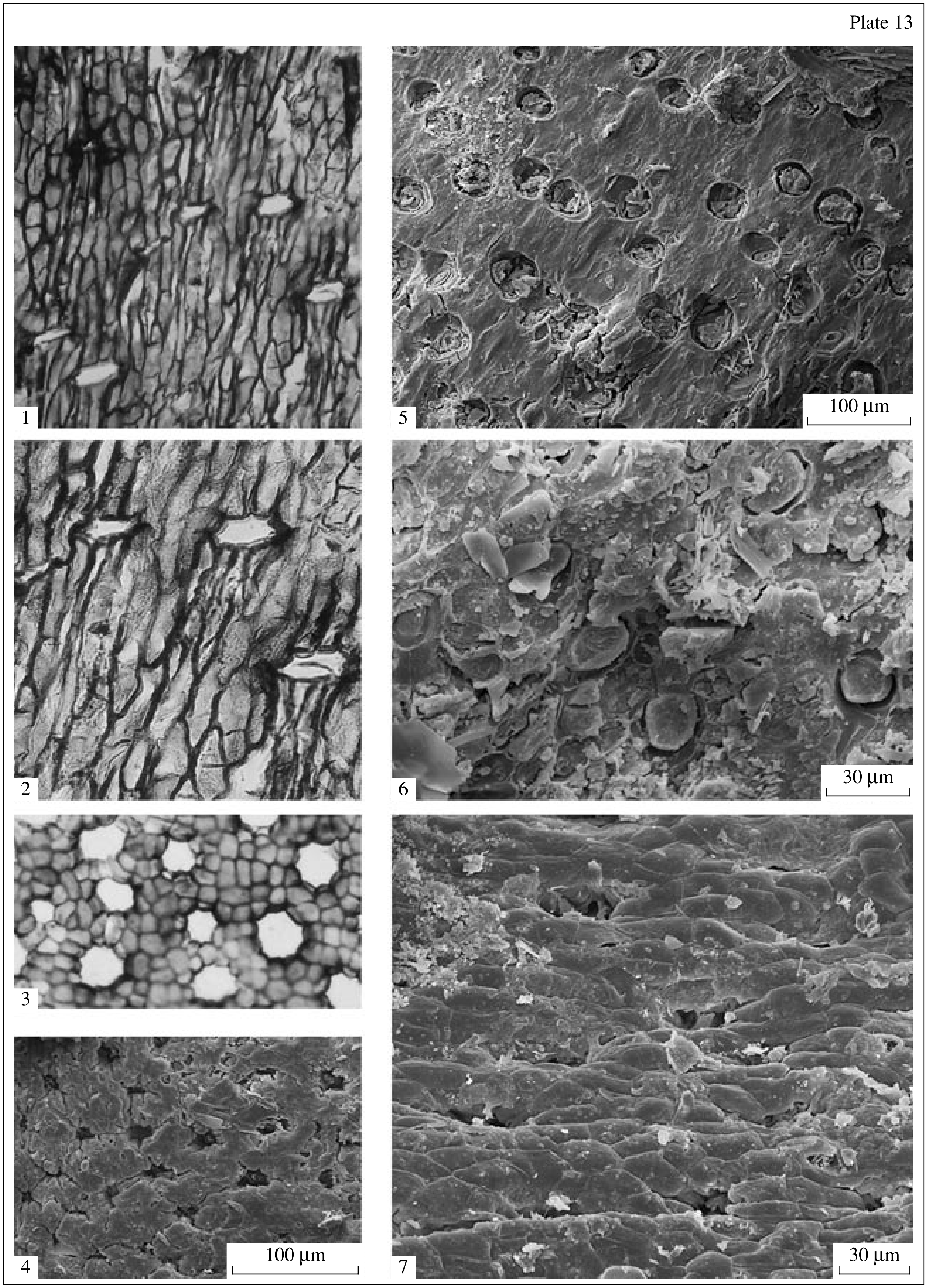


E x p l a n a t i o n   o f   P l a t e 12

Figs. 1–8. *Novgorodendron conoforum* gen. et sp. nov., holotype, no. 297/1: (1) a region of bark showing leaf cushions and their counterparts; (2) imprints of leaf cushions showing imprints of leaf scars; (3) leaf cushion showing scar with a trace, infrafoliar bladder, and a fragment of BCA, ×4.5; (4) imprint of a leaf cushion showing an imprint of a leaf scar and a secretory canal below, ×5; (5) a detail of the leaf cushion shown in Pl. 12, fig. 3 (leaf scar with a trace), ×10; (6) BCAs at the base of a leaf cushion, ×4.5; (7) BCA fused with a leaf cushion, SEM; and (8) three BCAs at the base of a leaf cushion, ×20.

The scale bar in figs. 1, 2 is 1 cm.

Plate 13



tichies (Fig. 2; Pl. 12, fig. 1). The lateral margins of the leaf cushions slightly overlap to form wings. The lateral angles of the leaf cushion are rounded; and the lower angle is pointed (Pl. 12, fig. 4). The leaf is approximately as wide as it is high: the average width is 10–11 mm, and the height is 10 mm. There is a leaf scar in the upper region of the leaf cushion. The leaf scar is a transversely elongated rhombus 2.5 mm high and 4–5 mm wide (Pl. 12, figs. 3–5). The lateral angles of the scar are pointed, and the upper and lower angles are arched. An elevation runs between the lateral angles, in the middle of which a 0.2-mm triangular trace is seen (Pl. 12, fig. 5). A thin keel is situated below the leaf scar. The keel is detectable only on counterparts under the cuticle and represents a hollow tube (Fig. 2). Laterally, two similar keel-like structures are present (Pl. 12, fig. 4). In addition, the leaf cushion has basal appendages shaped like elongated cones (Pl. 12, figs. 6–8). Each cushion bears three or more BCAs; the axial BCA is longer than the other BCAs and covers the base of the keel. The length and width of the axial BCA are 3.5–4 mm, and those of the lateral BCAs are 1–3 mm. A rounded or, more rarely, rounded-triangular infrafoliar bladder is situated in the middle part of the leaf cushion and is composed of spongy parenchyma (Pl. 12, fig. 3). Areas between cushions are not developed; ligule and parichnos were not found.

The cuticle of the leaf cushion is resistant to maceration and has a finely granular texture (Fig. 1a). The outer cells of the epidermis below the leaf scar, at the very base of the leaf cushion (under BCAs), are strongly laterally elongated and show traces of incomplete divisions of cells (Pl. 13, figs. 1, 3); thus, this region of the leaf cushion grew very rapidly. The cells are up to 60 μm long and 10–20 μm wide. The thickness of anticlinal walls is 0.75–1.5 μm. Occasional cup-like depressions are found (Fig. 1a; Pl. 13, fig. 3), in which trichomes are sunken. Outer epidermal cells hang over the depressions. The diameter of trichomes in this region of the leaf cushion is 10–25 μm.

The cells of the central and marginal parts of the leaf cushion are rounded, triangular–octagonal, and vary from nearly isometric to slightly elongated along the growth direction of the leaf cushion (Pl. 13, figs. 5, 6). The periclinal walls are convex (Pl. 13, fig. 7) or flat (Fig. 1b). The cells are 8–25 μm wide and 10–30 μm long. The thickness of anticlinal walls is about 1.5 μm. Trichomes are numerous, arranged in uneven longitudinal rows, which slightly curved during the growth of the leaf cushion. The trichomes are 25–35 μm in size. The distance between the nearest trichomes in the same row is equal to that between the closest trichomes of two adjacent rows: 30–50 μm.

Below the leaf scar (in upper third of the lower region of the leaf cushion), epidermal cells are more or less elongated with flat or concave periclinal walls (Figs. 1c–1f). Epidermal cells become nearly rhomboidal or fusiform. The width of the cells is 8–25 μm, and the length is 8–45 μm. The trichomes of this region of the leaf cushion are usually destroyed and are represented by shallow rounded or oval cutinized depressions (Fig. 1f; Pl. 13, fig. 2). Concentric thickenings are seen in these depressions. These are remnants of the walls of cells that constituted the trichomes. The diameter of trichomes is 30–45 μm. The distance between the rows of trichomes is larger: up to 60–100 μm.

Trichomes of *Novgorodendron conophorum* gen. et sp. nov. are multicellular. They are situated in cutinized depressions of the epidermis (Fig. 3) and are dissolved during maceration. They were held in the depressions by a cuticular ring and were covered with cutinized caps (Figs. 1b, 3; Pl. 13, fig. 4). They initiated in the marginal regions of the leaf cushion and were functional only in its lower third. Under the leaf scar, trichomes disintegrated, and outer epidermal cells died off (judging from their strongly concave periclinal walls, Fig. 1a).

No ligule pit was observed.

M a t e r i a l. Three specimens represented by parts, counterparts, and phytoleims of outer bark from the type locality.

DISCUSSION

Since both the keel and keel-like structures are not visible on the upper relief of the leaf cushions, but are detectable as tubes on counterparts directly under the cuticle, we believe that they could have been secretory canals. Keel-like structures that are visible in some imprints of leaf cushions of *Novgorodendron conophorum* gen. et sp. nov. closely resemble structures that are observable on bark imprints of *Lepidodendron volkmannianum* and are traditionally interpreted as infrafoliar parichnos. The mode of preservation of secretory canals in *Novgorodendron conophorum* gen. et sp. nov. suggests that they did not penetrate deep into the leaf cushion, but occupied a near-surface position. It is very possible that parichnos in leaf cushions of *Lepidodendron volkmannianum* were similarly situated; i.e., they

E x p l a n a t i o n o f P l a t e 13

Figs. 1–7. *Novgorodendron conoforum* gen. et sp. nov., holotype, no. 297/1: (1) cuticle of the base of a leaf cushion showing weakly cutinized bases of trichomes, ×600; (2) the same, a detail showing unfinished divisions of outer epidermal cells and a ridge on the cuticle of the base of a trichome, ×870; (3) upper surface of the cuticle of the central region of a leaf cushion showing remnants of trichomes as depressions, ×260; (4) incipient trichomes in the marginal zone of a leaf cushion, SEM; (5) surface of a leaf cushion under the leaf scar showing outer epidermal cells with flat periclinal walls and destroyed trichomes, SEM; (6) caps that cover trichomes (periclinal walls of epidermis are destroyed), SEM; and (7) outer epidermal cells with convex periclinal walls showing depressions where trichomes are sunken, SEM.

were not parichnos *sensu stricto*. As a result, identification and interpretation of seemingly usual structures in the Lepidodendrales present problems. This fact supports the necessity to revise the concept of leaf cushion morphology in the Lepidodendrales.

Most likely, no ligules existed on the leaf cushion of *Novgorodendron conophorum* gen. et sp. nov. However, it is not to be supposed that this plant was devoid of ligules. It is worth noting that the infrafoliar bladder is exceptionally well preserved: its well-preserved three-dimensional structure is lenticular in cross section. Below the infrafoliar bladder, there is a layer of prosenchymal cells. The presence of an infrafoliar bladder excludes the presence of infrafoliar parichnos.

The cuticle characteristic of areas between cushions is absent in *N. conophorum* gen. et sp. nov. The cuticle of the leaf cushion shows clear indications of growth. Thomas and Masarati (1982) hypothesized that there were two strategies of surface expansion during growth in the Lepidodendrales: in some members leaf cushions overgrew (*Lepidodendron*), in others overgrowth took place in areas between cushions (*Lepidodendron*). We believe that at early stages of stem growth cushions overgrew and, later, the overgrowth was accomplished at the expense of overgrowing areas between leaf cushions. Therefore, there was no significant difference between *Lepidophloyos* and *Lepidodendron* in the growth of spaces between leaf cushions during the secondary thickening. Consequently, *Novgorodendron conophorum* gen. et sp. nov. is a juvenile shoot.

Thomas (1970) and Thomas and Masarati (1982) considered depressions in the cuticle of the epidermis of leaf cushions as sunken stomata. Our results questioned the presence of stomata on leaf cushions of the Lepidodendrales. By maceration, we obtained well-preserved cuticles of leaf cushions with numerous cutinized depressions that are undistinguishable from those in members of the genus *Lepidodendron*. The cuticle of the depressions is considerably thinner than that of outer epidermal cells and, therefore, is easily damaged during maceration. However, in places, it is evident in transmitted light that the cuticle of the depressions is continuous and occasionally bearing a thickened shaped like an irregular incomplete ring or a middle ridge (Pl. 12, fig. 3). The cutinization in the depression resembles the guard cells of a stoma, and, if so, the thickened structures are inner cuticular ridges of these cells. This view was supported by Thomas (Thomas, 1970; Thomas and Masarati, 1982). The epidermis of the Lepidodendrales was studied not only by means of epidermal-cuticular analysis, but also in thin sections of coal balls. Snigirevskaya (1964, p. 17) studied leaf cushions of Carboniferous *Lepidodendron vasculare* Binney from coal balls of the Donets Basin and described very large peculiar cells "that resemble stomata in top view" on the surface of leaf cushions. Scanning electron microscopy, if applied without maceration, reveals a more complicated pattern. The depressions were occupied not by a single large cell, but by multicellular trichomes that are unstable to maceration. Some sections of leaf cushions clearly show that these structures had complex morphology and were composed of several cells (Figs. 1d–1f; Pl. 13, figs. 2, 4). A cuticular ridge that is prominent on the outer and inner sides of the trichome depression corresponds not to the margin between the guard cells of a stoma, but to the anticlinal wall between the cells at the base of a trichome. For example, this is the case of salt glands in some modern plants (Esau, 1977). Trichomes that are better preserved are covered with rounded cutinized caps.

Morphologically, these trichomes resemble absorbing hairs and, as previously mentioned, salt glands of some modern plants. Both variants of functions are applicable to members of the Lepidodendrales, which grew in areas with a constant shortage of fresh groundwater. Using trichomes, these plants might have excreted excess salts or, otherwise, absorbed atmospheric water that condensed on the stems.

ACKNOWLEDGMENTS

The authors are thankful to A.A. Kuz'makov (St. Petersburg State University, SPSU) for providing the material for the study, to Yu.V. Savitskii (SPSU) for valuable discussion on the stratigraphy of the region, and to V.A. Krassilov (Paleontological Institute, PIN), N.P. Maslova (PIN), and A.Yu. Jurina (MGU) for valuable suggestions. The study was supported by the Russian Foundation for Basic Research, project nos. 03-04-49351 and 03-05-64794.

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