

A New Species of the Conifer Genus *Oswaldheeria* with Well-Preserved Leaf Anatomical Elements from the Bathonian of the Kursk Region

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Abstract—A new species, *Oswaldheeria eximia* sp. nov., was discovered in the Bathonian continental deposits of an open-cast mine of Mikhailovskii Rudnik Mines, near the town of Zheleznogorsk in the Kursk Region. This is the first record of *Oswaldheeria* Bose et Manum from European Russia. The leaf anatomy of *Oswaldheeria*, reconstructed for the first time based on material of unique preservation, has shown that members of this genus were not closely related either to the Ginkgoales or to modern *Sciadopitys* Siebold et Zucc.

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Key words: Jurassic, leaf anatomy, gymnosperms, European Russia.

INTRODUCTION

The genus *Oswaldheeria* was erected by Bose and Manum (1990). In the same paper, these authors proposed a new family, Miroviaceae, for leaves of *Sciadopitys*-like morphology and placed the genera *Sciadopityoides* Sveshn., *Mirovia* Reymanówna, *Holcopitys* Bose et Manum, and *Oswaldheeria* in this family (Sveshnikova, 1981; Reymanówna, 1985; Bose and Manum, 1990; Manum et al., 2000). The species composition and geographical occurrence of *Oswaldheeria* were detailed by Nosova (2001). Later, Bose and Manum (1991) assigned the genus *Tritaenia* Mägdefrau et Rudolf (Mägdefrau and Rudolf, 1969) to the family Miroviaceae. Originally, the type genus of the family, *Mirovia* Reymanówna, was attributed to the Ginkgoales (Reymanówna, 1985). There is an opinion that the Miroviaceae is a conifer family closely related to the Taxodiaceae (Manum et al., 2000), although Bose and Manum established the family Miroviaceae based on significant differences between the leaves they studied and leaves of *Sciadopitys*. Currently there has been a tendency to place Miroviaceae into the Sciadopiaceae as a subfamily (Hvalj, 1997; Nosova, 2001). It should be noted that this family was erected based on general leaf morphology and micromorphology of the epidermis as a sole basis of classification. To date, no reproductive organs reliably related to leaves of this type are known. Accordingly, I prefer for the present to apply the term group rather than family to the Miroviaceae.

The discovery of leaf remains with well-preserved anatomical characteristics clarifies the position of the Miroviaceae within the system of gymnosperms.

MATERIAL AND METHODS

The material was collected in 2003 by the author from the continental Bathonian deposits of the Mikhailovskii Rudnik locality, near Zheleznogorsk in the Kursk Region. The plant remains come from cross-bedded fine- to medium-grained loosely consolidated quartz sandstones and from lignite layers, where abundant plant assemblages were formed. The material consists of leaf phytollems with well-preserved anatomical elements.

The phytollems were macerated by the standard method with nitric acid followed by KOH. The specimens obtained were first studied under an AXIOPLAN-2 light microscope and then under a CAMSCAN scanning electron microscope. In addition, some leaf fragments were not macerated before an SEM examination. Photomicrographs were taken through a CAMSCAN scanning electron microscope and light microscopes (Laboval and AXIOPLAN-2).

MATERIAL

Collection no. 5137 is housed in the Paleontological Institute of the Russian Academy of Sciences (PIN), Moscow.

SYSTEMATIC PALEOBOTANY

CLASS PINOPSIDA

Order Pinales

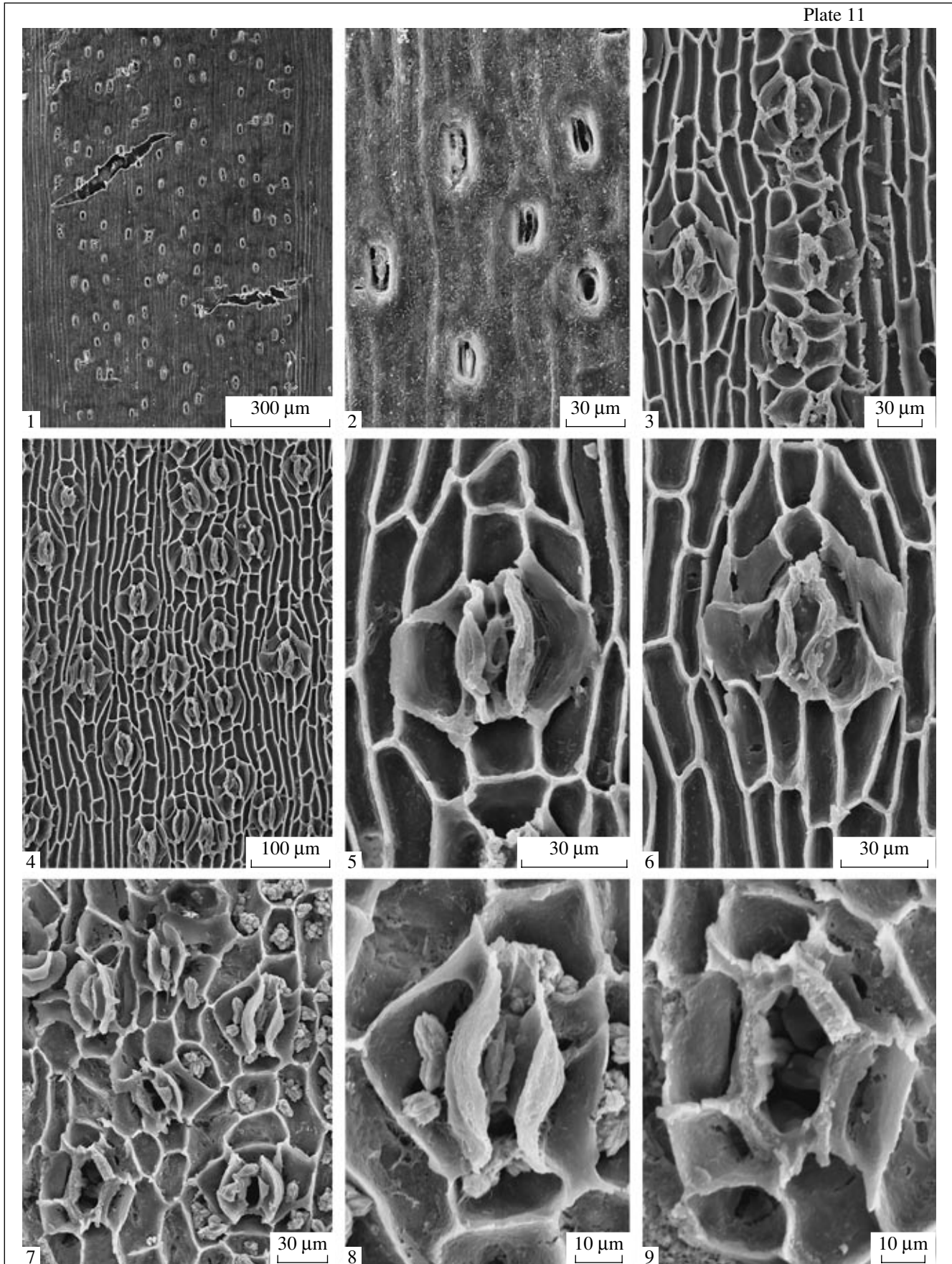
Family Miroviaceae Bose et Manum, 1990

Genus *Oswaldheeria* Bose et Manum, 1990

Oswaldheeria eximia Gordenko, sp. nov.

Plate 11, figs. 1–9; Plate 12, figs. 1–8

E t y m o l o g y. From the Latin *eximia* (excellent).



Holotype. PIN, no. 5137/1; phytolaim of a leaf fragment; northern open-pit mine of Mikhailovskii Rudnik Mines (Zheleznogorsk), Kursk Region; Middle Jurassic, Bathonian; Fig. 1q.

Diagnosis. Long linear leaves up to 150 mm long, 1–2 mm wide, with two veins and three intercostal resin ducts immersed in mesophyll, conspicuous in macerated leaves. Leaf apex rounded. Epidermis hypostomous. Lower cuticle thinner than upper, with one median stomatal zone. Upper surface of cuticle of stomatal zone distinctly ridged, that of nonstomatal zones ornamented by thin parallel ridges. Stomata longitudinally or, more rarely, obliquely orientated, monocyclic, incompletely amphicyclic, seldom amphicyclic. Subsidiary cells four to seven, non-papillate.

Short leaves 1–3 mm wide, 4–10 mm long, with two veins and three intercostal resin ducts. Leaf apices obtuse or rounded. Epidermal cells of stomatal zone have prominent periclinal walls. Subsidiary cells with prominent periclinal walls or with large hemispherical papillae.

Description (Figs. 1, 2). The collection contains numerous fragments of linear leathery leaves with a rather distinct median groove (Figs. 1k–1m, 1q) and short elliptical leaves with rounded apices gradually narrowing towards the base (Figs. 1a, 1e, 1f, 1g–1j, 1n–1p). The bases of the short leaves are widened and rounded (Figs. 1a, 1e, 1f). The bases of the long leaves have not been preserved. The width of leaves in the middle area ranges from 1 to 3 mm. The maximum length (revealed by a leaf impression and fragmentary phytolaims) is 150 mm, with a width of 2 mm. No venation is observed on the lower surface of either short or long leaves. In transverse sections and with the cuticle removed by maceration, two parallel non-inverted collateral conducting bundles and three intercostal resin ducts are visible (Pl. 12, figs. 3, 4; Fig. 2). The diameter of the conducting bundles is 80–85 μm . In conducting bundles, xylem elements are represented by protoxylem and metaxylem (Pl. 12, figs. 5, 7, 8). Metaxylem tracheids are supplied with inner spiral thickenings and araucarioid pitting (Pl. 12, fig. 8). Conducting bundles have a thin lining of mechanical tissue (Pl. 12, figs. 5, 6). The hypodermis consists of large rectangular cells, longitudinally elongated, 30–140 μm long, and 7–50 μm wide (Pl. 12, figs. 1, 7). The mesophyll of the leaf blade is more or less distinctly differentiated into palisade and spongy mesophylls (Pl. 12, figs. 2, 3, 5, 6), often with sclereids in the palisade mesophyll (Pl. 12, figs. 2, 7). The length of the cells of palisade mesophylls is 40–140 μm . Transfusion tissue is situated under conduct-

ing bundles (Pl. 12, fig. 3; Fig. 2). Endoderm was apparently lacking. Leaves are hypostomous. The cuticle is thick and maceration-resistant. The thickness of the upper cuticle is 5 μm on average but may reach up to 15 μm . The upper epidermis is formed of longitudinally elongated tetra- or pentagonal cells with slightly rounded corners, 30–60 μm long, and 10–20 μm wide. The anticlinal walls of the cells are straight or, more rarely, slightly curved. The outer surface of the upper epidermis and the marginal zones of the lower epidermis of the long leaves bears thin continuous longitudinal cutin strands (Pl. 11, fig. 1; Pl. 12, figs. 2, 4). In short leaves, no cutin strands have been found on the surface of the upper epidermis or on the marginal zones of the lower epidermis (Figs. 1a, 1b). Trichomes are lacking.

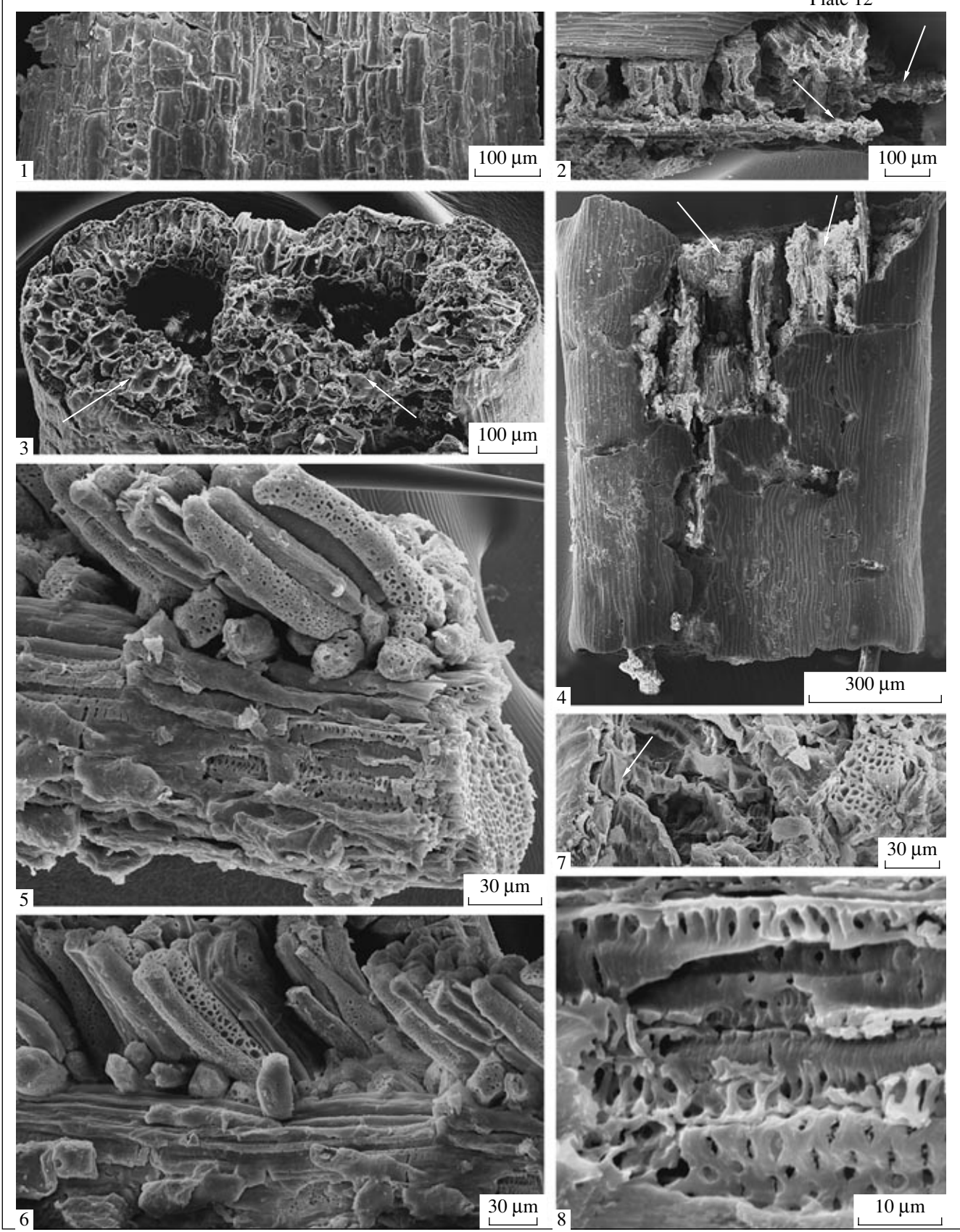
The lower cuticle of the marginal zones of the leaf is as thick as the upper cuticle, but becomes much thinner in the stomatal zone. A solitary stomatal zone is clearly visible on the lower epidermis, 450–600 μm wide in the long leaves and 750–2500 μm wide in the short leaves. The width of the marginal non-stomatal zones is about 300 μm in both types of leaves (Pl. 11, fig. 1; Figs. 1a, 1b, 1f, 1g, 1n, 1o). The ordinary epidermal cells have straight or weakly sinuous anticlinal walls and smooth periclinal walls. The epidermal cells located in the stomatal rows are rounded-rectangular or hexagonal. Usually, they are nearly isodiametric or slightly transversely (or, more rarely, longitudinally) elongated, 10–30 μm long and 15–20 μm wide. There are 10–15 stomatal rows within the width of the stomatal zone in the long leaves and 15–20 rows in the short leaves. The epidermal cells that are situated between the stomatal rows are longitudinally elongated, wedge-shaped, rectangular, or fusiform, 20–120 μm long, and 10–20 μm wide. The periclinal walls of the ordinary epidermal cells are flat in the long leaves and convex in the short leaves (Figs. 1c, 1d).

Within the stomatal zone, the stomata are arranged in longitudinal rows of different length (Pl. 11, figs. 3, 4, 7). The stomata are incompletely amphicyclic (Pl. 11, figs. 3, 6; Fig. 1s), monocyclic (Pl. 11, figs. 5, 8, 9), or, more rarely, amphicyclic. The outer periclinal walls of the guard cells are winged, with their outer margins often bent inwards (Pl. 11, figs. 5, 6, 8). The guard cells are more or less uniformly cutinized. The circumapertural rim is distinct (Pl. 11, figs. 5, 8). The guard cells are 40–45 μm long and 35–40 μm wide. The polar extensions are broad, long, with a thin median fringe (Pl. 11, figs. 5, 8). The polar extensions are 10 μm wide and 15 μm long.

Explanation of Plate 11

Figs. 1–9. *Oswaldheeria eximia* sp. nov., SEM: (1–6) holotype PIN, no. 5137/1; (1) stomatal zone and marginal zones of a long leaf; (2) stomatal apparatuses with Florin rings, long leaf; (3) anomalous stomata of a long leaf, inner surface of the cuticle; (4) epidermis topography in the area of a stomatal zone; (5) normal monocyclic stoma; (6) anomalous incompletely amphicyclic stoma; (7–9) PIN, no. 5137/4; (7) fragment of a stomatal zone, short leaf; (8) stoma; and (9) stoma, guard cells were removed to show papillae on subsidiary cells.

Plate 12



The guard cells of the stomatal apparatus are surrounded by two to four lateral subsidiary cells and two or three polar subsidiary cells, which in long leaves form a Florin ring over the aperture (Pl. 11, fig. 2). In short leaves, the periclinal walls of the subsidiary cells are either swollen (Fig. 1c) or have large wrinkled arcuate papillae (Fig. 1d). There are two or three encircling cells. Trichomes are lacking.

C o m p a r i s o n. The epidermal morphology of the long leaves of *O. eximia* sp. nov. closely resembles that of *O. scotica* (Florin) Bose et Manum from the Upper Jurassic of Scotland, *O. hallei* (Florin) Bose et Manum from the Lower Cretaceous of Arctic Canada and Spitsbergen (Bose and Manum, 1990), *O. orientalis* Nosova from the Lower Cretaceous of the Primorye Region (Russian Far East), and *O. neosibirica* (L.N. Abramova) Nosova from the Cretaceous of the New Siberian Islands (Nosova, 2001). In *O. orientalis* and *O. neosibirica*, Nosova (2001) pointed out the presence of cutin ridges on ordinary epidermal cells of both lower and upper faces of the leaf blade. This feature most probably also occurs in other species. In particular, I have found it in *O. eximia* sp. nov.

However, the short leaves of *O. eximia* sp. nov. differ from the long leaves in epidermal structure (swollen periclinal walls of epidermal cells and papillae on subsidiary cells). Papillae on subsidiary cells are known in *O. macrophylla* (Florin) Bose et Manum from the Middle Jurassic of northern Norway and the Lower Cretaceous of western Siberia, in *O. arctica* Bose et Manum from the Lower Cretaceous of Arctic Canada (Bose and Manum, 1990; Nosova, 2001), and *O. samylinae* (Sveshnik.) Hvalj from the Lower Cretaceous of eastern Siberia (Hvalj, 1997).

In all the other *Oswaldheeria* species the short and long leaves are identical in epidermal morphology. Therefore, the species described combines characters that usually occur in different species. Moreover, the long leaves of *O. eximia* sp. nov. are nearly twice as long as the leaves of *O. scotica*, which were previously considered to be the longest leaves in this genus.

R e m a r k s. The differences between the epidermal characters of the short and long leaves of the species described are remarkable. The short and long leaves might have been considered as two separate species. However, heterophylly is characteristic of the genus *Oswaldheeria*, and the short and long leaves have been found in association. Moreover, swellings and papillae are lacking on the inner surface of the epidermis (a

character that is also typical of the genus *Tritaenia*), and the micromorphology of stomatal apparatuses, as seen on the inner face of the epidermis, is identical in short and long leaves, that is a significant argument to refer the remains under consideration to one species.

The system of the genus *Oswaldheeria* requires a revision of the taxonomic values of epidermal characteristics. Thus, my observations show that elements described by Nosova (2001) as cuticular ribs and rims on epidermal cells in fact represent an outer sculpture consisting of thin elongated longitudinal cutin ribs that are longer than the epidermal cells. Such thin cutin ribs are characteristic of most conifers.

M a t e r i a l. Numerous fragmentary leaf phytolites from the type locality.

DISCUSSION

Recent data suggest that Miroviaceae were important in plant communities of the Northern Hemisphere both in Early Cretaceous and Middle Jurassic times, i.e., from their first appearance in the geological record. Gordenko (2004a, 2004b) has showed that members of this group occurred in European Russia in the Middle Jurassic. Nowadays, the systematic position of the Miroviaceae is still a matter for discussion. Although the type genus of the family was originally attributed to the Ginkgoales (Reymanówna, 1985), most scientists are inclined to assign this family to conifers.

The anatomical study of *Oswaldheeria eximia* sp. nov. has revealed that *Oswaldheeria* had two conducting bundles, as Bose and Manum (1990) supposed. At first glance, this fact in combination with the presence of a solitary stomatal zone may support a relationship with *Sciadopitys*. However, the present study has revealed that these two conducting bundles were not inverted; therefore, the leaves of this genus cannot be considered an analogue of the very peculiar double leaves of *Sciadopitys*. In the present case, two conducting bundles are evidence of a many-veined leaf blade, a character better developed in *Tritaenia*, which has more than two veins (Gordenko, 2004a, 2004b). There is a close similarity in the ratio between resin ducts and conducting bundles to the Pseudotorelliaceae, Araucariaceae, and some members of the Podocarpaceae.

The group "Miroviaceae" resembles the Ginkgoales and Araucariaceae, and considerably differs from the modern Podocarpaceae, in the pitting of the tracheids in the conducting bundles. However, the position of the

Explanation of Plate 12

Figs. 1–8. *Oswaldheeria eximia* sp. nov., SEM: (1, 2, 4–6, 8) PIN, no. 5137/8; (1) hypodermis of a long leaf (cuticle and epidermis is removed); (2) longitudinal section of a long leaf fragment, note two resin ducts and sclereids in mesophyll; (3) holotype PIN, no. 5137/1, transverse section of a long leaf (mesophyll, two conducting bundles, and transfusion tissue under them are visible); (4) fragment of a long leaf, view from the stomatal side, note two conducting bundles and three resin ducts in the section; (5) fragment of a conducting bundle; (6) detail of fig. 5; (7) PIN, no. 5137/9, detail of a transverse section of a long leaf, note epidermis, hypodermal layer, sclereids, and a conducting bundle; and (8) detail of a conducting bundle, note inner spiral thickenings of tracheids and araucarioid arrangement of rounded bordered pits.

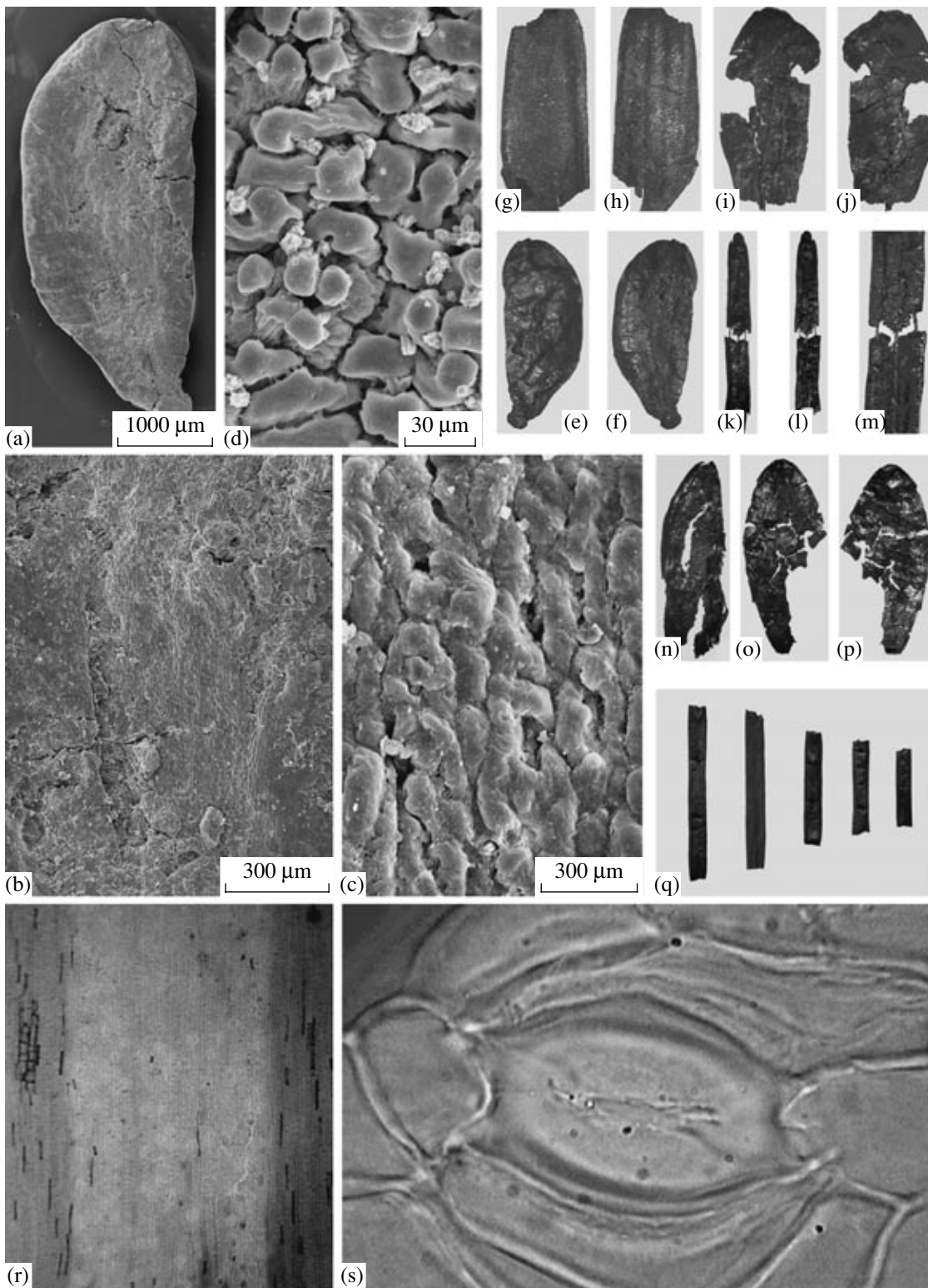


Fig. 1. *Oswaldtheeria eximia* sp. nov.: (a–c, e) PIN, no. 5137/2; (a) completely preserved short leaf, note the stomatal zone, SEM; (b) detail of the stomatal zone shown in Fig. 1a, SEM; (c) stomata with swollen periclinal walls of subsidiary cells, SEM; (e) lower face of a leaf, $\times 7.8$; (f) fragment of a short leaf, lower face, $\times 7.8$; (d, g, h) PIN, no. 5137/4; (d) stomata with papillose subsidiary cells, SEM; (g) short leaf, lower face, $\times 3.5$; (h) the same leaf as shown in Fig. 1g, upper face, $\times 3.5$; (i, j) PIN, no. 5137/3; (i) short leaf, note three resin ducts, $\times 5.3$; (j) the same, lower face, $\times 5.3$; (k–m) PIN, no. 5137/7; (k) short leaf fragment, lower face, $\times 4$; (l) apex of a long leaf, lower face, note three resin ducts, $\times 4$; (m) apex of a long leaf, upper face, $\times 12$; (n) PIN, no. 5137/5, fragment of a short leaf, note a stomatal band, $\times 4.6$; (o, p) PIN, no. 5137/6; (o) short leaf, lower face, $\times 3.1$; (p) upper face, $\times 3.1$; (q–s) holotype PIN, no. 5137/1; (q) fragments of the same long leaf, $\times 3.3$; (r) cuticle of a long leaf, the cuticle is thinner in the stomatal zone than in the marginal zones, $\times 44$; (s) incompletely amphicyclic stomatal apparatus, $\times 2000$.

transfusion tissue relative to the conducting bundle in the Miroviaceae differs from all the three above-listed taxa. In the Ginkgoales, the transfusion tissue forms a continuous ring around the conducting bundle, unlike *Oswaldheeria* where it is situated below the conducting bundles. In the Araucariaceae and Podocarpaceae, a distinct mass of sclerified mechanical tissue adjoins the conducting bundle, whereas in *Oswaldheeria* the mechanical tissue is nearly non-sclerified and forms only one layer around the conducting bundle, overlain by mesophyll and underlain by transfusion tissue. *Oswaldheeria eximia* sp. nov. has hypodermis; however, it is composed of fairly large peculiar rectangular cells forming no hypodermal strands (Pl. 12, figs. 1, 7). The modern *Ginkgo biloba* L. and the majority of modern conifers (in particular, the Podocarpaceae, Araucariaceae, and Sciadopityaceae) have hypodermal strands.

The morphology of the bases of the short leaves of *Oswaldheeria* (similar to that in the modern *Abies* Miller) suggests that they have no brachyblasts. The absence of brachyblasts is a convincing argument against a relationship between this genus and the modern *Sciadopitys*.

Gordenko (2004) showed that, in spite of some differences, there is much in common between *Tritaenia* and *Oswaldheeria* and the Podocarpaceae in their epidermal morphology. Numerous fragmentary trunks of *Podocarpoxyton* sp. found in the Mikhailovskii Rudnik locality in association with the foliage of *Oswaldheeria eximia* sp. also support this conclusion.

The main feature differentiating the “Miroviaceae” from the Araucariaceae and Podocarpaceae is deciduousness: the fact that all members of the group “Miroviaceae” were deciduous, unlike Araucariaceae or Podocarpaceae (except for *Agathis* Salisbury). The lifespan of a leaf in some members of the Araucariaceae and Podocarpaceae may reach several dozen years. Dead leaves are not shed, but decay attached to the twig. In some members of the Araucariaceae and Podocarpaceae, repeated shedding of leafy shoots takes place (Harris, 1976). In conifers *Taxodium* Richard, *Metasequoia* Miki, and *Glyptostrobus* Endlicher, shortened annual shoots develop, which shed at the end of the vegetative period. Hence, the group “Miroviaceae” differs from the majority of the Araucariaceae and Podocarpaceae as well as from the Taxodiaceae.

Seasonal deciduousness when a plant sheds all leaves at the end of the vegetative period is characteristic of some modern members of the Pinaceae: *Larix* Miller, *Pseudolarix* Gordon, and *Cathaya* Chun et Kuang. Seasonal deciduousness when only old dead leaves are shed is known in some members of the Pinaceae (e.g., *Picea* Dietrich and *Abies* Miller) and in the Taxaceae. These two types of deciduousness are extremely difficult to differentiate in fossil state, since in both cases significant agglomerations of shed leaves may be accumulated. The total absence of shoots in the burial or the occurrence of naked shoots in association

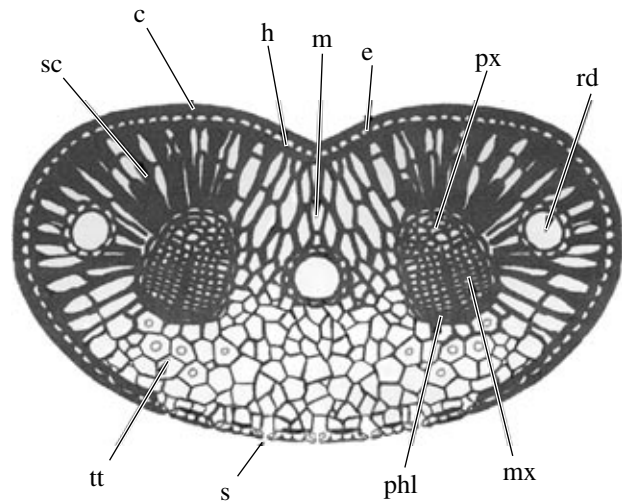


Fig. 2. Idealized transverse section of the leaf of *Oswaldheeria eximia* sp. nov.: (e) epidermis; (h) hypodermis; (m) mesophyll; (sc) sclereids; (tt) transfusion tissue; (px) protoxylem; (mx) metaxylem; (phl) phloem; (rd) resin duct; (c) cuticle; (s) stoma.

with shed leaves may serve as indirect evidence of complete seasonal leaf shedding (Harris, 1976). Bose and Manum (1990) described in *Oswaldheeria* a few fragments of naked shoots, which may indicate deciduousness of the first type. Other members of this group (*Mirovia* and *Sciadopityoides*) are characterized by the presence of shed leaves and small fragments of leafy shoots (Bose and Manum, 1990), implying incomplete shedding of leaves.

Of interest is the fact that complete leaf shedding is characteristic of the conifers with shortened shoots, and incomplete shedding is characteristic of the conifers without such shoots. The Ginkgoales, plants with brachyblasts, are characterized by complete seasonal shedding of leaves. Since there were definitely no shortened shoots in the Miroviaceae, it is most probable that these plants shed only a part of their foliage. Consequently, the Miroviaceae, the Taxaceae, and some Pinaceae constitute a single group according to their type of deciduousness.

The leaf micromorphology of Miroviaceae is quite diverse. The constant characters are hypostomous leaf blade, incompletely amphicyclic stomatal apparatuses, and wide guard cells of stomata with distinct polar extensions. Members of the Miroviaceae have some transitional epidermal characteristics. Thus, a leaf blade of *Tritaenia* usually has both monocyclic and amphicyclic stomata, i.e., the group “Miroviaceae” shows a transition from monocyclic to amphicyclic stomatal apparatuses. The former type of stomatal morphology is characteristic of the Pseudotorelliaceae and other members of the Ginkgoales, whereas the latter is typical of the Araucariaceae and Podocarpaceae. The orientation of stomata in the group varies from longitudinal and oblique (*Tritaenia*, *Oswaldheeria*, and *Hop-*

kopitys) to oblique and transverse (*Mirovia* and *Sciadopityoides*). The first type is characteristic of the Pseudotorelliaceae and Podocarpaceae, and the second is typical of the Araucariaceae.

Therefore, we are dealing with a quite independent group of gymnosperm plants (at least, judging from their leaf blade morphology), an affinity of which with the Ginkgoaceae and Sciadopityaceae lacks any supporting evidence.

The close resemblance of the Miroviaceae to the Podocarpaceae and *Araucariodendron* Krassilov (Krassilov, 1965, 1967) in stomatal morphology and the topography of the epidermis implies the parallel development of similar epidermal characters in these three groups.

The geographical distribution of Miroviaceae differs from that of Mesozoic Podocarpaceae. They occurred in relatively high latitudes of the Northern Hemisphere, not below the present-day 45° parallel. In the case of the Podocarpaceae, we can apparently assume their invasion from the south (through Central Asia and Japan). The Miroviaceae might have separated from ancient Podocarpaceae with subsequent isolation under new climatic conditions. Such isolation probably shaped the peculiar general outlook of the leaves, but did not change the wood anatomy.

As previously noted, so far the placement of *Tritaeonia* and morphologically close genera in a separate family Miroviaceae has appeared poorly justified, since the reproductive organs of these plants have not been adequately studied, and the classification of conifers at the level of families has been conventionally carried out based on reproductive characteristics. On the other hand, the accumulated data (including anatomical data) testify to the taxonomic uniqueness of this group, showing some similarities to the Podocarpaceae rather than being an ancestor of the modern *Sciadopitys*.

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