

A New Species of *Pachypteris* (Brongniart) Harris (Corystospermales) from the Bathonian Continental Deposits of the Kursk Region, Russia

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Abstract—A new species, *Pachypteris rutenica* sp. nov., is described from the Bathonian continental deposits of the Mikhailovskii Rudnik opencast mine, near the town of Zheleznogorsk in the Kursk Region of Russia. This is the first report of *Pachypteris* (Brongniart) Harris from European Russia. The systematics and ecology of the genus is discussed.

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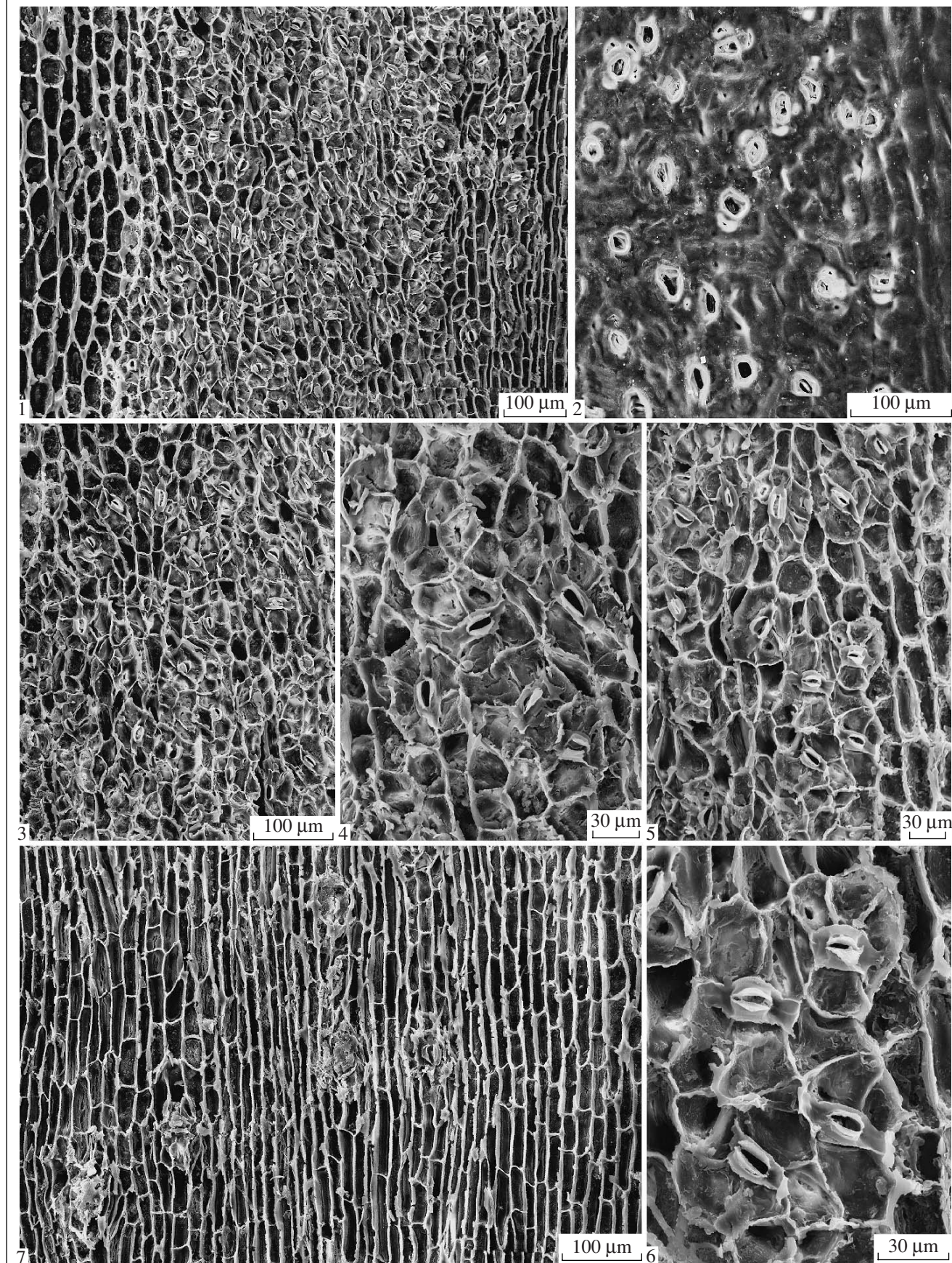
INTRODUCTION

Members of the genus *Pachypteris* are found for the first time in European Russia. Although the material under study seems fragmentary, it is interesting both from a systematic and a paleoecological perspective.

Pachypteris, with the type species *P. lanceolata* Brongniart, was established by Brongniart (1828) on the basis of poorly preserved fragmentary material, which led to further problems with application of this generic name and understanding of the composition of the genus. Thus, Ettingshausen (1952) erected the genus *Tinnfeldia* with the type species *T. rhomboidalis* Ettingshausen. Andrae (1855) believed that *Pachypteris* and *Tinnfeldia* were synonyms and transferred the type species *T. rhomboidalis* to *Pachypteris rhomboidalis* (Ettingshausen) Andrae. However, since the genus *Pachypteris* was insufficiently characterized, paleobotanists continued to describe new species of *Tinnfeldia*. A detailed morphological description of *Pachypteris lanceolata* and its emended diagnosis was published by Harris (1964), who also emended the generic diagnosis. It was again stated that the genera *Pachypteris* and *Tinnfeldia* were identical (Reymanówna, 1963; Harris, 1964), although not all species of *Tinnfeldia* were transferred to *Pachypteris*. Doludenko (Doludenko, 1969, 1971, 1974; Doludenko and Svanidze, 1969; Doludenko et al., 1998) studied the morphological variability and epidermal structure of the two genera, and showed that *Tinnfeldia* is a junior synonym of *Pachypteris*, and confirmed the correctness of the combination proposed by Andrae. However, she did not create new combinations for other species of *Pachypteris*, thus leaving the problem pending. Barbacka (1994) removed the genus *Komploteris* from *Pachypteris* (including *Tinnfeldia*).

Komploteris nordenskiöldii (Nathorst) Barbacka, transferred from *Pachypteris* (*Tinnfeldia*) *nordenskiöldii* (Nathorst) Doludenko, is the type species of *Komploteris*. Barbacka believed that wide costal non-stomatal zones in *Komploteris* that correspond to lateral veins is an important generic character, since Harris mentioned in the diagnosis of *Pachypteris* that stomata occur all over the surface, except the midrib. The consideration of data published by Doludenko (1969) and Doludenko and Svanidze (1969) shows that this character is very variable, and narrow or (more rarely) relatively wide non-stomatal zones correspond to lateral veins in segments of *Pachypteris*. It is not excluded that a wider non-stomatal zone is no more than a specific character. Other characteristics that were used to establish this genus are also equivocal. Thus, stomatal apparatuses in *Komploteris* differ from typical stomata of *Pachypteris*, but resemble those in *Cycadopteris* (Zigno) Barale. However, Popa (2000a) showed that *Pachypteris* is connected with *Cycadopteris* by transitional forms, having described *Pachypteris gradinarui* Popa from the Lower Jurassic of Romania. Consequently, such stomata occur in *Pachypteris* as well. One more character, the length and degree of dissection of segments, is also highly variable and cannot be used. Judging from the data by Doludenko and Svanidze (1969) on Callovian members of *Pachypteris* from Georgia, both bipinnate leaves with short and dissected segments and simple pinnate leaves with entire-margined segments occur in one species. In all probability, such a situation was normal for *Pachypteris*. However, transitional forms are not always traceable, and it is difficult to prove the relationship between extreme members of a row. Hence, species of *Pachypteris* described

Plate 7



to date are far from natural taxa representing relatively conventional morphotypes. All the above factors additionally complicate the uneasy understanding of the composition of the *Pachypteris*. Popa (2000a) reviewed in detail nearly all species of *Pachypteris* described to date.

Summarizing all of the above mentioned points, I adhere to the opinion that species of *Pachypteris* and *Tinnfeldia* should be treated as *Pachypteris*, and separation of the genus *Komploteris* by Barbacka (1994), is as yet poorly justified.

MATERIALS AND METHODS

The material was collected by the author, Valentin Krassilov, and Natalia Zavialova (Laboratory of Paleobotany, PIN) from the Bathonian continental deposits of the Mikhailovskii Rudnik locality, near the town of Zheleznogorsk (Kursk Region, Russia). The plant remains were extracted from cross-bedded fine- to middle-grained weakly cemented quartz sandstones as well as from lignite sublayers, where the plant remains formed mass agglomerations. The material is leaf phytoliteims with preserved anatomical elements.

The phytoliteims were macerated by conventional methods, using nitric acid and, then, alkali (KOH). The obtained specimens were studied with an AXIOPLAN light microscope and a CAMSCAN scanning electron microscope. Some leaf fragments were placed on stubs for scanning electron microscopy, without maceration.

The material is housed at PIN, collection no. 5137.

SYSTEMATIC PALEOBOTANY

Order Corystospermales

Family Corystospermaceae Thomas, 1933

Genus *Pachypteris* (Brongniart) Harris, 1964

Pachypteris rutenica Gordenko, sp. nov.

Plate 7, figs. 1–6; Plate 8, figs. 1–6

E t y m o l o g y. From the Latin *rutenica* (Russian).

H o l o t y p e. PIN, no. 5137/12, phytoliteim of a leaf fragment, northern opencast mine of the Mikhailovskii Rudnik locality, town of Zheleznogorsk, Kursk Region, Russia; Middle Jurassic, Bathonian; Figs. 1a, 1b.

D i a g n o s i s. Segments linear 10–54 mm long or longer and 2–5 mm wide. Segment apex rounded or acute. Midrib distinct on both upper and lower surfaces. Secondary veins simple or dichotomous, not visible macroscopically and usually also indistinct in lower

epidermis topography as costal non-stomatal zones. Epidermis hypostomous. Lower and upper cuticles 10–15 µm thick. Lower epidermis with two distinct stomatal zones. Stomata randomly orientated within stomatal zones, forming small groups. Stomata non-avoiding zones of secondary veins. Stomata mainly monocyclic, more rarely with one or two encircling cells or bicyclic. Subsidiary cells four to six, more rarely three or seven, with or without papillae. Some stomatal apparatuses share subsidiary cells. Guard cells sunken and finely cutinized. Covering cells of stomatal zones prominent, cuticle of non-stomatal zones with thin parallel ridges. Trichomes absent.

Description (Figs. 1–4). The collection contains numerous fragments of linear leathery leaf segments (Figs. 1a–1p), which are 10–54 mm long and longer, 2–5 mm wide in the middle area, with a more or less distinct keel on the lower surface, 0.6–1.8 mm wide (Fig. 1a), and a midrib 0.25–1.25 mm wide, which relieves over the upper surface (Fig. 1b). The apices of the segments are rounded to acuminate (Figs. 1l–1o). There is a segment bearing a small lobe parallel to the apex (Fig. 1m). The segments are slightly narrowing towards both the basiscopic and acroscopic parts. Bases of the segments are not preserved. Hypodermal strands and resin ducts are lacking. The area of the midrib is ornamented with thin interrupted parallel ribs (Figs. 3a–3c). The axial conducting bundle occupies up to one-quarter of the leaf width. Lateral veins are simple or dichotomizing, deviating from the midrib at an angle of 15°–30°, rarely once dichotomizing, entering the segment margin, and visible only in cleared leaves (Fig. 1q). Very rarely (only in the widest segments), lateral veins appear in the topography of the lower epidermis as chains of one or two rows of elongate cells, deviating at an acute angle from the central non-stomatal zone, which corresponds to the midrib (Fig. 1r, Pl. 8, fig. 4). These chains are sorts of costal zones that, unlike the midrib, do not reach the segment margin and mark no more than one-third of its length. Stomatal apparatuses occur in costal zones.

Only spongy mesophyll is found by maceration.

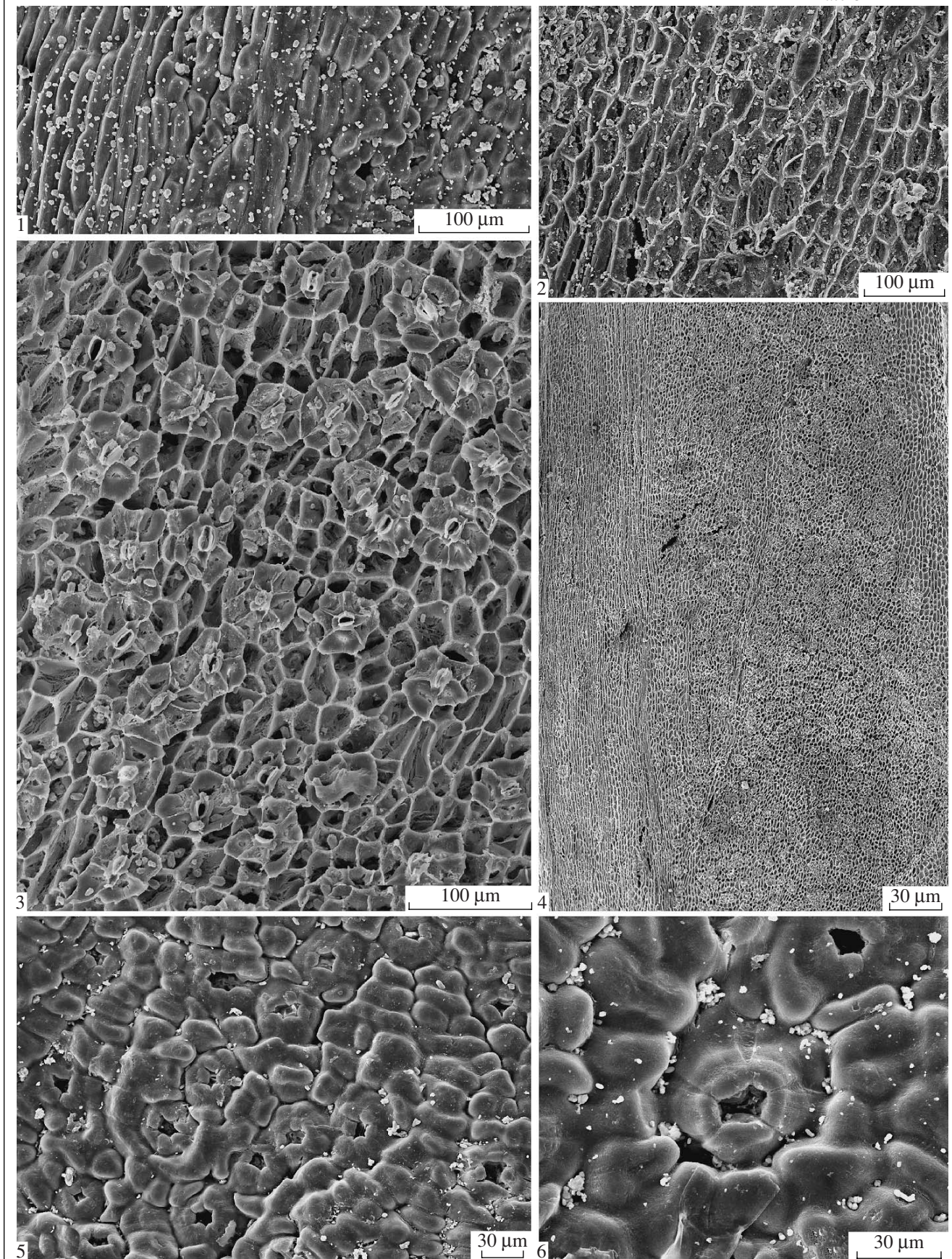
The cuticle is very thick (10–15 µm). The cuticle of the upper epidermis is virtually as thick as that of the lower epidermis.

The segments are hypostomous. The upper epidermis may be divided into zones according to the outline, size, and orientation of ordinary epidermal cells: two marginal zones, one middle zone, and two zones that

Explanation of Plate 7

Figs. 1–7. *Pachypteris rutenica* sp. nov., northern opencast mine of the Mikhailovskii Rudnik locality, town of Zheleznogorsk, Kursk Region, Russia; Middle Jurassic, Bathonian, holotype PIN, no. 5137/12, SEM: (1) fragment of a stomatal zone, outside view, note stomatal apertures; (2) stomatal zone, cells of a marginal zone are visible to the left, and cells of the middle non-stomatal zone are visible to the right; (3) fragment of a stomatal zone, small groups of stomata are visible; (4) groups of stomata that share subsidiary cells, thin striation is visible on subsidiary cells; (5) aggregations of stomata; (6) detail of fig. 5 showing stomata with contacting or common subsidiary cells; (7) longitudinally orientated abortive and fully developed stomatal apparatuses in a zone that corresponds to the midrib.

Plate 8



are situated over the stomatal zones of the lower epidermis. In marginal zones, epidermal cells are triangular to hexagonal, longitudinally orientated, 36–127 μm long and 18–46 μm wide (Figs. 2a, 3d). The width of the marginal zones is 210–600 μm . Epidermal cells of the middle zone (Figs. 2c, 3a, 3d, 3e), which corresponds to the midrib, are mostly tetra- or pentagonal, forming longitudinal rows, and strongly longitudinally elongated. The cells are 6–33 μm long and 27–110 μm wide. The cuticle of the zones over stomatal zones shows triangular to hexagonal, more rarely heptagonal, epidermal cells, 20–60 μm long and 20–57 μm wide (Figs. 2b, 3d, 3e). Cells of these zones are slightly elongated and form indistinct chains at an angle of 15°–30° to the midrib. The tilt of the cells marks the angle of deviation of the lateral veins from the midrib. The anticlinal cells are either straight, relatively thin, and evenly cutinized (Fig. 2b), or thick, with cutinization that increases at the contact with the periclinal cells (Fig. 1s, Pl. 8, fig. 2). Often, both types of cutinization of anticlinal cells are visible in the same segments. However, there are segments showing only one of the two types. The periclinal walls of the cells are convex or swollen (Fig. 3a).

The lower epidermis shows two stomatal zones, 430–1560 μm wide, separated by a zone 600–920 μm wide, corresponding to the midrib (Figs. 1q, 1r, 2a, 3c), in which scanty longitudinally orientated abortive (or, more rarely, functional) stomatal apparatuses occur (Figs. 2f, 3b, 3c, Pl. 7, fig. 7). In this zone, epidermal cells are trapezoidal, rectangular, or fusiform, longitudinally elongated, 20–120 μm long and 10–20 μm wide. Epidermal cells within marginal non-stomatal zones are 27–100 μm long and 27–37 μm wide. The width of marginal non-stomatal zones is 200–600 μm . Epidermal cells of stomatal zones are triangular to hexagonal, usually nearly isodiametric, or slightly obliquely elongated parallel to lateral veins (Fig. 2d, Pl. 8, fig. 3), more rarely longitudinally elongated (Fig. 2e, Pl. 7, figs. 2, 3), 10–30 μm long and 15–20 μm wide. Epidermal cells have straight anticlinal walls and swollen periclinal walls (Figs. 3b, 3c, Pl. 7, fig. 1, Pl. 8, figs. 1, 5). In the lower epidermis, the cutinization of the anticlinal walls of ordinary epidermal cells is as variable as that of ordinary cells of the upper epidermis (Fig. 4).

Stomata are irregularly distributed in stomatal zones (Figs. 2d, 2e, Pl. 7, fig. 2, Pl. 8, figs. 3, 5) and form small groups, where they share lateral, polar encircling

and, occasionally, subsidiary cells (Pl. 7, figs. 3–6, Pl. 8, fig. 3). Some stomatal apparatuses share up to two subsidiary cells. Stomatal apparatuses are predominantly obliquely orientated (parallel to lateral veins) or, more rarely, transversely or longitudinally.

Stomatal apparatuses are monocyclic, more rarely incompletely amphicyclic with one or two encircling cells; amphicyclic stomata occur as an exception. There are (3)4–6(7) subsidiary cells. Usually, polar subsidiary cells are not expressed. The cuticle of subsidiary cells often shows a thin radial striation on the external and internal surfaces, which is visible both in cleared leaves and SEM (Fig. 2g, Pl. 7, fig. 4, Pl. 8, fig. 6). Occasionally, the periclinal walls of subsidiary cells are much more weakly cutinized than the anticlinal walls (Figs. 2e, 4; Pl. 7, fig. 1). In some segments, subsidiary cells lack papillae (Fig. 4a, Pl. 7, fig. 1), whereas in other segments they bear small, but distinct proximal papillae (Fig. 4b, Pl. 8, figs. 5, 6). Occasionally, small proximal papillae develop on ordinary epidermal cells that adjoin subsidiary cells (Pl. 8, fig. 6). In some cases, subsidiary cells both with and without papillae are present on the same segment. The cutinization of external periclinal walls of guard cells is rodlike, thin, and more or less uniform (Fig. 2g, Pl. 7, fig. 6). The cutinization of internal periclinal walls is expressed by flanges between guard cells (Pl. 7, fig. 6). The stomatal aperture is 13–15 μm long. The length of guard cells, including polar extensions, is 26–30 μm , the width of the pair of guard cells in the middle area is 13–21 μm . The polar extensions are broad, long, and with a thin median ridge (Pl. 7, fig. 6). The length of the polar extensions is 10–15 μm , and the width is 10–15 μm .

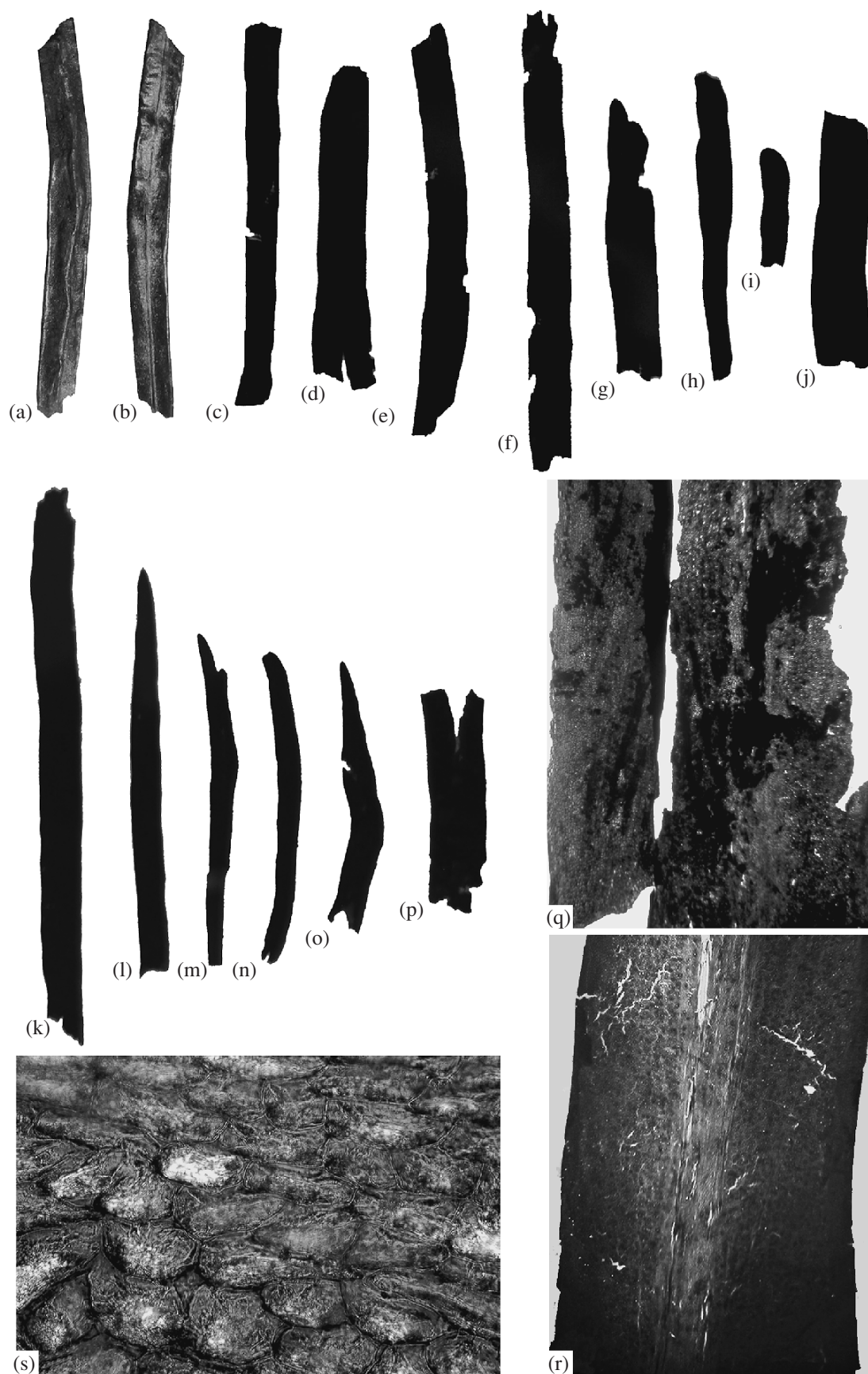
Trichomes are lacking.

Comparison. The patterns of venation and epidermal morphology of segments suggest the unequivocal affinity of the remains studied to the genus *Pachypteris*. The presence of segments with an additional lobe (Fig. 1m), parallel to the segment apex, indicates that an originally bipinnate leaf was reduced by assimilation of ultimate segments. A similar situation was described by Doludenko and Svanidze (1969) in leaves from the Cretaceous of Georgia assigned to *Pachypteris lanceolata*.

P. rutenica sp. nov. differs substantially from the type specimens of *P. lanceolata* from the Middle Jurassic of Yorkshire (England) by the size of segments and epidermal morphology. In *P. rutenica* sp. nov., stomatal apparatuses often bear papillae and can share subsid-

Explanation of Plate 8

Figs. 1–6. *Pachypteris rutenica* sp. nov., northern opencast mine of the Mikhailovskii Rudnik locality, town of Zheleznogorsk, Kursk Region, Russia; Middle Jurassic, Bathonian, PIN, no. 5137/13, SEM: (1) external surface of the lower epidermis in the contacting area between the midrib and stomatal zones; (2) inner cuticle surface of the upper epidermis, note rows of cells at an acute angle to the midrib; (3) fragment of a stomatal zone with the predominantly oblique orientation of stomata and ordinary epidermal cells, internal surface of the cuticle of the lower epidermis; (4) detail of the lower epidermis topography, a distinct trace of a lateral vein represented by a chain of elongate cells, inside view; (5) papillose stomatal apparatuses and ordinary epidermal cells with swollen periclinal walls; (6) stomatal apparatus with papillose subsidiary cells which form an elevation over it, some ordinary epidermal cells also bear small papillae.



iary cells, a phenomenon which is not observed in *P. lanceolata*. There is a similarity between the species under consideration and some specimens from the Callovian of Georgia described as *P. lanceolata* (Doludenko and Svanidze, 1969). Doludenko and Svanidze traced a transition from bipinnate leaves with elliptic segments to simple pinnate leaves with narrowly lanceolate segments by the reduction of segments of lateral axes; thus, they once more demonstrated that *Pachypteris* and *Tinnfeldia* are identical. Although a similarity to simple pinnate leaves is observed, the morphology of stomata in these leaves does not differ from that in type specimens of *P. lanceolata*. Moreover, their segments differ from segments of *P. rutenica* sp. nov. in the distinct non-stomatal costal zones that are present in the topography of the lower epidermis.

The fragments under study obviously belonged to simple pinnate leaves of the '*Tinnfeldia*' morphotype. Although the genus *Pachypteris* includes many species, leaves with long linear segments are quite rare.

Pachypteris ('*Tinnfeldia*') *speciosa* (Ettingsh.) Popa from the Lower Jurassic of Romania shows the greatest similarity (Popa, 1997, 2000b). However, in this species, the lateral veins are distinct in the topography of the lower epidermis. In addition, no stomatal apparatuses share subsidiary cells or bear papillae on the subsidiary cells.

There is a vague morphological similarity between the new species and *P. ('Tinnfeldia') major* (Raciborsky) Reymanówna from the Jurassic of Poland (Reymanówna, 1963). *P. major* has simple pinnate leaves with relatively long segments up to 32 mm long. Unlike those in *P. rutenica* sp. nov., they are lanceolate. Moreover, *P. major* bears papillae on ordinary epidermal cells, whereas *P. rutenica* sp. nov. has swollen periclinal walls of epidermal cells, and subsidiary (or, more rarely, encircling) cells supplied with papillae.

In epidermal morphology, the new species resembles *P. papillosa* (Thomas et Bose) Harris from the Middle Jurassic of Yorkshire (Harris, 1964). Like *P. rutenica* sp. nov., *P. papillosa* does not show non-stomatal zones in the topography of the lower epidermis that correspond to lateral veins, and its subsidiary cells bear papillae. Unlike *P. rutenica* sp. nov., *P. papillosa* has broader segments that are distinctly amphistomatic.

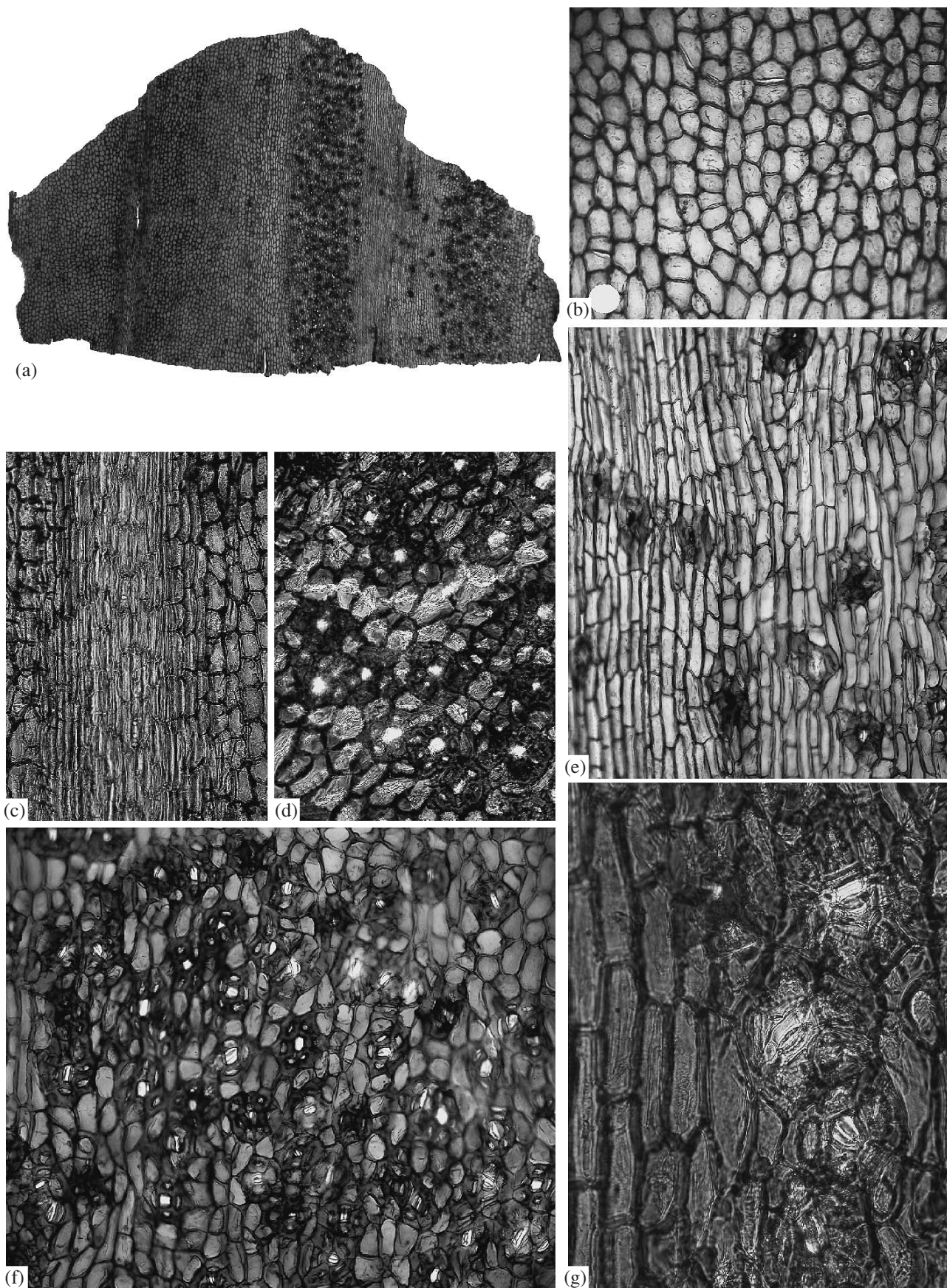
The similarity of the new species to *P. ('Tinnfeldia') banatica* (Hummel) Doludenko from the Lower Jurassic of Romania (Doludenko, 1974) lies in the fact that half of its stomata bear papillae and half of them are devoid of papillae. However, *P. rutenica* sp. nov. differs from *P. ('Tinnfeldia') banatica* in the linear segments contrasting to elliptical or elongated segments of the latter species. In addition, in *P. ('Tinnfeldia') banatica* papillae are present on subsidiary cells of the upper epidermis, a feature uncharacteristic of the new species. It should be pointed out that the structures interpreted by Barbacka (1994) as hair bases and supposed hydathodes are actually abortive stomatal apparatuses. Similar stomatal apparatuses were described by Harris (1964) in costal zones of *P. papillosa*. I observed such abortive stomata in the area of the midrib.

The new species resembles *P. ('Tinnfeldia') rhomboidalis* in the epidermis topography, but differs from it significantly in the segment morphology. In *P. ('Tinnfeldia') rhomboidalis*, segments are rhomboidal and half as long as in *P. rutenica* sp. nov. In addition, encircling cells and papillae on subsidiary cells are absent in *P. ('Tinnfeldia') rhomboidalis*.

The new species resembles *P. multiformes* Delle from the Middle Jurassic of Georgia in epidermis topography, but differs substantially in the outlines and greater sizes of pinnules (Delle, 1967). In *P. multiformes*, pinnules are usually oval and relatively small (5–21 mm long and 3–7 mm wide). Usually, stomata are incompletely amphicyclic; they are circled by five or six subsidiary cells, which are slightly smaller than other cells. Encircling cells form an incomplete ring and do not differ from other cells.

The segment outline closely resembles that of *P. aff. speciosa* from the Middle Jurassic of Georgia; some degree of similarity in the epidermal morphology also exists (Doludenko, 1969). Like the new species, *P. ('Tinnfeldia') aff. speciosa* has hypostomous leaves. However, in the latter species lateral veins are visible only on the outer surface of the segments; epidermally, they are expressed as bands of three to five rows of longer cells. In *P. ('Tinnfeldia') aff. speciosa*, stomata are amphicyclic or incompletely amphicyclic, rather sunken and densely situated, whereas *P. rutenica* sp. nov. has mostly monocyclic, or, more rarely, incompletely amphicyclic, or amphicyclic stomata with more or less

Fig. 1. *Pachypteris rutenica* sp. nov., northern opencast mine of the Mikhailovskii Rudnik locality, town of Zheleznogorsk, Kursk Region, Russia; Middle Jurassic, Bathonian: (a, b) holotype PIN, no. 5137/12; (a) fragment of a segment, view from the lower surface, note a keel, $\times 2.7$; (b) fragment of the same segment, view from the upper surface, the midrib is projecting, $\times 2.7$; (c) PIN, no. 5137/14, fragment of a segment, $\times 2$; (d) PIN, no. 5137/15, fragment of a segment, $\times 2$; (e) PIN, no. 5137/16, fragment of a segment, $\times 2$; (f) PIN, no. 5137/17, fragment of a segment, $\times 2$; (g) PIN, no. 5137/18, fragment of a segment, $\times 2$; (h) PIN, no. 5137/19, fragment of a segment narrowing toward the base, $\times 2$; (i) PIN, no. 5137/20, fragment of a segment with a preserved apex, $\times 2$; (j) PIN, no. 5137/21, fragment of a segment, $\times 2$; (k) PIN, no. 5137/22, fragment of a segment, $\times 1.7$; (l) PIN, no. 5137/23, fragment of a segment with a preserved apex, $\times 1.7$; (m) PIN, no. 5137/24, fragment of a segment with preserved apex and additional lobe, $\times 1.7$; (n) PIN, no. 5137/25, fragment of a segment with a preserved apex, $\times 1.7$; (o) PIN, no. 5137/26, $\times 1.7$; (p, r, s) PIN, no. 5137/13; (p) fragment of a segment, $\times 1.7$; (r) topography of the lower epidermis with two broad stomatal zones with weakly visible narrow costal zones corresponding to lateral veins, $\times 10$; (s) cuticle of the upper epidermis shows strongly cutinized anticlinal walls, $\times 9.8$; (q) PIN, no. 5137/27, spread of a partially macerated fragment of a segment, lateral veins are visible, $\times 370$.



developed papillae on subsidiary cells. In *P. ('Tinnfeldia')* aff. *speciosa*, encircling cells of two neighboring stomata often contact, but stomata rarely share encircling cells; in *P. rutenica* sp. nov., stomata often share both encircling and subsidiary cells.

An important distinctive feature of *P. rutenica* sp. nov. is the presence of groups of stomata sharing subsidiary cells. Stomatal apparatuses sharing encircling cells are also common.

The new species differs more substantially from other members of *Pachypteris*, both in morphology and epidermal characteristics.

Remarks. Epidermal characters are relatively highly variable in the new species. The study of *Pachypteris rutenica* sp. nov. additionally confirmed that intrageneric variability is also very high among members of the genus. Although the outline and size of the segments implies the assignment of the new species to *Komlopteris*, all other characters (including the morphology of the stomata) unequivocally indicates that it belongs to *Pachypteris*. Popa (2000a) noticed that *Pachypteris ('Tinnfeldia')* *speciosa* (in my opinion, the closest species to *P. rutenica* sp. nov.) shows transitional characteristics between the genera *Pachypteris* and *Komlopteris*. Consequently, *Komlopteris nordenskioeldii* and *Pachypteris rutenica* sp. nov. could be the extreme members of the same morphological row.

Some species of *Pachypteris* are often confused with members of *Cycadopteris*, in which the presence of hairs is among the diagnostic features. In transmitted light, either mesophyll cells that were incompletely macerated or inner periclinal walls of stomatal apparatuses, which in *Pachypteris* are quite resistant to maceration, are taken for hairs. For example, in my opinion, *P. bendukdzei* Doludenko et Svanidze (Doludenko and Svanidze, 1969) was erroneously transferred (Doludenko et al., 1998) into *Cycadopteris jurensis* (Kurr) Barale (Barale, 1982) because of the hairs, that are actually inner periclinal walls of stomatal apparatuses, partially dissolved during maceration. This is obvious because of their characteristic shape and position directly below stomatal apparatuses. Moreover, Doludenko and Svanidze (1969) remarked that the "hairs" can be dissolved by longer maceration. Trichomes in members of *Pachypteris* are lacking, in contrast, for example, to *Cycadopteris*.

In the Mikhailovskii Rudnik locality, segments of *P. rutenica* sp. nov. are associated with fragments of pinnate leaves of *Pachypteris* sp., which is remarkably

different both in the morphology and epidermal structure. Unfortunately, the paucity of the material has so far prevented a more exact determination of these leaves.

Material. Phytoliteims of numerous leaf fragments.

DISCUSSION

The Mikhailovskii Rudnik locality, where *P. rutenica* was discovered, is apparently the richest locality for the Bathonian flora in Central European Russia. Members of the Corystospermales (*Pachypteris* sp. and *P. rutenica* sp. nov.), Miroviaceae (*Oswaldheeria eximia* Gordenko; Gordenko, 2007), and Ginkgoales (*Ginkgo huttoni* Harris and *Leptotoma prinadae* Travina) were found. Microphyllous conifers are represented by solitary leaves. It is of interest that beds dominated by leaves of *Oswaldheeria eximia* with rare ginkgoaleans are laterally substituted by beds dominated by segments of *Pachypteris rutenica* sp. nov. combining with rare leaf fragments of *Pachypteris* sp., *Oswaldheeria eximia*, and ginkgoaleans. Further laterally, this mixed taphocenosis gives way to a taphocenosis that consists exclusively of ginkgoaleans. An association of *Pachypteris*, *Oswaldheeria* Bose et Manum, and ginkgoaleans was earlier recorded in the Middle Jurassic of northern Norway (Manum et al., 1991). It is conceivable that such communities were relatively common. The community of the Mikhailovskii Rudnik locality grew in a swamped delta of a river that entered a freshwater body. *Oswaldheeria* prevailed in less swampy river bank sites, whereas *Pachypteris* and ginkgoaleans preferred swampier sites. Consequently, *P. rutenica* sp. nov. did not grow in marshes, but preferred swampy river valleys. It is evident that *Pachypteris* is not a strict indicator of coastal marshes, since it occurs in definitely freshwater deposits (Barbacka et al., 2006).

In the context of the environmental preferences of *P. rutenica* sp. nov., its extremely thick cuticle is noticeable. Thick cuticle is conventionally considered as a xeromorphic character. Indeed, modern inhabitants of raised bogs show xeromorphic features because of physiological dryness. However, *P. rutenica* sp. nov. grew in lowland bogs, not in raised bogs. Nor did it inhabit brackish marshes, where plant physiological dryness is also known. If the thick cuticle of leaves of *P. rutenica* sp. nov. appeared as an adaptation to intense insolation, the absence of palisade mesophyll in its

Fig. 2. *Pachypteris rutenica* sp. nov., northern opencast mine of the Mikhailovskii Rudnik locality, town of Zheleznogorsk, Kursk Region, Russia; Middle Jurassic, Bathonian: (a–g) holotype PIN, no. 5137/12; (a) spread of the cuticle showing the topography of the lower and upper epidermises, $\times 19$; (b) fragment of the cuticle of the upper epidermis over a stomatal zone, $\times 150$; (c) cuticle of the upper epidermis in the area of the midrib, $\times 150$; (d) stomatal apparatuses showing contacting or even common subsidiary cells, $\times 150$; (e) stomatal zone with unevenly distributed stomata, $\times 150$; (f) longitudinally orientated normal and abortive stomata of the lower epidermis in the keel area, $\times 150$; (g) stomatal apparatuses forming a longitudinal chain at the margin of a stomatal zone and sharing subsidiary cells. Note a significantly weaker cutinization of guard cells and periclinal walls of subsidiary cells in comparison to ordinary epidermal cells, $\times 460$.

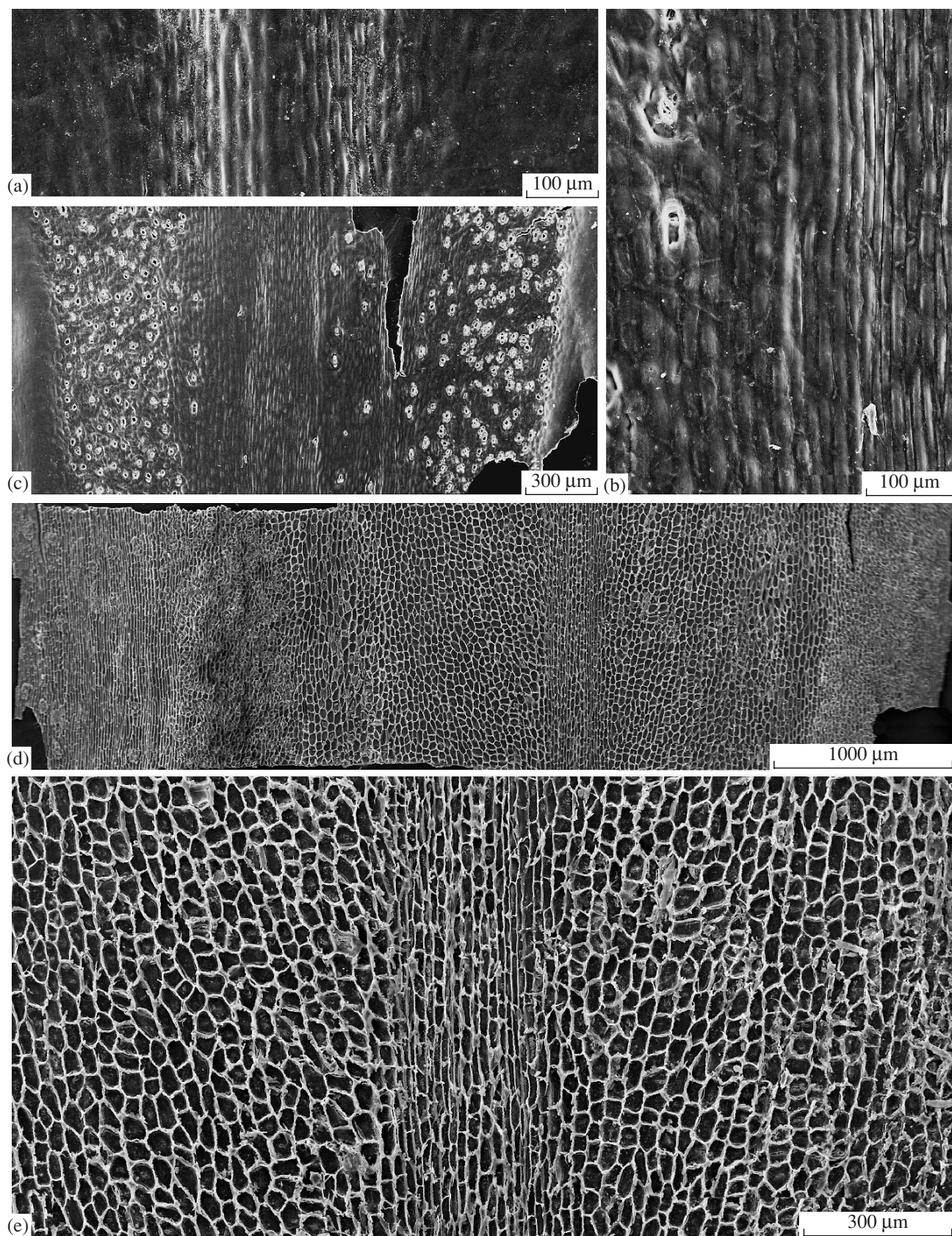


Fig. 3. *Pachypteris rutenica* sp. nov., northern opencast mine of the Mikhailovskii Rudnik locality, town of Zheleznogorsk, Kursk Region, Russia; Middle Jurassic, Bathonian: (a–e) holotype PIN, no. 5137/12; (a) outer surface of the upper epidermis in the area of the midrib; (b) detail of the lower epidermis at the stomatal zone/keel contact, note abruptly lengthened epidermal cells; (c) outer surface of the lower epidermis, note two stomatal zones and individual stomata in the keel area; (d) spread of a cuticle showing the topography of the epidermis, arrows indicate stomatal zones; (e) inner surface of the cuticle of the upper epidermis showing chains of cells orientated at an acute angle to the midrib zone, the oblique orientation becomes nearly longitudinal at a distance from the midrib.

leaves is very peculiar. Palisade mesophyll is well developed in xerophytes and plants inhabiting well-illuminated sites, but poorly developed or totally lacking in plants growing in shade, e.g., in the understory (Larcher, 1976). Therefore, apparently xeromorphic characters do not always indicate that the plant was a xerophyte or grew under physiological dryness. So far, the only obvious thing is that the thick cuticle of *Pachypteris* served as a skeleton, since the hypoderm in members of this genus was absent.

Thick cuticle is known in many Mesozoic plants, such as *Pagiophyllum* Brongniart, *Brachyphyllum* Brongniart, *Bilsdalea* Harris (Harris, 1979), and members of the Miroviaceae (e.g., *Oswaldheeria eximia*, Gordenko, 2007). Some members of *Pagiophyllum* have stomatal apparatuses that resemble those in *Pachypteris*. This similarity between different plant groups may indicate convergent epidermal adaptations, although we have not so far known what exactly these adaptations were. Although the above-mentioned plants are widely believed to be xerophytes, it is not excluded that some of them were not always xerophytes.

Similarly to many other members of *Pachypteris*, *P. rutenica* sp. nov. has a thick but unevenly thickened cuticle (Fig. 4b). The thickness is mostly reached at the expense of a characteristic cutinization of anticlinal

walls, which are triangular in transverse section. The periclinal walls are overlain by strongly widened bases of anticlinal walls and virtually indistinguishable from the inside surface. Such an epidermis might have functioned as an optic system that intercepted sunbeams passing through the leaf. Similar adaptations effectively intercepting sunlight by means of its back reflection by the lower surface of the epidermis are not a rarity among modern shade-requiring plants (Larcher, 1976).

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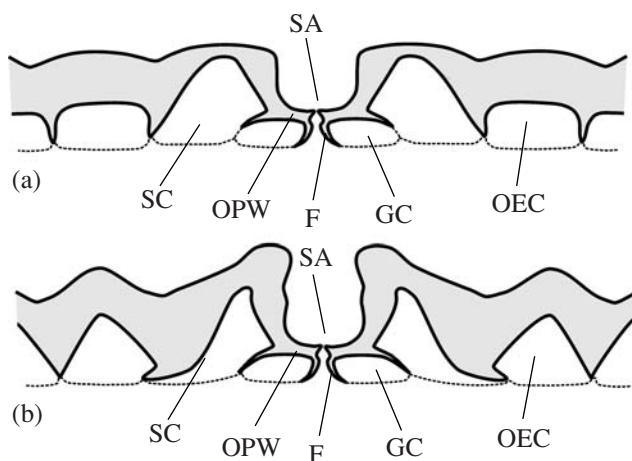


Fig. 4. Reconstructed transverse sections through stomatal apparatuses and ordinary epidermal cells of *Pachypteris rutenica* sp. nov. showing variable cutinization: (a) stomatal apparatus lacking papillae; (b) papillose stomatal apparatus; (SC) subsidiary cell; (OPW) outer periclinal wall; (F) flange between guard cells; (GC) guard cell; (OEC) ordinary epidermal cell; (SA) stomatal aperture. Cutinization is in gray, rough outlines of cells are shown by dotted line.

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