

ON THE MOSS GENUS *GOMANKOVIA* FROM THE UPPER PERMIAN
OF THE RUSSIAN PLATFORM

О РОДЕ *GOMANKOVIA* ИЗ ВЕРХНЕПЕРМСКИХ ОТЛОЖЕНИЙ
РУССКОЙ ПЛАТФОРМЫ

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Abstract

The Upper Permian moss genus *Gomankovia* was described in 1990 and remained poorly known, mostly by a single, well-preserved leaf. Recently collected additional material revealed more than 40 new specimens of this genus. Its variation in leaf shape and laminal cell areolation is described. The specimens were cut, showing the transverse costal structure, which is formed mostly of large, moderately thick-walled cells, with only a few cells with thicker walls. The costa has several lateral branches, which preclude an immediate comparison of *Gomankovia* with any modern moss group. Sections of costa are studied with transmission electron microscopy, and, despite the compression type of preservation, it appeared possible to reconstruct the original structure of the costa. Generally, it lacks differentiation similar to costa of extant mosses of similar size of plants and leaf shape and size. There is no way to refer *Gomankovia* to any extant group; however, its relationship to some extinct lineages is possible.

Резюме

Новые коллекции верхнепалеозойского мха из рода *Gomankovia* позволяют дать более подробную его характеристику по сравнению с той, которая была сделана ранее, поскольку на момент первоописания в 1990 г. он был известен только по одному листу. В то же время в недавно собранных дополнительных коллекциях выявлено более 40 новых образцов этого рода. Описано варьирование морфологии листьев *Gomankovia* и их клеточной сети. Были сделаны поперечные срезы листьев, позволяющие увидеть строение жилки, которая образована большей частью крупными клетками с умеренно утолщенными стенками, лишь с немногочисленными более толстостенными клетками. Жилка *Gomankovia* имеет несколько боковых ответвлений, что не позволяет сравнивать этот род с современными мхами. Поперечные срезы жилки были изучены с помощью трансмиссионного электронного микроскопирования, в результате чего, несмотря на то, что образцы представлены в виде компрессии, стало возможно реконструировать первоначальное строение жилки. Жилка *Gomankovia* не имела дифференциации, сходной с таковой у современных мхов со сходными размерами растений и листьями сходной формы и размеров. Невозможно отнести этот род к какой-либо из современных групп мхов, но его родство с некоторыми другими известными линиями ископаемых мхов не исключено.

KEYWORDS: fossils, bryophytes, Russian Platform, TEM, anatomy, costa structure

INTRODUCTION

Paleozoic mosses remain rather little known, and the localities with well-preserved fossils remain quite few in the world (Tomescu *et al.*, 2018; Ignatov & Maslova, 2021). The northern Asia, the Angaraland in Late Paleozoic time, is one of exceptions. Protosphagnalean mosses were a rather common component of the Upper Permian vegetation there, as described by Neuburg (1956,

1960). It is likely that they not only dominated locally, but were the only group of mosses in that area, and this group became totally extinct.

However, at the western edge of this huge territory where protosphagnalean mosses grew, there were several localities where protosphagnalean and likely non-protosphagnalean mosses co-occurred. Gomankov & Meyen (1986) described in their “*Tatarina flora*” a great diversity of

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mosses from the territory which is situated now in the NE of the European Russia. The richest locality among described by these authors is Aristovo. For mosses this is a real Klondike, where as much as twelve moss genera were found, eight being described as new (Ignatov, 1990).

The genus *Gomankovia* is one of them. This monospecific genus has been described based on a single leaf, which, however, had many unique distinctive features. Only a small leaf fragment in addition to the holotype was mentioned in the protologue (Ignatov, 1990), and this fragment even could not be attributed to this genus with certainty. During a long time after the description of *Gomankovia*, no new records of mosses from that area appeared, until our collection of 2022 from the same place provided numerous samples of mosses. The description of new collections of the genus *Arvilidia* has already been published (Ignatov *et al.*, 2023), while several other genera are still waiting an expanded study. The material of *Gomankovia*, which allowed us to expand the knowledge of this genus significantly, is described in the present paper.

MATERIAL AND METHODS

Locality. The material was collected from the Aristovo, Vologda Region, Velikoustyugskii District, right bank of the Lesser Northern Dvina River 100 m upstream the Aristovo pier. Details of the locality is given in Gomankov & Meyen (1986).

Gomankov & Meyen (1986) referred the deposits from Aristovo to the Vyatkian Horizon, the Upper Tatarian Substage, the Upper Permian, now referred to the Wuchiapingian of the Lopingian Series (Gomankov, 2002). Moss remains were associated with *Tatarina* pteridosperms and numerous leaves of *Cordaites*. There also were numerous oogonia of Charophyta, supporting, among others, an assumption that the material comes from deposits of the ancient riverbed, or oxbow lake (Gomankov & Meyen, 1986).

Entomofauna of the same deposits has been described by Aristov *et al.* (2013), with the other useful reference regarding this locality and its dating.

Material. The plant-bearing deposits consist of grey and dark-grey argillites. Wet argillites were delivered into the lab with some precautions to avoid possible fragmentation that happens if argillite dries. During the transportation, pieces of argillites were placed in plastic boxes and wetted by water with fungicide. In the lab, the material was sunk for four weeks in a mixture of aqueous saturated solution disodium EDTA (to extract calcium) and hydrofluoric acid (1:2), then washed in distilled water. Plant remains were sorted and most of them were mounted on slides with glycerol-gelatin using a standard protocol. Before embedding, a few larger specimens were studied and photographed in water under both light and compound microscopes.

Microscopy and photography. Before mounting in glycerol-gelatin on slides or in epon-araldite resin for

sectioning, material was photographed in water slides under light microscope Olympus CX43 with camera Infinity 1-2. Z-stacks of several images were obtained by HeliconFocus 4.50 (Kozub *et al.*, 2008).

Destructive studies. *Gomankovia* specimens were much less numerous than protosphagnalean mosses, but we decided that three large leaf fragments (easily attributable to the genus by characteristically darker marginal cells) can be used for destructive studies. Those included (1) the general procedure for embedding to cutting medium and (2) TEM preparation, as follow:

1) Anatomical sections studies. The material kept in water with fungicide was washed in distilled water, then dehydrated in an alcohol series (20%, 40%, 60%, 80% and 96% alcohol), alcohol-acetone mixture (1:1), and acetone for 15 minutes in each solution, soaked in an acetone-resin mixture series (3:1, 1:1, 1:3) for 6, 12 and 1 hours respectively, and then embedded in epon-araldite resin as recommended by the manufacturer. The resin was polymerized at 37°C for 24 hours and then at 60°C for another 24 hours.

For light microscope observations, serial sections of 2 or 1 µm thick were made with LKB ultramicrotome with glass knives. At the point of special interest, the resin block was proceeded further for the ultrathin section preparation.

2) For TEM observations, the ultrathin 60 nm thick sections were made with LEICA ARTOS 3D with diamond knife (with 45° angle). TEM sections were studied without any staining, or contrasted by either uranyl acetate and lead citrate.

Sections were studied under JEM-1011 TEM (Jeol, Japan) at 80 kV and a CCD ORIUS SC1000W under control of GATAN Digital Micrograph in the Laboratory of electron microscopy at the Faculty of Biology of Lomonosov Moscow State University.

Specimens of Aristovo collections have the prefix 'Aristovo-', which is omitted in the foregoing figure legends, as no material from other collections is shown in this paper.

MATERIAL DESCRIPTION

Identification. The material of this genus is rather easy to sort out among other moss leaf fragments. Ignatov's (1990) diagnosis of *Gomankovia* included: (1) leaves oblong-ovate, (2) margin entire, (3) marginal cells similar in shape to lamina cells, but darker in color, (4) laminal cells thin-walled, in the upper part of leaf isodiametric, near the base rectangular with length to width ratio 2–3:1, (5) costa multistratose, moderately pronounced, extending to 4/5 of the leaf length, with lateral branches, in leaf apex forked.

This diagnosis allowed us to select 40 fragments of *Gomankovia* from the mixture of moss fragments obtained from balk maceration. Basing on these, we describe here the available entire leaves and their fragments focusing on the variation of the mentioned features.

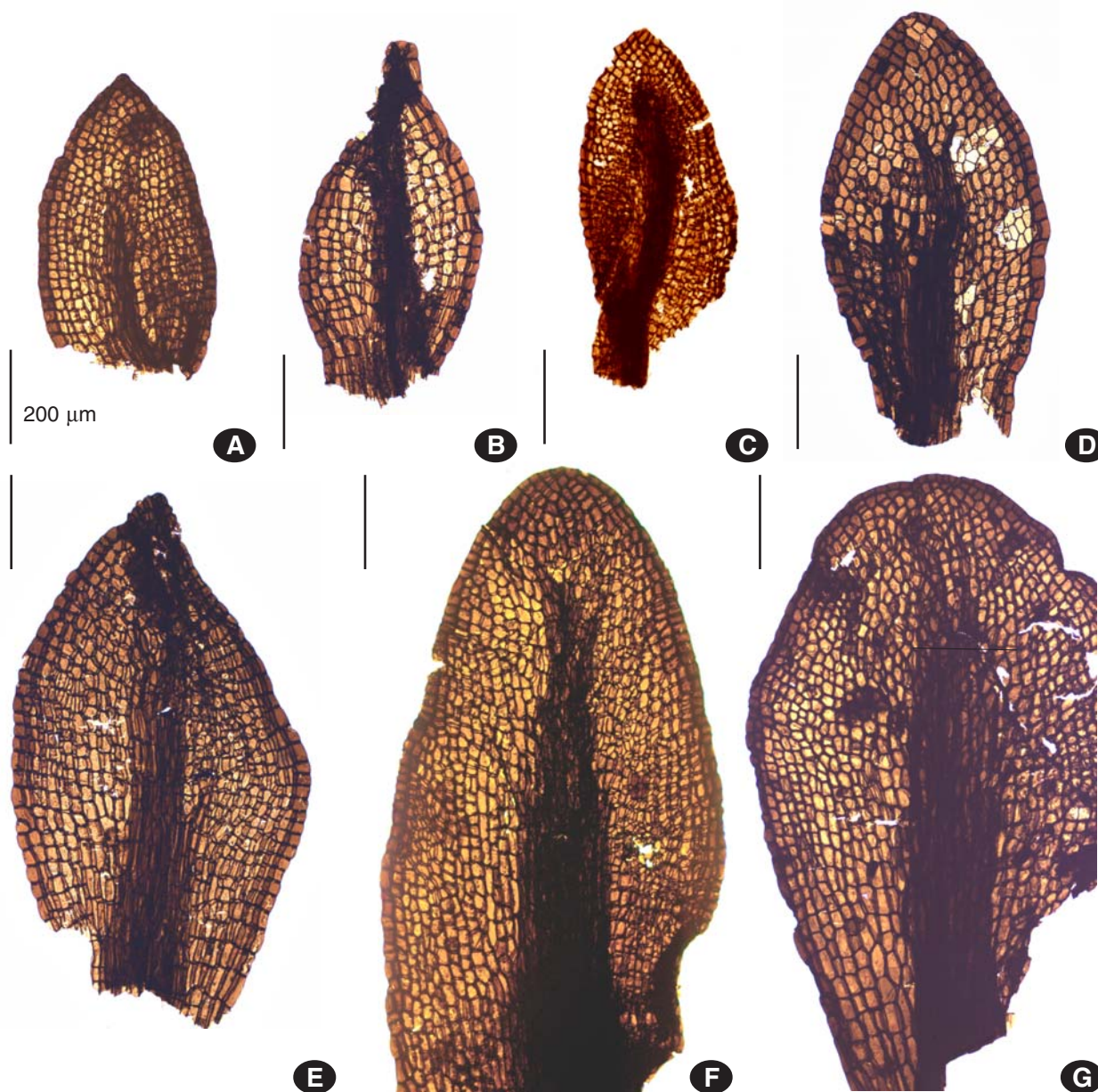


Fig. 1. *Gomankovia latifolia*, Aristovo, Upper Permian. Leaf shape variation. A: 121A-1, B: 102A-8, C: 102B-12, D: 106B-13, E: 107A-9, F: 115A-7, G: 120A-6.

Leaves. The holotype leaf is 1.1×0.45 mm, e.g. has size slightly below the average in extant acrocarpous mosses with broad leaves, e.g. those without long, narrow acumina, while the latter usually have longer leaves.

In the present collections some leaves are smaller, being 0.65×0.38 mm (Fig. 1A), 0.78×0.39 mm (Fig. 1B), 0.78×0.22 mm (Fig. 1C), but the conspicuous border, as well as more or less lingulate leaf shape ensure us that these leaves belong to *Gomankovia*. One small leaf in Fig. 1 B looks narrower acute, although it is somewhat damaged in the upper part, and the shape of its apex is not clear. Gentle narrowing of these small leaves towards the base apparently indicate that they likely were from the lower parts of stems, in a manner of leaf differentiation along the stem in extant mosses.

Other leaves from the new collections are somewhat larger than holotype, 1.35×0.70 mm or a little longer, considering somewhat incomplete preservation (Figs. 1F-G).

Leaf shape is variable, as they are widest above mid-leaf (Fig. 1G), near it (Figs. 1D-E), or below it (Fig. 1F).

Leaf apices vary from bluntly acute to broadly rounded. The holotype has an acute apex with apparently one apical cell; similar apices were observed in leaves shown in Figs. 1B, 1C, and 1E, though in some of them, e.g. in Fig. 1B, leaf apex is partly damaged. In most cases, however, leaf apices are rounded, and cells in apical region look fairly even, so it is difficult to recognize the leaf apical cell among neighboring cells (e.g., in Fig. 2E, F). However, in some cases even in leaves with rounded api-

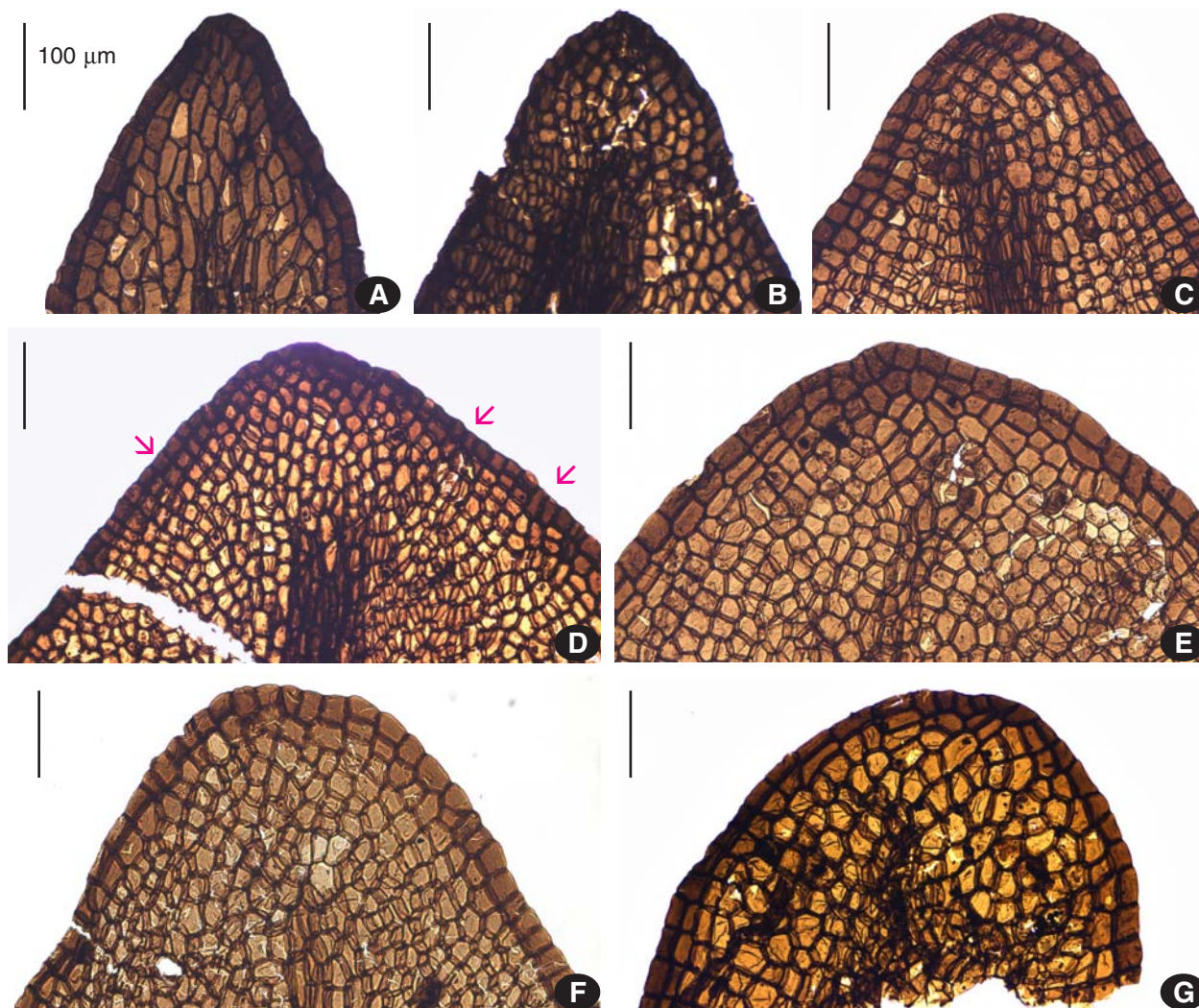


Fig. 2. *Gomankovia latifolia*, Aristovo, Upper Permian. Variation of the leaf apical part. A: 108B-5, B: 121B-6, C: 101B-1, D: 118A-20, E: 107A-6, F: 104A-2, G: 107B-8. The colored leaf border is biseriate at places (Figs. 1F, 2D), having a pattern of broadening towards the base (arrowed).

ces, the apical cell can be recognized by its triangular shape and characteristic surrounding cell arrangement (e.g., in Fig. 2G) inherited from the apical cell bifacial division (Frey, 1970; Donskov, 2015).

The angle at which the leaf sides meet at apex ranges from 45 to 90° (most leaves in Figs. 1–3), not regarding the very narrowly tapering leaf in Fig. 1B, which can be caused by damage. In case of large leaves with very broad, rounded apices, it is difficult to estimate an angle formed by leaf sides, unless to consider it being about 180° (Figs. 1G, 3D).

Minimal angle between leaf sides occurs in the leaf shown in Figs. 2A and 3A. This leaf differs from most other leaves in having elongate cells in the apical region; actually, isodiametric cells are totally absent in it. Nevertheless, other diagnostic characters of *Gomankovia*, such as 1–2 rows of darker cells at margins and costa with side branches, are present in this leaf, and we are inclined to consider this difference within the range of species variation. This is also supported by the presence

in our collection of another, similarly narrow, but poorer preserved leaf, not shown here.

Leaf margins are always entire, though the marginal cell walls faced outwards are somewhat convex, making an aspect of a very slight dentation (e.g., Fig. 4E). Leaf margins are perfectly plain, without any evidence of the recurvation or incurvation. This fact can probably be explained by the presence of a border. The darker color of the latter can be due to thicker walls of marginal cells, which provide a rigid stature of leaf with plain margins.

Marginal cell differentiation in *Gomankovia* is conspicuous, first of all in its invariable presence in all leaf parts. In most cases, shape and size of marginal cells do not differ from those of the neighboring cells inwards the leaf lamina. However, occasionally, a particular cell at leaf margin can be subtended by two neighboring cells or be longer than neighboring cells of inner leaf lamina. More rarely, the marginal cell is divided longitudinally. The colored leaf border is biseriate at places, having the

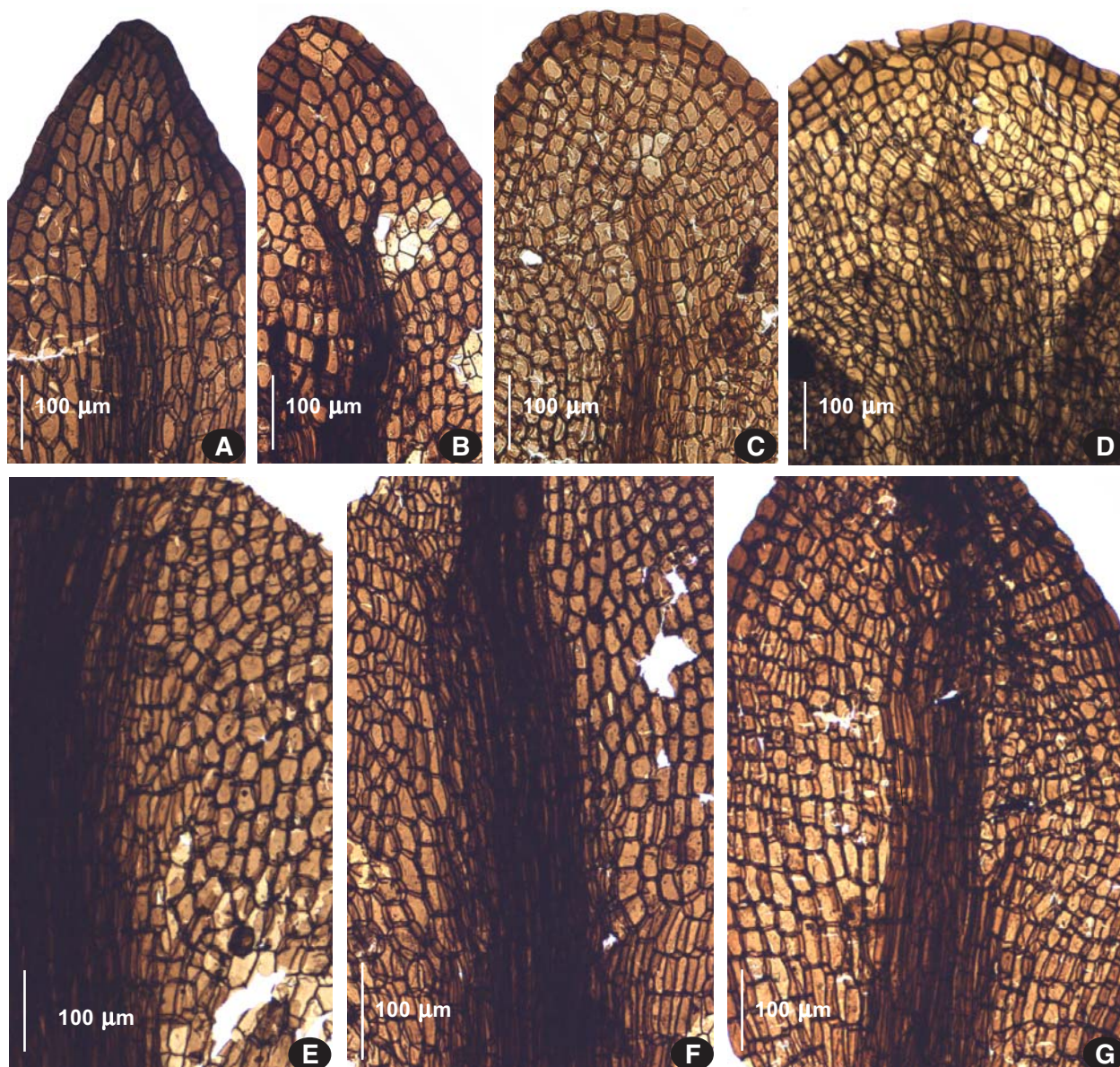


Fig. 3. *Gomankovia latifolia*, Aristovo, Upper Permian. Costa is branching in the upper, middle and lower parts of leaves. A: 108B-5, B: 106B-13, C: 104A-2, D: 107A-6, E: 105B-6, F: 107A-7, G: 107A-9.

pattern of broadening towards the base (Figs. 1F, 2D, arrowed).

Marginal cells are 15–45 μm long and 17–33 μm wide.

Laminal cells of *Gomankovia* are described in the protologue as isodiametric, ca. $30 \times 30 \mu\text{m}$ in the upper part of leaf; in recently collected material, cell size is largely the same. Cells are more variable in subapical region of leaves, where some cells are $40 \times 30 \mu\text{m}$ or even $45 \times 50 \mu\text{m}$ (Fig. 2C, E, G), while in other parts of leaves, cells are smaller, 17–25 μm (Fig. 2B, D). The maximal difference in cell size was observed in leaves with narrower apices (Figs. 1D, 2A), where cells around the end of costa are 70–80 μm long, making the outline of costa poorly defined.

Laminal cells in the basal part of leaf were described in the protologue as having length to width ratio 2–3:1,

being maximally 80 μm long and 40 μm wide. In the new collections, size of basal leaf cells almost never exceeds these limits, with only solitary cells being ca. 85 μm long.

The transition from isodiametric upper cells to elongate basal cells in most cases starts at 1/3 to 1/2 of the leaf length. Note, however, that in leaves with narrower apices (Fig. 3A), the elongate laminal cells are arranged along the costa, so that in the juxtacostal area cells are wider than in submarginal area (Figs. 1F, 4A).

Costa is described in the protologue of *Gomankovia* as multistratose, having lateral branches. In our opinion, an apical furcation of costa is merely a variant of lateral branching, so it will not be discussed separately.

Costa reaches 0.8 the leaf length in well-developed, large leaves, whereas in smaller leaves it is shorter, to

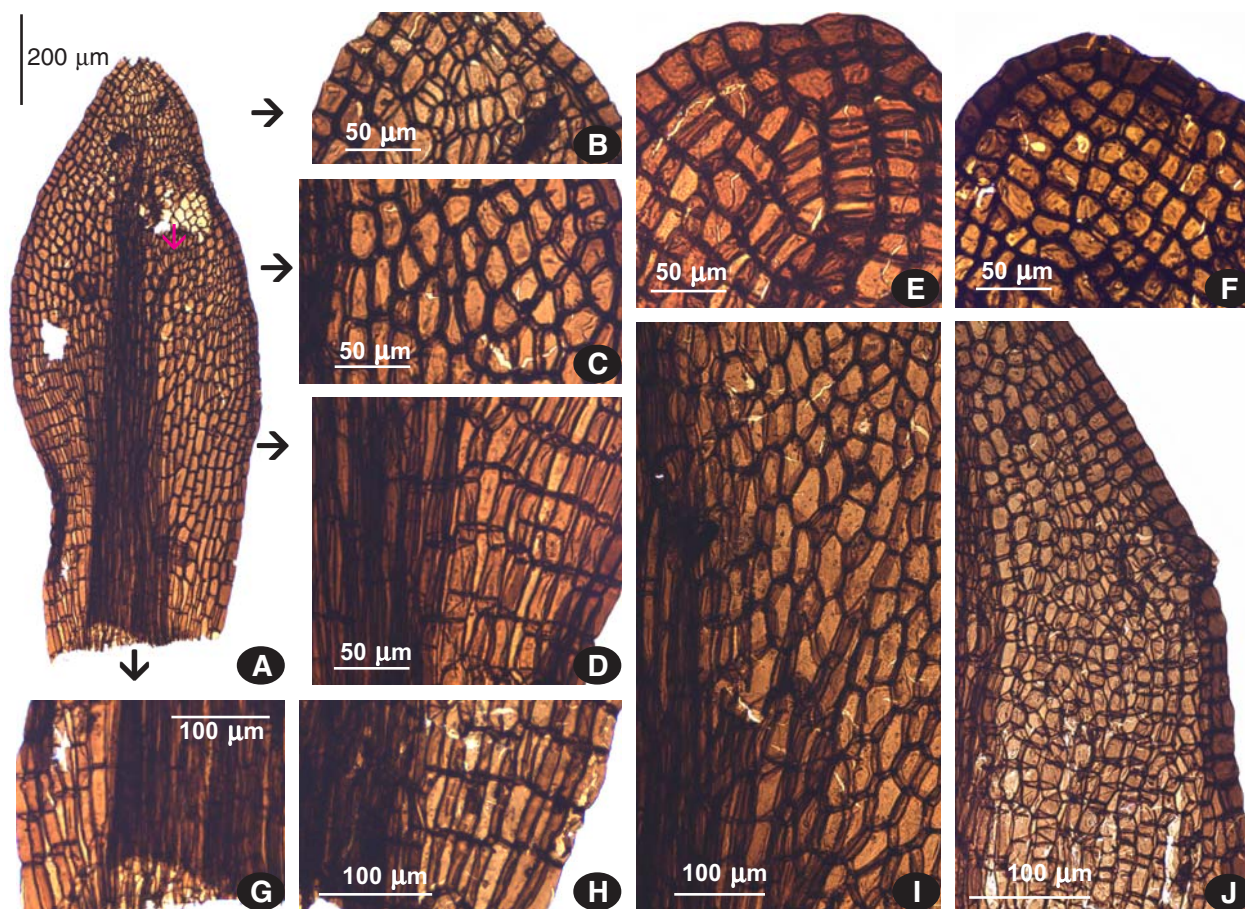


Fig. 4. *Gomankovia latifolia*, Aristovo, Upper Permian. Cells areolation in the different parts of leaf, showing variants of cells in distal part of leaf, transition from costal to laminal cells, and variation in border differentiation. A–D, G: 107B-6, E: 104A-2, F: 117B-4, H: 107A-9, I: 108A-6, J: 101B-1. Pink arrow in 'A' point the dark colored cells at the tip of lateral costa.

0.65 the leaf length. Although being described as only a moderately pronounced, at leaf base costa usually constitutes 0.3–0.35 of the leaf width. In distal part of leaf, e.g. below the last furcation, costa becomes narrower, being 0.15–0.20 of the leaf width at this level.

Costa is translucent, at least at its margins, where cell outlines are apparent, and their size is mostly $60\text{--}70 \times 15\text{--}20 \mu\text{m}$.

In the distal portion of costa, 2–5 lateral branches 1–2 cells wide appear, spreading at narrow angle of $20\text{--}30^\circ$. These lateral branches are $20\text{--}40 \mu\text{m}$ wide, and the main part of the costa becomes markedly narrower after each branch spreads off.

Costa multistratosity. The costae in their marginal and distal parts (Fig. 3C, D) and in lateral branches (Figs. 3F, G, 4A) look unistratose. This partially disagrees with the original description of the costa of *Gomankovia* as multistratose, also challenging the costa definition and a way of its delimitation from the lamina. This is not the first time this question has been raised in the description of Permian mosses. Thus, Neuburg (1960) in the description of a number of Permian moss genera already mentioned that costa is multistratose but at some places it is unistratose. TEM observations of the costa

transverse sections of three specimens were done for *Gomankovia* (Figs. 5–6).

Since the material of *Gomankovia* was compressed due to multi-ton pressure, its cellular structure was strongly modified. However, the relative thickness of cells walls, their curvature, and rare occurrence of thick-walled cells allowed us to restore leaf costa anatomy to a certain extent.

Width of laminal cells, ca. $30 \mu\text{m}$, could be measured in TEM images as a distance between the neighboring joints of longitudinal and surface cell walls (Fig. 5G, arrowed); it agrees well with what can be measured under light microscope (Fig. 5A–C). In TEM images of leaf transverse sections, longitudinal cell walls are mostly strongly curved; however, their measurements in better seen sections (Fig. 5D) revealed that thickness of leaf lamina in *Gomankovia* was between 10 and $15 \mu\text{m}$. Leaf lamina may look as bistratose at places, with alternating ticker and thinner strips (Fig. 5G); however, it is likely the result of a very tight pressure which caused deformation of leaves and their irregular compression. True bistratose places in the marginal part of costa can be recognised by the unequivocal joints of three cells walls (Fig. 5D), whereas in Fig. 5G, numerous 'pseudo-joints', resulted from strongly curved and partly broken cell walls,

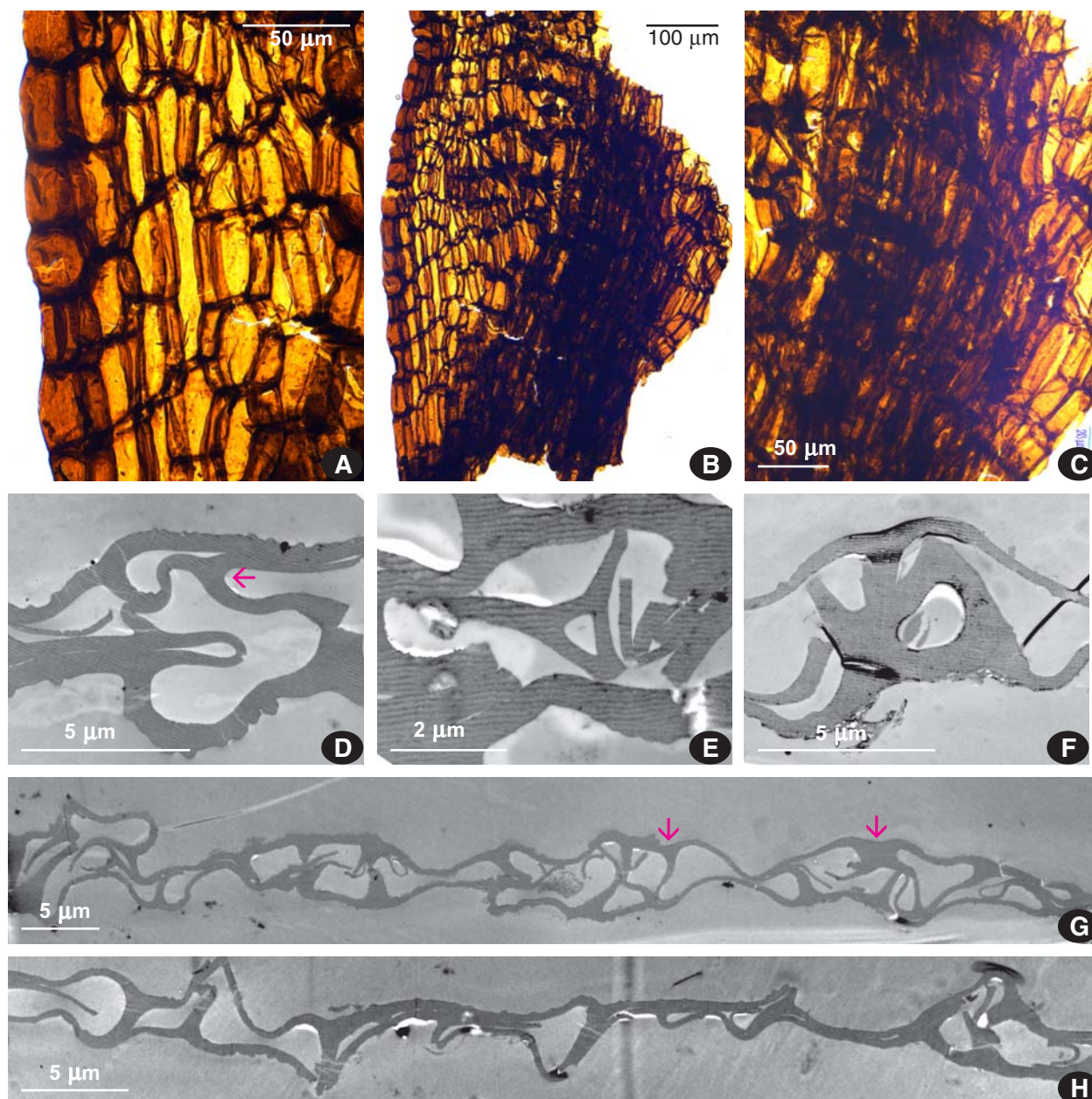


Fig. 5. *Gomankovia latifolia*, Aristovo, Upper Permian, Series CUT_P5. A–C: Leaf fragment, light microscopy; D–H: transverse sections of its costa (D–E) and lamina (F–H), TEM images. ‘B’ is a whole specimen, ‘A’ and ‘C’ are its close-ups. ‘E’ shows thick-walled cell within costa, and ‘F’ thick-walled cell within unistratose lamina. See text for discussion.

are seen. Even in the obviously bistratose part of costa, places with apparent joints of three cell walls were rather few (Fig. 6B, arrowed).

Surface cell walls are relatively equally thickened on both sides of leaf (Figs. 5G–H, 6A), being 0.4–0.7 μm thick. In bi- or multistratose part of the leaf, i.e. in the costal part, the abaxial cell walls are 10–25% thicker than adaxial ones, ca. 0.8–1.1 μm vs. 0.7–0.9 μm . Internal cells walls are still thinner (Figs. 5–6), considering the thinnest of them, because the thicker ones could appear due to an oblique position to sectioning.

However, few cells with thicker walls are noteworthy. Fig. 5E shows the section of one triangular, thick-walled cell within bistratose costa. Its relation to neigh-

boring cells is unclear because their walls are strongly broken. It is interesting that only one such cell, resembling stereid cells in costae of extant mosses, was observed in costa section of this specimen. It is also surprising that the second thick-walled cell was found within unistratose part of lamina (Fig. 5F). The only possible explanation of its position is that it belonged to the tip of lateral branch of costa, similar to that shown in Fig. 4A (arrowed), where thicker walls of its cells are apparent. This ‘unicellular costa’ was found so far only once (unless Fig. 5E is not considered as one of its variants). Likewise, in the section of another series (CUT_P10), a similar triangular thick-walled cell was found only once (Fig. 6C) within the bistratose part of section.

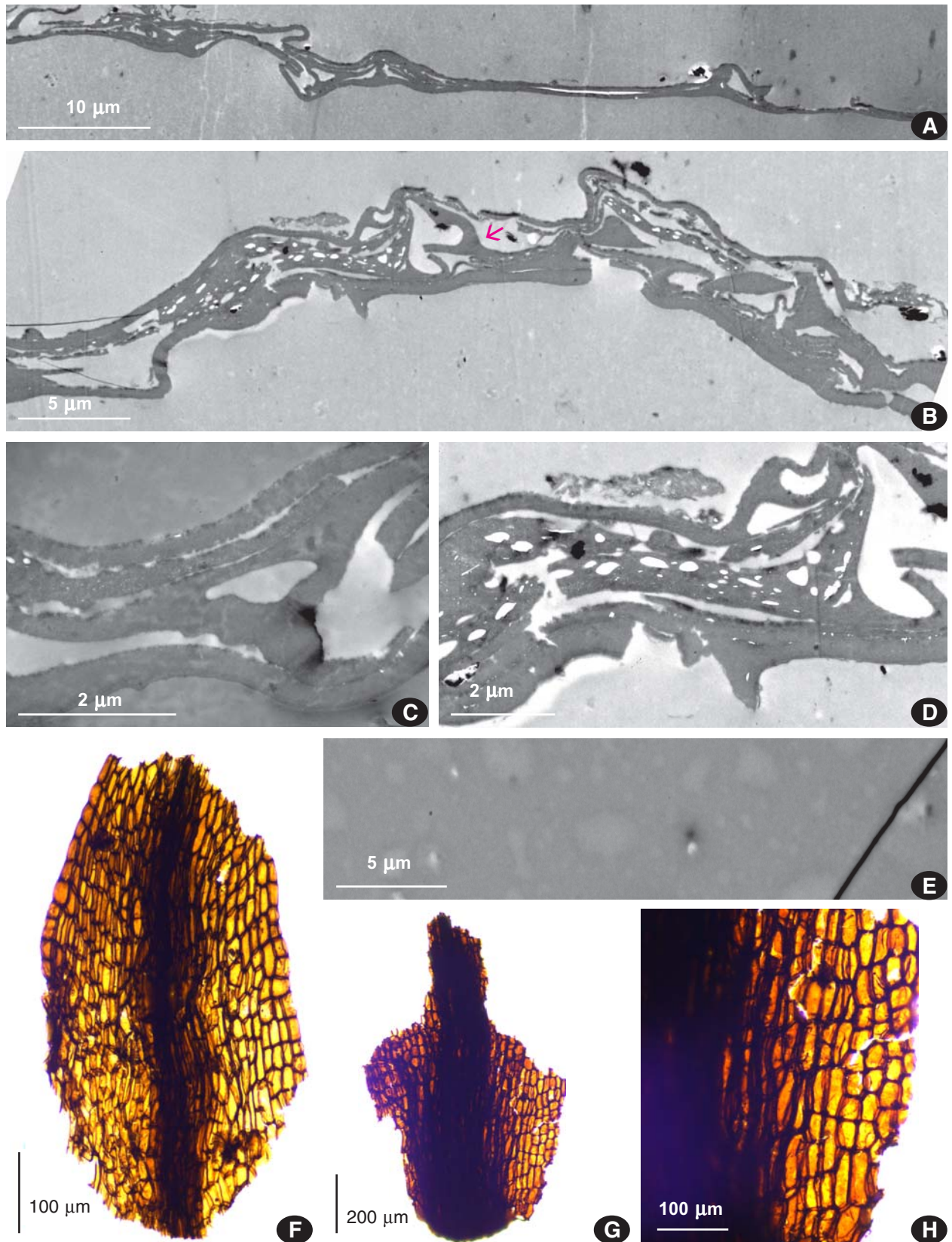


Fig. 6. *Gomankovia latifolia*, Aristovo, Upper Permian. A–E: Transverse sections of costa and lamina (A) and costal parts (B–E) of leaf fragments show in F–H (light microscopy). Series: CUT_P10: A–D, F and CUT_P4: E, G–H. 'C' shows thick-walled cell within costa, 'B' and 'D': transverse sections of costa, showing perforated cell walls. 'F' and 'G' are whole specimens, 'H' is close-up of 'G'.

Another interesting structure in the series CUT_P10 is the strongly perforated transversal or subtransversal cell wall within the costa (Fig 6B, D). Numerous perforation are ranging in size from 0.07 to 0.5 μm , which might represent food-conducting cells (Ligrone *et al.*, 2000), though the excluding of artifact requires additional studies.

The CUT_P4 series comprises the section of thick costa near leaf base (Fig. 6 E), where it has a complex multistratose structure, albeit with numerous broken cell walls.

Small papillae occur on some outer cell walls in *Gomankovia* (Fig. 5D, G–H); however, their presence is not regular, so the artifact caused by fossilization is also possible.

DISCUSSION

The original description of *Gomankovia* included its comparison with the extant family Funariaceae, especially with *Physcomitrium*, and with Splachnobryaceae, the genus *Splachnobryum* (Ignatov, 1990). Both these groups have superficial similarity with *Gomankovia* in lamina areolation, but differ from it in a complex and regular structure of costa.

In the transverse sections of costa in *Gomankovia*, many cell walls were broken, thus hampering understanding of its structure; however, the absence of stereid bands and regularly differentiated epidermal layers was apparent.

The most outstanding feature of this genus is the lateral costa branching. In extant mosses, the costa is forked in many hypnalean taxa, but one costa with several branches is known only in *Atrichia*, and even in the latter genus, the branches are spreading from the central costa only at its base, i.e. the main costa is perfectly unbranched almost throughout.

An occasional and vestigial costa branching was reported for protosphagnalean mosses by Neuburg (1960, Fig. 3), but in their case this pattern is never that conspicuous as in *Gomankovia*; furthermore, superficially these two groups look completely different. Nevertheless, the circumscription of the order Protosphagnales was recently challenged by Ignatov & Maslova (2021), who suggested to include in it the genus *Rhizinerites*, a moss which lacks most specific features of protosphagnalean mosses. The invariably differentiated leaf border and costa strongly broadened to the leaf base are other similarities between *Gomankovia* and protosphagnalean mosses. These features, however, are not rare among other mosses, so they contribute only a little to the decision on the systematic position of *Gomankovia*. Further data on either *Gomankovia*, or other similar Paleozoic mosses may help to approach the solution.

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