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ARVILDIA, AN UPPER PERMIAN MOSS AND ITS POSSIBLE RELATIONSHIPS

ARVILDIA, ВЕРХНЕПЕРМСКИЙ МОХ И ЕГО ВОЗМОЖНОЕ РОДСТВО

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Abstract

New collections of a Late Paleozoic moss *Arvildia* allowed us to circumscribe its morphology more precisely than it has been done earlier. Despite of the compression type of the material preservation, it was possible to embed the material from bulk maceration in epon-araldite resin and study it by a series of thin and ultrathin sections with light and transmission electron microscopy. The weakly differentiated leaf costa in the transverse section and thick-walled and strongly bulging leaf cells support possible relationships of *Arvildia* with Andreaeopsida rather than with Dicranidae, as it was supposed earlier. This study also shows that the cell damage differs in different parts of leaf and therefore such studies of compression highlight some biomechanical properties of moss leaves.

Резюме

Новые коллекции верхнепалеозойского мха из рода *Arvildia* позволили описать его морфологию более точно, чем это было сделано ранее. Несмотря на компрессионный тип сохранности материала, было возможно после объемной мацерации залить его в эпон-аралдитовую смолу, сделать тонкие и ультратонкие срезы и изучить их с помощью световой и электронной трансмиссионной микроскопии. Такие признаки, как слабо дифференцированная на поперечном срезе жилка и клетки с сильно выпуклыми стенками, свидетельствуют скорее в пользу гипотезы о родстве *Arvildia* с Andreaeopsida, чем с Dicranidae, как предполагалось ранее. Было также показано, что повреждение клеток в результате компрессии различается в разных частях листа; подобные исследования подчеркивают некоторые биомеханические особенности листьев мхов.

KEYWORDS: fossils, bryophytes, Russian Platform, Andreaeales, Dicranales, SEM, TEM, anatomy

INTRODUCTION

The recent advances in the reconstruction of moss phylogeny are conspicuous (Liu *et al.*, 2019; Bechteler *et al*., 2023). However, calibration of the origin of different moss lineages differs greatly in various reconstructions (Newton *et al.*, 2007; Laenen *et al.*, 2016; Bechteler *et al.*, 2023), mainly because of the differences in selection of fossils records for the molecular tree calibration. This makes the study of the moss fossils of a great importance for best calibration of evolutional events and understanding their evolution in a whole.

Paleozoic moss fossils are known so far from a limited number of localities in the world (Tomescu *et al.*, 2016; Ignatov & Maslova, 2021). The only exception is the territory of the northern Asia, the Angaraland in Late Paleozoic time. All mosses known from most localities in that area belong to protospagnalean and their closest relatives. Neuburg (1956, 1960) described as many as nine genera of mosses from the Angaraland, referring three of them to the order Protosphagnales, and six to the order Bryales. However, Ignatov (1990) doubted that Permian mosses from the Angaraland comprise two distinct lineages. Later, Maslova *et al.* (2012a, b) and Ivanov *et al.* (2018) concluded that most mosses described by Neuburg are likely protosphagnalean, a lineage probably not represented in the modern flora at all.

Mosses other than protosphagnalean were found in the Late Permian deposits of the Russian Platform by Gomankov & Meyen (1986), and the richest of them appeared to be Aristovo. Ignatov (1990) additionally studied collections of Gomankov and Meyen, as well as collections of Ignatiev from the same locality and reported for Aristovo nine moss genera: *Arvildia, Gomankovia, Aristovia, Protoochyraea, Ignatievia, Serviktia, Protosphagnum, Palaeosphagnum*, and *Vorcutannularia*. Three latter species have a protosphagnalean cell dimorphism in the leaf lamina, while the former six species have a bryoid areolation pattern.

These mosses from the bulk maceration were excellently preserved, retaining almost complete leaf cell structure. However, these samples were collected along with embryophyte fossils for the general paleobotanical exploration, and therefore the number of moss samples was limited. No other methods than the study samples mounted in

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Canadian balsam were applied for that collection in the course of preparation of publication of Ignatov (1990).

In 2022 we had an opportunity to collect an additional material in Aristovo, and it was studied with some additional methods, revealing features not studied previously. Additional data on the structure of already known and putatively new moss genera is under preparation for other papers. Here we provide an expanded description of only one species, *Arvildia elenae* Ignatov. The only other species of the genus, *A. obtusifolia* Ignatov, was known solely by the holotype (Ignatov, 1990), and in a new collection we obtained only one its leaf fragment, thus it will be discussed here only briefly.

The excellently preserved material of *Arvildia elenae* shed some more light on the structure and possibly on the affinity of the genus *Arvildia*. Also, the present study explores the possibilities of obtaining new data from the fossils preserved as a compression.

MATERIAL AND METHODS

Locality. The material for the present study was collected from the Aristovo, Vologda Region, Velikoustyugskii District, right bank of the Lesser Northern Dvina River 100 m upstream the Aristovo pier.

Meyen & Gomankov (1986) referred the deposits from Aristovo to the Vyatkian Horizon, the Upper Tatarian Substage, the Upper Permian, now referred to the Wuchiapingnian of the Lopingnian Series (Gomankov, 2002).

Gomankov & Meyen (1986) provided a description of the vegetation of this locality. Moss remains were associated with *Tatarina* pteridosperm 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.

Material. The plant-bearing deposits consist of grey and dark-grey argillites. Collected argillites were wet, and we tried to bring all this material into the lab in a wet state, avoiding possible fragmentation that happens if argillite dries. Pieces of argillites were placed in plastic boxes and wetted by water with fungicide compounds. In the lab, the material was sunk in disodium EFTA solution for two weeks to extract calcium content before the further solution in hydrofluoric acid. After washing, the plant remains were sorted and most of them were mounted in slides in glycerol jelly using a standard protocol. Few larger specimens, before embedding, were studied and photographed in water under a light microscope and compound microscope.

Microscopy and photography. Before mounting in glycerol-gelatin slides or in epon-araldite resin, material was photographed under the light microscope Nikon SMZ-25 with objective lens 2x and Olympus SZX16 with objective lens 1.6x with digital camera Infinity 4-4. Most specimens in glycerol-gelatin slides were photographed under light microscope Olympus CX43 with camera Infinity 1-2 and Olympus BX53 with camera Infinity 3-3. Z-stacks of several images were obtained by Nikon SMZ-25. Olympus SZX16 images were processed by Helicon-Focus 4.50 (Kozub *et al.*, 2008).

Destructive studies. *Arvildia* remains were not numerous, some of them were broken and incomplete, and therefore providing not as much additional information about the overall structure of this moss. Four specimens (one shoot, one almost complete leaf and two leaf fragments) were selected for anatomical destructive studies. The following methods were used:

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. Sections were placed on glass slides without mounting medium, arranged in four rows by 10 sections on each slide, which makes easy to find out the distance from the end of a specimen. Sections were photographed under light microscope Olympus BX53 with long working distance objective lens 100x/0.80.

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, or lead citrate, or ammonium molybdate.

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.

2) SEM SNE-4500M observations. Material from bulk maceration has been glued on carbon tape upon aluminum stubs and coated by gold without any additional preparation. Studies were conducted at 20 kV, using SE mode, with the specimen inclinations up to 50°.

3) SEM Thermoscientific Quattro S equipped with field emission gun studies. Material from bulk maceration has been glued on carbon tape upon aluminum stubs and observed without any further preparation. We did not use gold or platinum coating in order to avoid a risk of material damage during such a coating. Observations were conducted at the accelerated voltage 15 kV, at environmental SEM (ESEM) mode, at the air pressure ca. 500 Pa, under 15 kV, using SE mode.

MATERIAL DESCRIPTION

General comments. The plant fragments referred here to the genus *Arvildia* are fairly diverse. Ignatov (1990) combined in this genus moss remains with thick costa and dull, isodiametric, round-hexagonal laminal cells, which are hardly transmitted by lower light of microscopes, so the cells in many leaves illustrated in the original description are not clearly seen. Even in the holo-

type, the border between costa and lamina is not apparent in the upper part of leaf (Ignatov, 1990, plate 1, fig. 14), despite the laminal cells in *Arvildia* are unistratose, as far as it is known.

The smaller shoots with less opaque lamina and the smooth, short rectangular (vs. bulging, isodiametric) laminal cells can be assumed to belong to another taxon, but the presence of intermediates suggests better to retain them as one taxon.

When evaluating a variation, we also kept in mind the variation patterns common in extant mosses. By this reason, we refer to the same species one much larger and broader leaf, which will be illustrated and discussed below, as a putative perichaetial leaf, because it: (1) has hardly translucent, isodiametric and bulging laminal cells and stout costa; (2) fits the pattern of differentiation of perichaetial leaves in modern mosses; (3) co-occurs with 'average' leaves and shoots of *Arvildia*.

The descriptions and illustrations of *Arvildia* in the present paper are arranged mostly by methods of observation rather than the morphological traits. The general observations are followed by high vacuum SEM observations, anatomical section studies under light microscope (LM) and then TEM studies for the same specimens. Finally, the observations on low vacuum SEM illustrate possibilities of that approach.

Light microscopy

In our new collections, *Arvildia elenae* is represented by six fragments of shoots. Four of them were mounted in slides, one was used for transverse cutting series (CUT2), and one was used for low vacuum SEM observation and then mounted in slide.

Shoot fragments are up to 2–3 mm long (Figs. 1–2), they were probably erect, as their foliage is julaceous, dense, and 8–10 leaves are crowded in the apical part of shoots (Fig. 1). Leaves are overlapping each other by their bases, comprising the leaf arrangement in dense spiral, which is common for extant mosses. Below the apically crowded leaves, as well as in thinner shoots and in shoot fragment with broken off apical part (Fig. 2), the leaves are more remote. In places where the stem is exposed, it is 0.25 mm wide, its epidermal cells look inflated, ca. 25–30 μm wide and 120–200 μm long and maybe still longer, but this is not clearly seen.

On one shoot, we observed a group of several round cells and a conspicuously larger cell in the center of this group; they were markedly contrasting with other epidermal cells (Fig. 1C). We interpret the larger central cell as an apical cell of the branch bud. Arrangement of cells around it and also their position in the leaf axil supports this assumption. Cells around branch apical cell do not form foliose structures, comprising the pattern characteristic for most extant mosses except for the terminal group of subclass Bryidae (especially orders Hypnales, Bartramiales, and Hedwigiales). There is no evidence if this dormant bud comprises a primordium of vegetative or generative shoot.

Leaves of shoots in Fig. 1 are appressed or erect, straight or slightly incurved or recurved in distal part. The longest leaves are up to 1.5 mm long (in the previous collection, one exceptionally long linear-lanceolate leaf was as long as 2 mm), while most leaves are about 1 mm long and 0.25–0.30(–0.35) mm wide; width of costa at leaf base is ca. 100 μm, as seen in leaves on shoots in Fig. 1.

Cells of upper leaves are mostly distinctly bulging, isodiametric, ca. 12 μm on average. However, remotely arranged leaves, which are situated below the crowded apical leaves (see Fig. 1A"), are more similar in their areolation to the leaves from smaller shoots, as shown, e.g., in Fig. 2. In such shoots leaves are more remote, many cells are short rectangular, similar to the pattern found in a previous study (Ignatov, 1990). However, towards the leaf apex laminal cells become shorter and somewhat bulging (Fig. 2A), and a similar tendency to cell shortening is observed in the basal part of leaf (Figs. 2D, F).

Stem epidermal cells in smaller shoots are 15–20 mm wide and over 100 mm long (Fig. 2E), e.g. narrower that in the previously described specimen (Fig. 1C). Among these cells, one triangular structure has been noticed (Fig. 2E), with a smaller triangle inside the bigger triangle. The triangle may point to a branch primordial structure; however, as its position is not axillary, the assumption of its possible identity would be too insufficiently based.

Rhizoids are axillary, rare. One rhizoid was clearly seen in the previous material in axil of leaf in small-leaved flagellate shoot, referred to *A. elenae* because of dull leaves with broad costa (Ignatov, 1990). The new collection includes only transverse and oblique sections, which we interpret as rhizoids (see below).

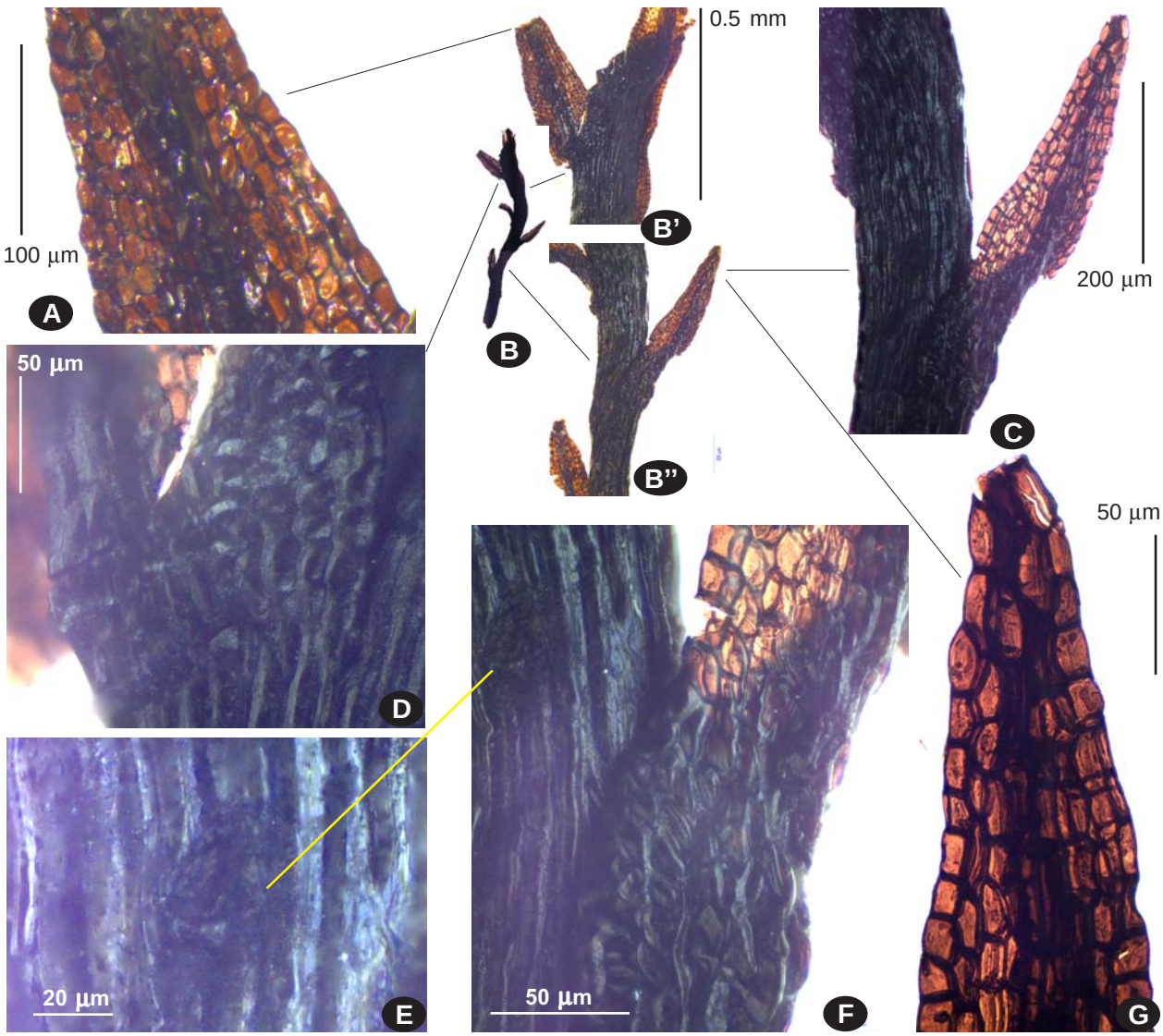
Leaves. In addition to foliate shoots, the bulk maceration material includes several leaves of lanceolate shape, gradually tapered to apex, and therefore referred to *Arvildia elenae* (Fig. 3). One almost complete leaf has an obtuse apical part, and therefore it is referred to *A. obtusifolia* (Fig. 4, A–C). Another large leaf of *Arvildia* sp. (Fig. 4, D–G) is discussed below.

Leaves of *Arvildia elenae* are mostly lanceolate (Fig. 3), long acuminate or moderately acuminate, apparently quite fragile, so leaf acumina in most specimens do not retain, but their approximated size is as was already mentioned for leaves on shoots: (0.7–)1.0–1.5(–2.0) mm long, 0.25–0.30(–0.35) mm wide; leaf costae constitute from quarter to more than a half the leaf width, they are opaque, and the juxtacostal cells are also hardly translucent. Margins are plane and entire or crenulate due to lateral bulgings of marginal cells, especially in acumina (Fig. 3A–C, H), but in leaves where cells are mostly isodiametric (Fig. 3E), they make margin crenulate further down to the basal part of leaf where cells are short rectangular. A less prominent bulgings occur in the area, where marginal cells are transversely rectangular (Fig. 3G).

Leaf laminae in some leaves of *Arvildia elenae* consist of isodiametric cells almost throughout (Fig. 3G, H), or only distally (Fig. 3E), or otherwise most cells in the broad part of the leaf are rectangular (Fig. 3F).

Fig. 1. *Arvildia elenae.* Three shoots (A: A111_2; B: A112_1; C: A111_1) from new collections from Aristovo, showing their habit, foliage and in 'C' also the apical cell of branch bud. It is in the axil of leaf that almost totally fell off (the basal row of leaf cells is marked by arrows). Bud cells differ contrastingly from the stem epidermal cells: the latter are elongate to linear, whereas the apical cell and cells around it are round.

Isodiametric cells are 10–20 µm in diameter, in leaf acumen sometimes to 29 µm; rectangular cells towards the base are longer, but of the same width or even slightly narrower, 15–25×10–18 µm (Fig. 3F), although in the previous collection from Aristovo there are cells up to 45 µm. Transversely rectangular cells along the margins are sometimes 9–12 µm long and to 15 µm wide. The cell walls in *Arvildia*, as well as in other fossil moss compressions obtained from the bulk maceration, are apparent as a double lines on junctions of the cells: one is on the upper surface of a studied specimen, while another one is on the lower surface. These junctions are fairly contrasting, looking almost black, and mostly well seen through the material of the dark brown substance of cell walls.



2. *Arvildia elenae* (A110_3), a rather small shoot with leaf laminal cells mostly short rectangular. A: leaf middle part, showing slightly shorter and more strongly bulging cells towards the apex; B: habit; C: leaf and its closeup in G; D & F: leaf bases clasping the stem, showing subquadrate cells in alar region; E: a putative dormant branch primordium, seen as a triangle among stem epidermal cells, with a smaller triangle in it (exposed tetrahedtal cell?).

Epi illumination makes leaves and other parts of the *Arvildia* plants black, which is seen in Fig.3A; it is especially contrasting by comparison between the same leaves photographed with epi (Fig. 3I) and transmitted illumination (Fig. 3J). Many specimens were therefore photographed with the combined epi and transillumination, which revealed a dark substance upon the cell surface, looking just as dirt, in *A. elenae* (Figs. 3B, D, E & 4F), *A. obtusifolia* (Fig. 4B) and *A.* sp. (Fig. 4D–F, 5B). At places, this dark layer looked quite homogeneous and continuous (Fig. 3B; Fig. 4F, left, below), but in other places it appeared as an irregular, patchy remains of a probably continuous layer. A similar and likely the same dark substance fills the fissures along the cell junctions. Another look at this dark layer under SEM is shown in Fig. 5H (and partly also 5C, F, I, N).

Leaf tips of *Arvildia elenae* are often broken off. However, even in the retained apices their cell structure is difficult to observe, because cells near leaf apex are strongly bulging and quite dull (Fig. 3B, C). One leaf acumen where the cell arrangement is clearly seen is shown in Fig. 3D. Its apical cell is bifacial, dividing obliquely and resulting in alternate cell arrangement, i.e. not unifacial, dividing transversely, and resulting in opposite cell arrangement as in most species of *Andreaea*. The areolation of leaves from small shoots (Fig. 2) also indicate most likely bifacial apical cells. The only case that can be tentatively interprted as unifacial, will be discussed below (Fig. 6A).

Two specimens shown in Fig. 4. we refer to *Arvildia* without serious doubt: both are similar to *Arvildia elenae* in having stout costa, dull, hardly translucent laminal cells of the same shape and with dark surface material providing them dirty appearance. The latter is consid-

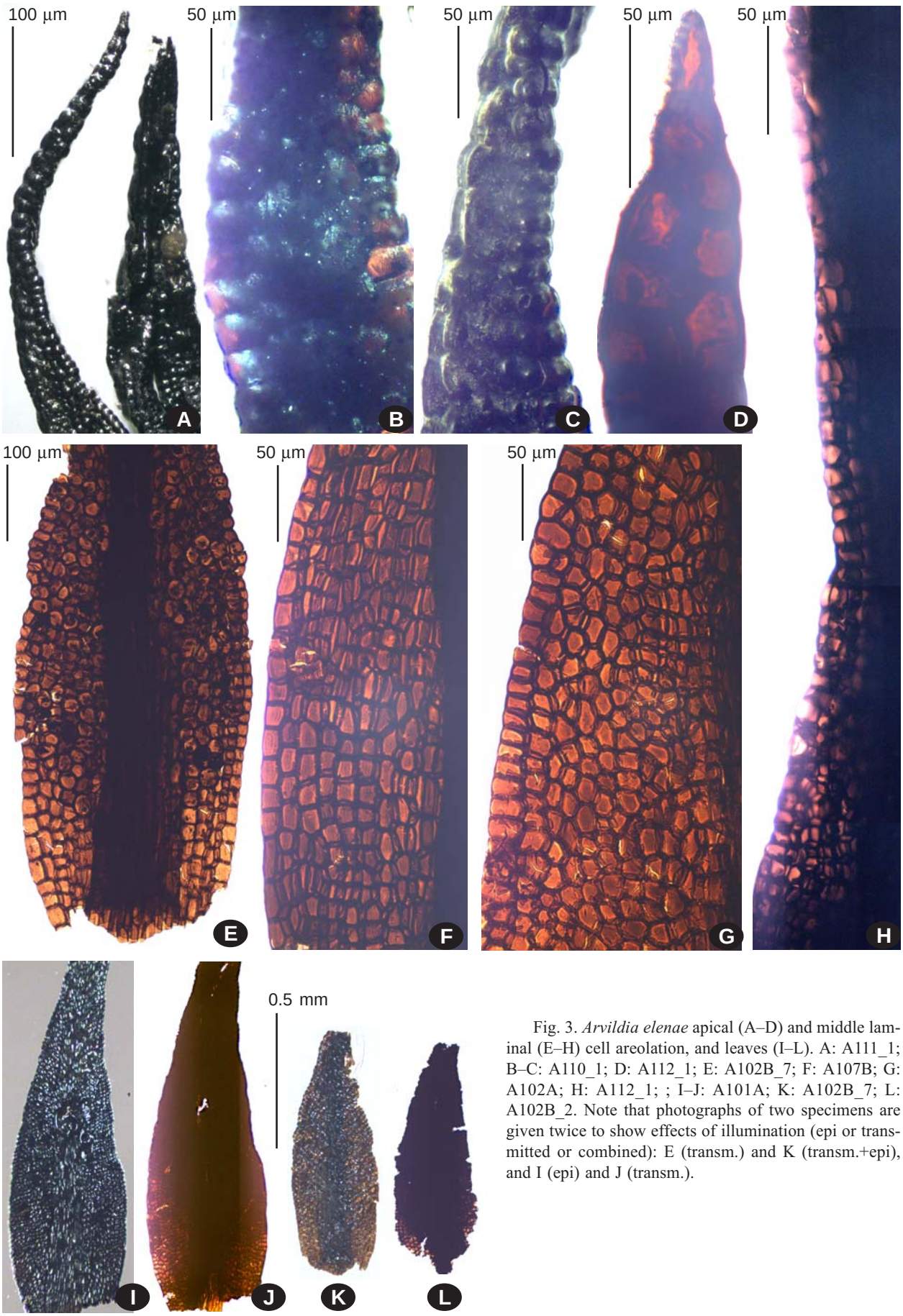


Fig. 3. *Arvildia elenae* apical (A–D) and middle laminal (E–H) cell areolation, and leaves (I–L). A: A111_1; B–C: A110_1; D: A112_1; E: A102B_7; F: A107B; G: A102A; H: A112_1; ; I–J: A101A; K: A102B_7; L: A102B_2. Note that photographs of two specimens are given twice to show effects of illumination (epi or transmitted or combined): E (transm.) and K (transm.+epi), and I (epi) and J (transm.).

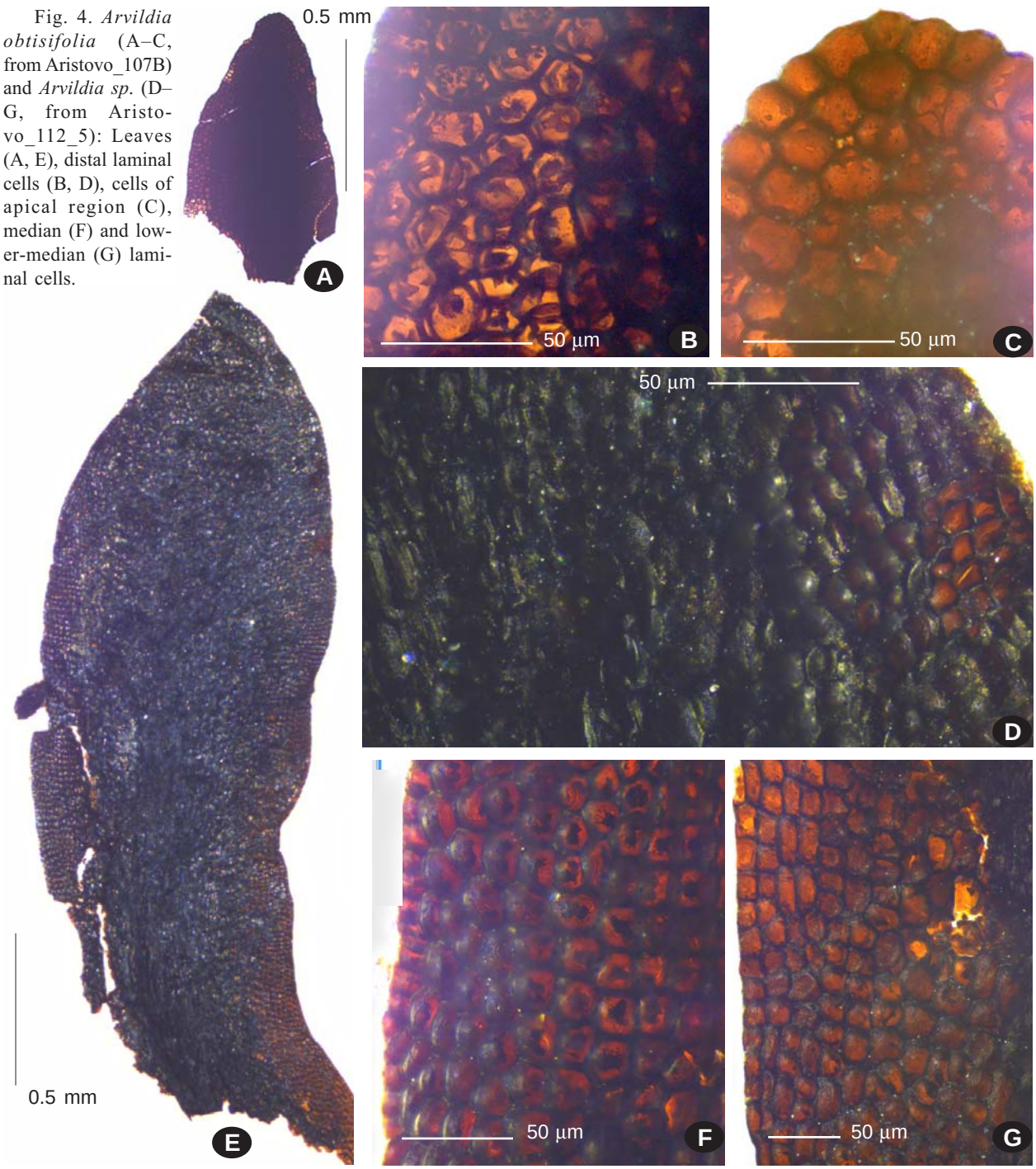


Fig. 4. *Arvildia obtisifolia* (A–C, from Aristovo_107B) and *Arvildia sp.* (D–G, from Aristovo_112_5): Leaves (A, E), distal laminal cells (B, D), cells of apical region (C), median (F) and lower-median (G) laminal cells.

ered as specific to *Arvildia*, as nothing similar was observed in about ten moss genera known from the same collection from Aristovo. However, these specimens differ from *A. elenae* in having rounded (Fig. 4A–C) or broadly acute (Fig. 4D–F) leaves, and the latter leaf is also considerably larger: its fragment (likely representing nearly complete leaf) is 2.9 mm long and 0.9 mm wide. We refrain from the description of one more species of *Arvildia* in this case. As it was already mentioned in general comments, we consider the variation patterns common in extant mosses. For example, the perichaetial leaves in species of the extant genus *Andreaea* differ similarly from much smaller stem leaves.

The paucity of *Arvildia* specimens precludes a well-based assumption that *Arvildia* sp. (Fig. 4D–F) and some larger leaves more broadly tapered to apex from the previous collection, and even *A. obtusifolia* comprise a series of perichaetial leaves, from smaller outer ones to the largest, called '*A.* sp.', which is treated as a putative inner perichaetial lead. Considering this indefinity in *Arvildia* taxonomy, the further discussed specimen will be referred to the genus *Arvildia* without the species level attribution.

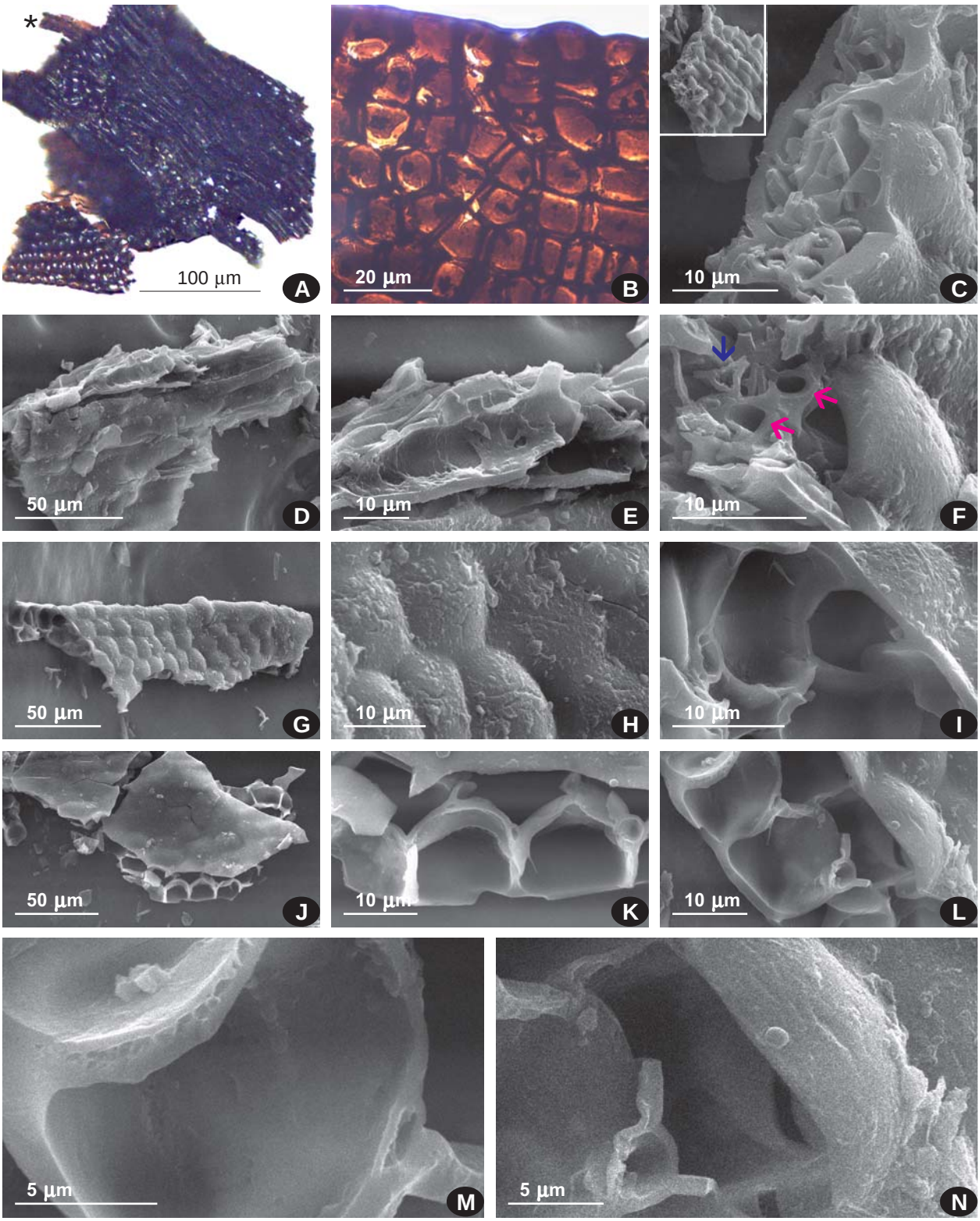


Fig. 5. *Arvildia elenae* leaf fragment (Aristovo_101A). A–B: LM images combined trans and epi illumination, showing main part of fragment used for SEM study (A), and its cells (B); C–N: SEM_SNE images; coated by gold, observations at 20 kv, high vacuum, SE detector. C, F: Costa breakage, showing a transverse view on its structure: note thick outer cell walls, mostly broken inner cell walls, and several intact cells with moderately thick-walled walls, having either round lumen (red arrow) or three-point star lumen (blue arrow). D and its closeup in E comprise the costal cells after partial removal of dorsal epidermis (place marked by asterisk in A): cells are elongate, with irregular material deposited on their inner surface; G–J: dorsal lamina surface; cell walls of lamina cells are convex, roughened from outside by minute raisings of cell walls; K–N: views of laminal cells from transverse and partly paradermal breakages: note that laminal cell walls are porose at places (M), and have moderately regular holes at the joints of three cell walls (K–N).

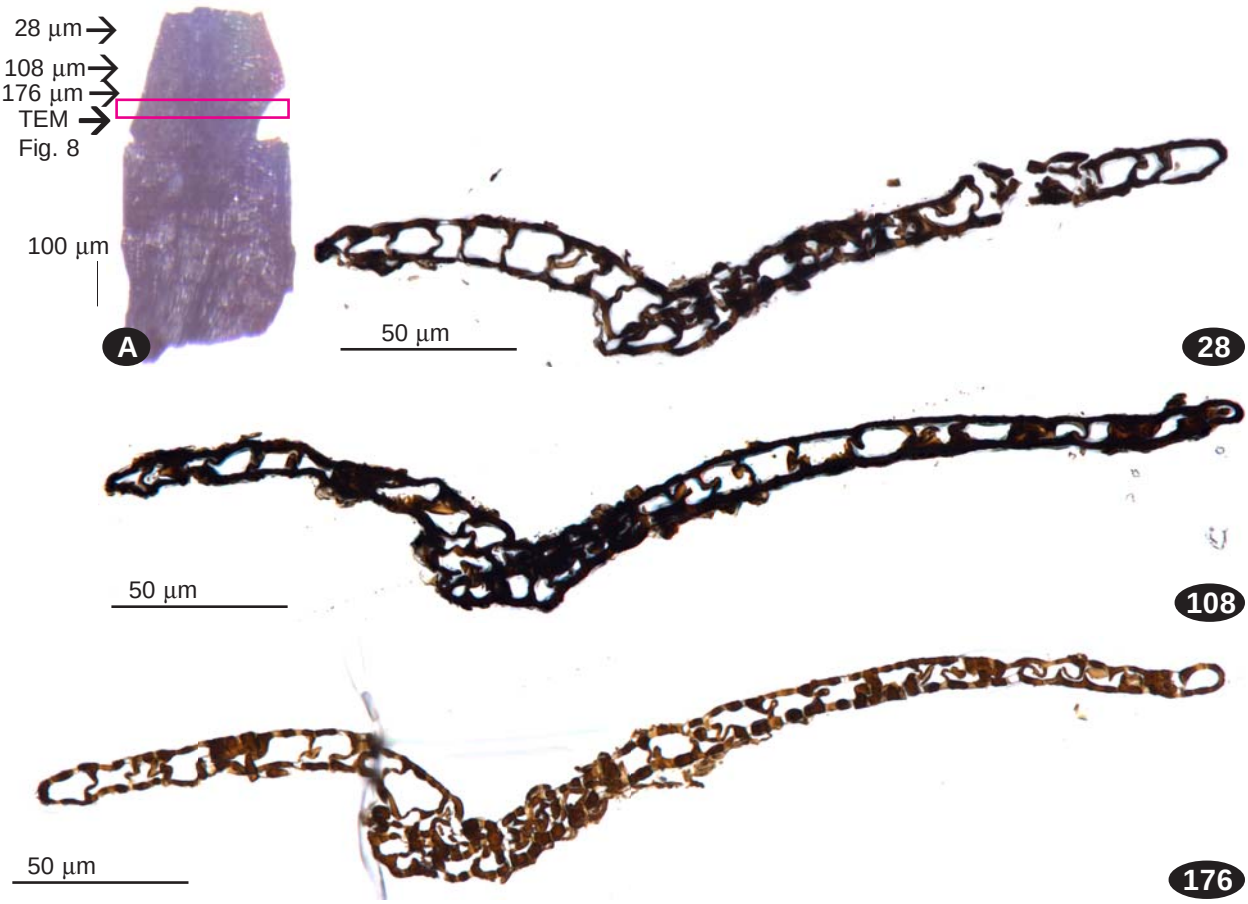


Fig. 6. *Arvildia elenae* (Aristovo_CUT3; LM). Leaf fragment (A) and its transverse sections, made at 28, 108 and 176 µm from upper end of the leaf fragment (see scheme in A). Sections 28 and 108 are 2 µm thick and section 176 is 1 µm thick. The cell walls in the two former sections are evenly dark brown, while in the 1 µm thick section they are variegate, with alternation of lighter and darker brown color (the color changes depending on breakages of cell wall material).

Leaf structure as it is seen under SEM

One fragment of *Arvildia elenae* leaf was selected for SEM studies (Fig. 5). It was partly broken already during bulk maceration. It was glued to the carbon tape, and additionally broken to see costa structure, which was possible by inclination of specimen to 50°. An observation confirmed that leaf of *Arvildia* has unistratose lamina with rather strongly bulging dorsal cell walls (Fig. 5B, G, H), which are well seen after the specimen inclination to 50°, while the similar surface looks much less bulging without inclination (Fig. 5J). Cells are isodiametric, 10–15 µm long and wide, and 10–15 µm thick, being up to 15 µm at the cell center, in the highest point of mammillae (5K–M), and ca. 10 µm at cell joint.

Thick-walled costal epidermal cells appeared to be only moderately damaged compared to thinner-walled inner costal cells (Fig. 5C, F), which failed to resist the pressure of fossilization and were comprised by a mess of broken cell walls. We were able to find among them only few unbroked cells with either round or three-point star lumina.

Outer walls of laminal cells are rough from outside, which probably corresponds to a dark layer seen under LM (Figs. 3, 4 and 5B), but under SEM this layer looks continuous (Fig. 5D, H).

Dorsal cell walls are convex, over 2 µm thick (M); ventral cell walls are slightly thinner, 1.0–1.5 µm (I–L). The cell junctions as they are seen in the subtransverse breakages (Fig. 5I–N) appear to have somewhat unexpected pattern: there are small round hollows in many junctions, although not in all of them. Ignatov (1990) discussed three types of irregular swelling found at the cell junction. Most of them occur irregularly and therefore they are referred to a probable effect of fossilization.

Series of anatomical sections

Three series of transverse sections of *Arvildia elenae* were done. They include a small leaf fragment (Figs. 6–8), an almost complete leaf (Figs. 9–10), and a small shoot (Fig. 11).

Sections were 2 and 1 µm thick, each having a certain advantage. The thicker sections were more stable in preparation, while the thinner ones were partly crumbling. In return, the 1 µm thick sections were more translucent, while 2 µm ones were dull and with fewer details visible (Fig. 6). The cell walls in 1 µm sections are variegate from the alternation of small, 1–3 µm long com-

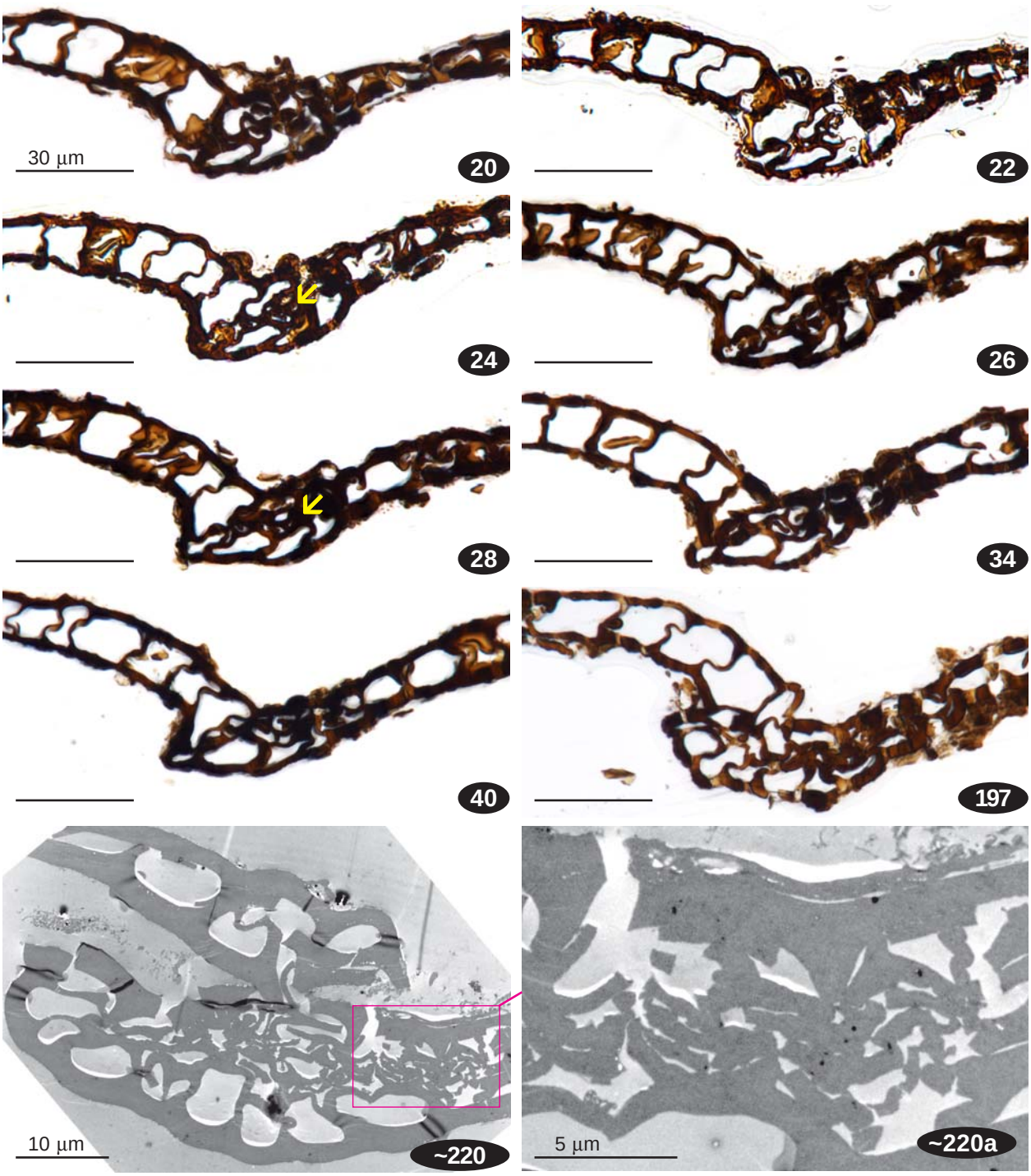


Fig. 7. *Arvildia elenae* (Aristovo_CUT3). Leaf transverse sections. Images '20'–'40' and '197' are LM photographs of 2 µm thick sections. All their scale bars are 30 µm. Two TEM images ~220 and ~220a are from 60 nm thick sections. Section positions are shown in Fig. 6A and the number of an image is its distance from the upper end on this leaf fragment, in µm. Cells with small lumens in costa are apparently substereids, showing a rather limited presence in the middle of costa (e.g. arrowed in '24' and '28'). However, they can not be detected for sure in other sections, because they could be misinterpreted as such among distorted cell walls (cf. ~220 and ~220a). TEM sections ~220 and ~220a also illustrate a very thick cell walls on dorsal leaf surface, so cells of the dorsal epidermis remained almost intact, contrary to mostly broken inner cells of the costa.

partments, differing in color saturation. The darker and paler parts are separated one from another by very thin, hardly visible cracks precluding spreadings of the color beyond these limits. It apparently is an effect of fossilization.

Series from a leaf fragment (Fig. 6) are relatively short, as the leaf was damaged in the middle. The studied part comprises a leaf portion, which is tapered from 350 µm wide (Fig. 6,'176') to 300 µm (Fig. 6,'28'). Despite the rather short distance between these sections, they differ

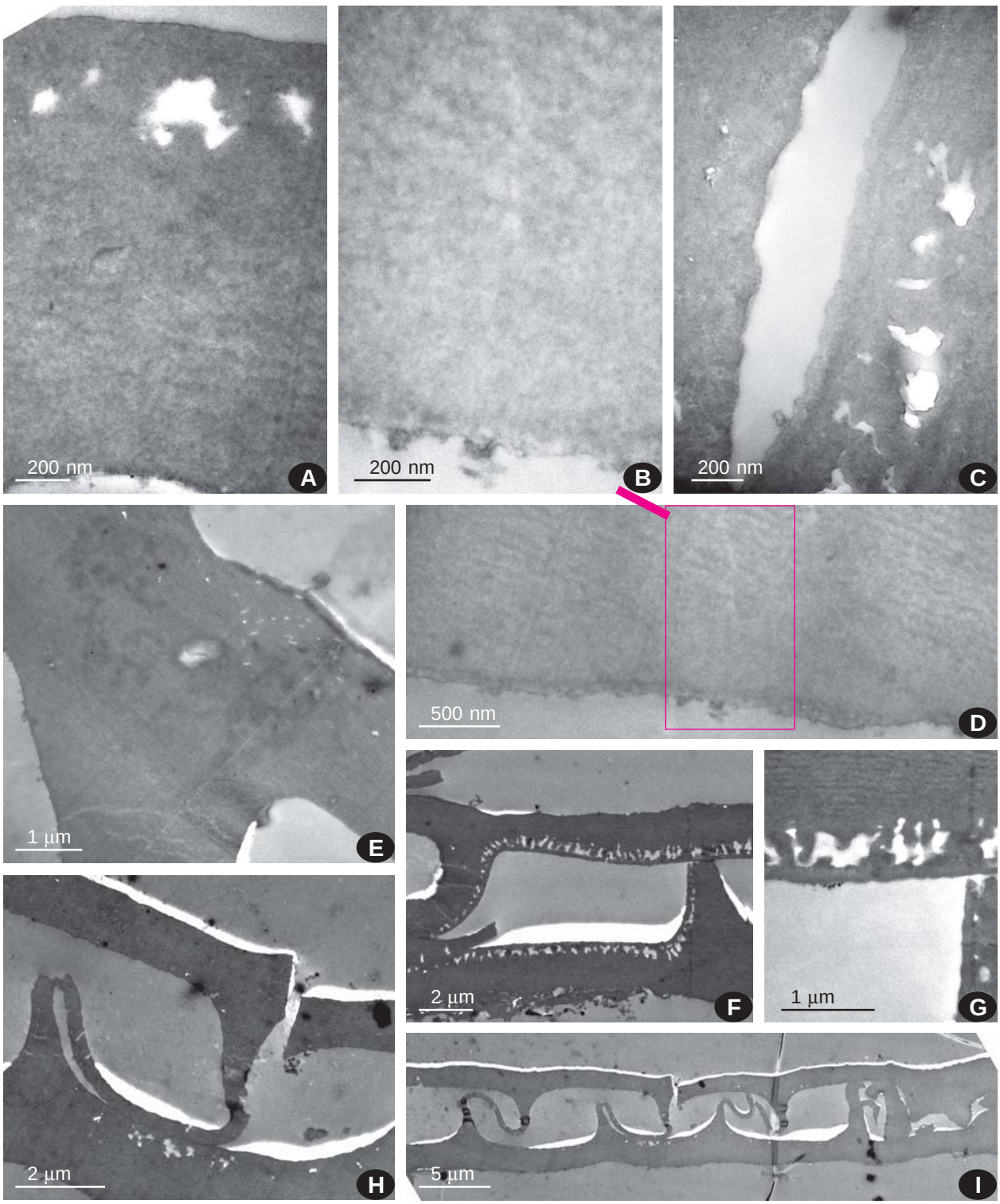


Fig. 8. *Arvildia elenae* (Aristovo_CUT3). Leaf transverse sections, TEM images of 60 nm thick sections, showing details of cell wall structure. Most cell walls are electron homogeneous, with slightly differentiated thin surface layer less than 100 µm thick (A–B, D). This thin layer is developed on the outer surfaces of cell walls and mostly on the dorsal side of leaves, which allows us to suggest their protective function, probably correspondent to the roughened surface of leaves shown in Fig. 6 F, H, I, N. Otherwise, the cell walls lack any apparent stratification. Cell walls faced inwards are usually lacking a well-developed layer on their surfaces, rarely it is indistict (C). Occasionally, cell walls are porose, having either a single pore at three cell joints (E), or extensive porosity shortly below the inner cell surface (F–H). The distortion during fossilization is severe (H, I): from the curved cell walls in between cells we may measure that the original leaf thickness was ca. 15 µm, i.e. twice thicker than after fossilization, when the leaf became only 7 µm thick.

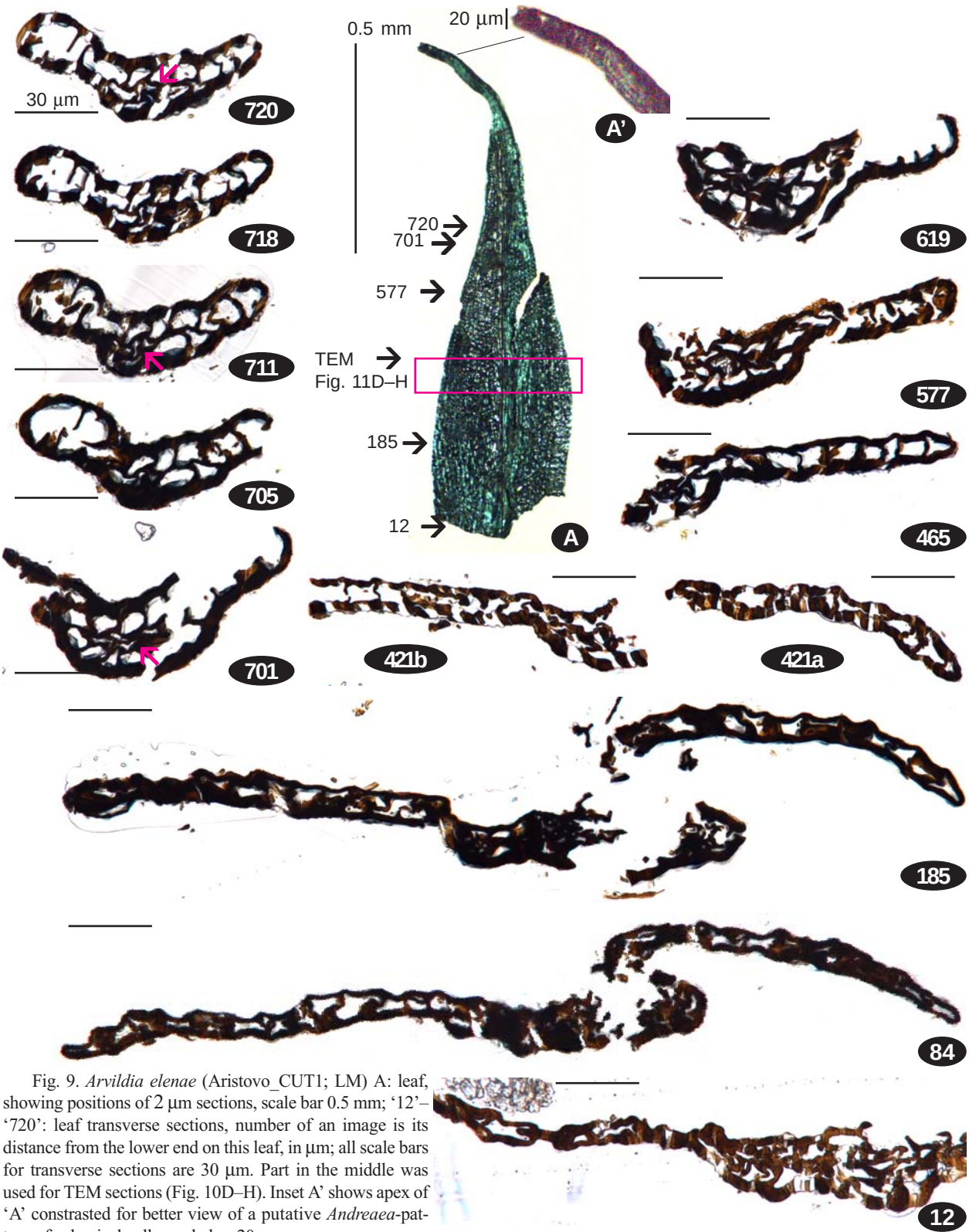


Fig. 9. *Arvildia elenae* (Aristovo_CUT1; LM) A: leaf, showing positions of 2 µm sections, scale bar 0.5 mm; '12'–'720': leaf transverse sections, number of an image is its distance from the lower end on this leaf, in µm; all scale bars for transverse sections are 30 µm. Part in the middle was used for TEM sections (Fig. 10D–H). Inset A' shows apex of 'A' constrasted for better view of a putative *Andreaea*-pattern of subapical cells; scale bar 20 µm.

markedly in that the intracellular walls are almost intact in the distalmost section, while they are severely distorted in the proximal ones. This effect can be, of course, due to unknown occasional circumstances, but, as it will be seen in further series, the same difference between upper and median laminal cells occurs there as well. Therefore, this is likely a rule that the intracellular walls are firmer in the distal part of leaf, while in the proximal leaf portion intracellular walls are thinner and become damaged much stronger.

Costa is poorly differentiated, but few cells with smaller lumina are seen in its middleup to the lowest section '12'.

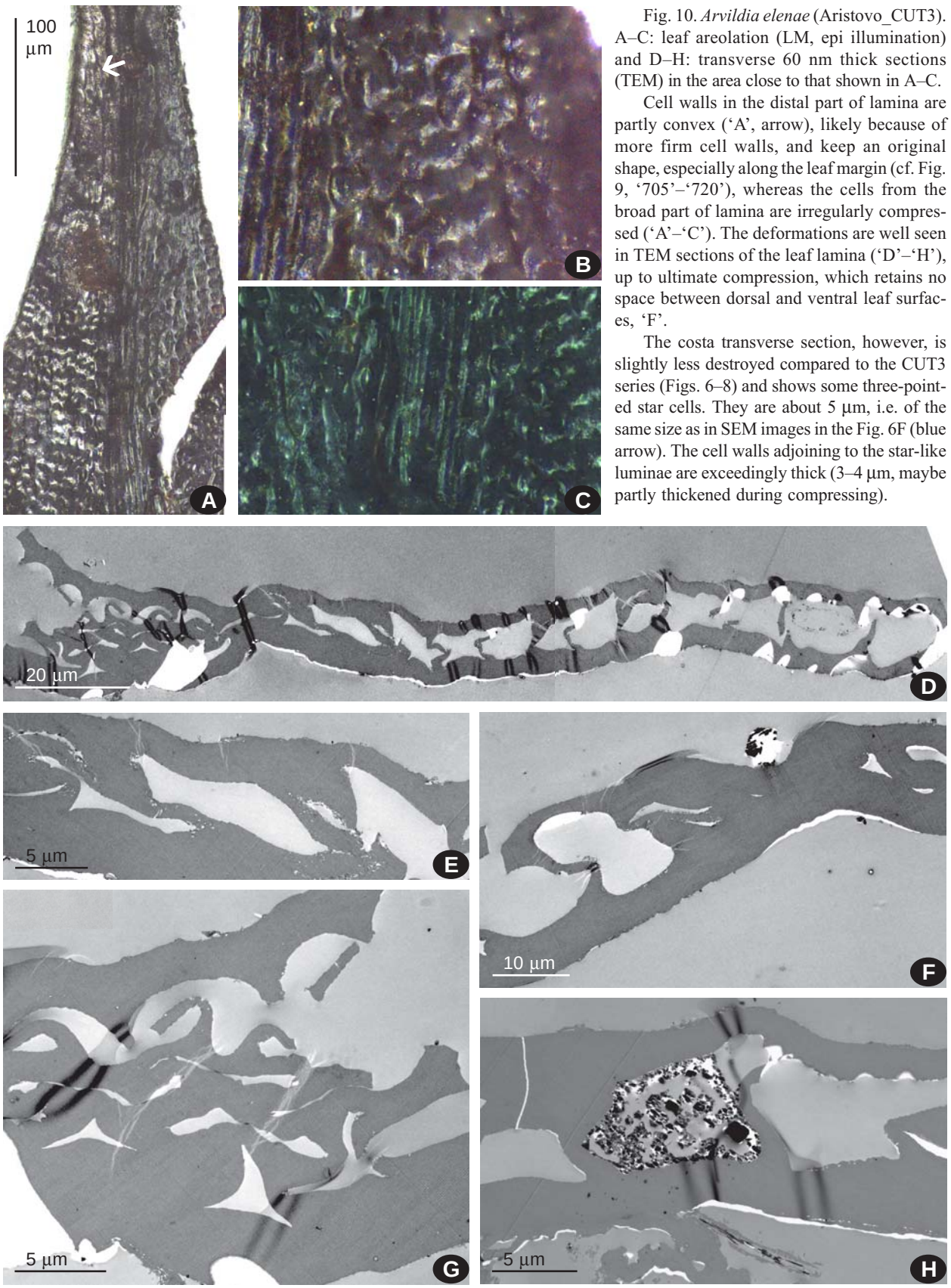


Fig. 10. *Arvildia elenae* (Aristovo_CUT3). A–C: leaf areolation (LM, epi illumination) and D–H: transverse 60 nm thick sections (TEM) in the area close to that shown in A–C.

Cell walls in the distal part of lamina are partly convex ('A', arrow), likely because of more firm cell walls, and keep an original shape, especially along the leaf margin (cf. Fig. 9, '705'–'720'), whereas the cells from the broad part of lamina are irregularly compressed ('A'–'C'). The deformations are well seen in TEM sections of the leaf lamina ('D'–'H'), up to ultimate compression, which retains no space between dorsal and ventral leaf surfaces, 'F'.

The costa transverse section, however, is slightly less destroyed compared to the CUT3 series (Figs. 6–8) and shows some three-pointed star cells. They are about 5 µm, i.e. of the same size as in SEM images in the Fig. 6F (blue arrow). The cell walls adjoining to the star-like luminae are exceedingly thick (3–4 µm, maybe partly thickened during compressing).

Considering an importance of costa differentiation, a separate plate is compiled for sections with clearer differentiation of a substereid group within the costa. This series comprises sections at the distance from 20 to 40 μm (Fig. 7). The substereids, e.g. the cells with smaller lumina, are apparent in images '22', '24' and '28'. In other sections, the flexuose and broken cell walls raise doubts in such interpretation. As it is seen in TEM images (Fig. 7, 220A, B), the narrow 'lumina' that might be assumed as such in many places, in fact, are an artifact. Therefore, a clear differentiation of costa is not invariably present in *Arvildia*, and the main proof of the substrereid presence in this genus comes from the SEM study (Fig. 5F).

Cell walls in TEM sections of *Arvildia* leaf lamina look almost totally electron homogeneous (Fig. 8). Only a thin surface layer less than 100 nm thick is somewhat differentiated in texture (Fig. 8A, B, D), probably partly corresponding to the black material in LM observations (Figs. 3–4) and SEM (Fig. 5F, H, I, N). These thin layers are developed on the outer surfaces of leaf cells, mostly on the dorsal side (Fig. 8B, D, I). Inner cell walls have only very subtile differentiation on their surface (Fig. 8C). Occasionally cell walls are porose, having either single pore at three cell junction (Fig. 8E), or shortly below the inner cell surface (Fig. 8F–H). The fact of their rarity indicates that they likely represent an effect of fossilization. However, as such porosity is much stronger expressed in the inner parts of cell walls, it also points to the cell wall differentiation which is otherwise unseen in TEM images.

The second series of sections is shown in Figs. 9–10. The specimen used for it represents the nearly complete leaf (Fig. 9A) and therefore is supposed to be more promising compared to the small fragment used for the first series (Fig. 6A). However, its sections appeared to be largely broken and crumbled, even when they were cut by 2 μm. The fallen off small pieces of cell walls do not preclude seeing the leaf features and cell wall details, such as their thickness and the fossilization deformations.

In the uppermost available sections, '720'–'711', the lamina is only three cells wide, the costa includes few cells with a small lumina, the substereids (arrowed). Similar to the first section series (Fig. 6), the most distal cells have fewer deformations in the walls between lamina cells (Fig. 9, '720'–'711'), so some of them are straight. The section at ca. 150 μm lower, '577', is much more damaged. Some sections further downwards have less damage, e.g. '465', but the general trend to the bigger deformations towards the leaf base is apparent.

TEM sections (Fig. 10 D–H) were done from this leaf at 300–400 μm from the base of its fragment. Cells at this level are rather strongly distorted, as seen from the photographs under the LM at about the same part of leaf. The deformations are well seen in TEM sections of the leaf lamina, up to ultimate compression, which retains no space between dorsal and ventral leaf surfaces (Fig. 10F).

The cell walls in the costa transverse section are slightly less destroyed compared to the CUT3 series (Fig. 7 '220'), and some three-pointed star cells are observed. They are about 5 μm, i.e. of the same size as in SEM images in the Fig. 5F (blue arrow), therefore we admit that their star-shape was original, despite the exceedingly thick (3–4 μm) cell walls near these star-shaped lumina suggest that their shape may appear during compressing. The available material does not allow us to solve the problem of the three-pointed star original shape.

The cell wall porosity in the section of the second series was never so strongly expressed as in the first series (e.g. Fig. 8F), although the stronger porosity was seen in few cell walls between laminal cells which are more strongly distorted (Fig. 10E).

The third series is shown in Fig. 11. The cuttings in this case were made transverse to stem of small shoot of *Arvildia elenae,* which is similar in many aspects to that shown in Fig. 2. The stem is only slightly wider than 100 μm and leaves are small, less than 0.5 mm long, with more rectangular, although slightly bulging cells. Leaves are remotely arranged.

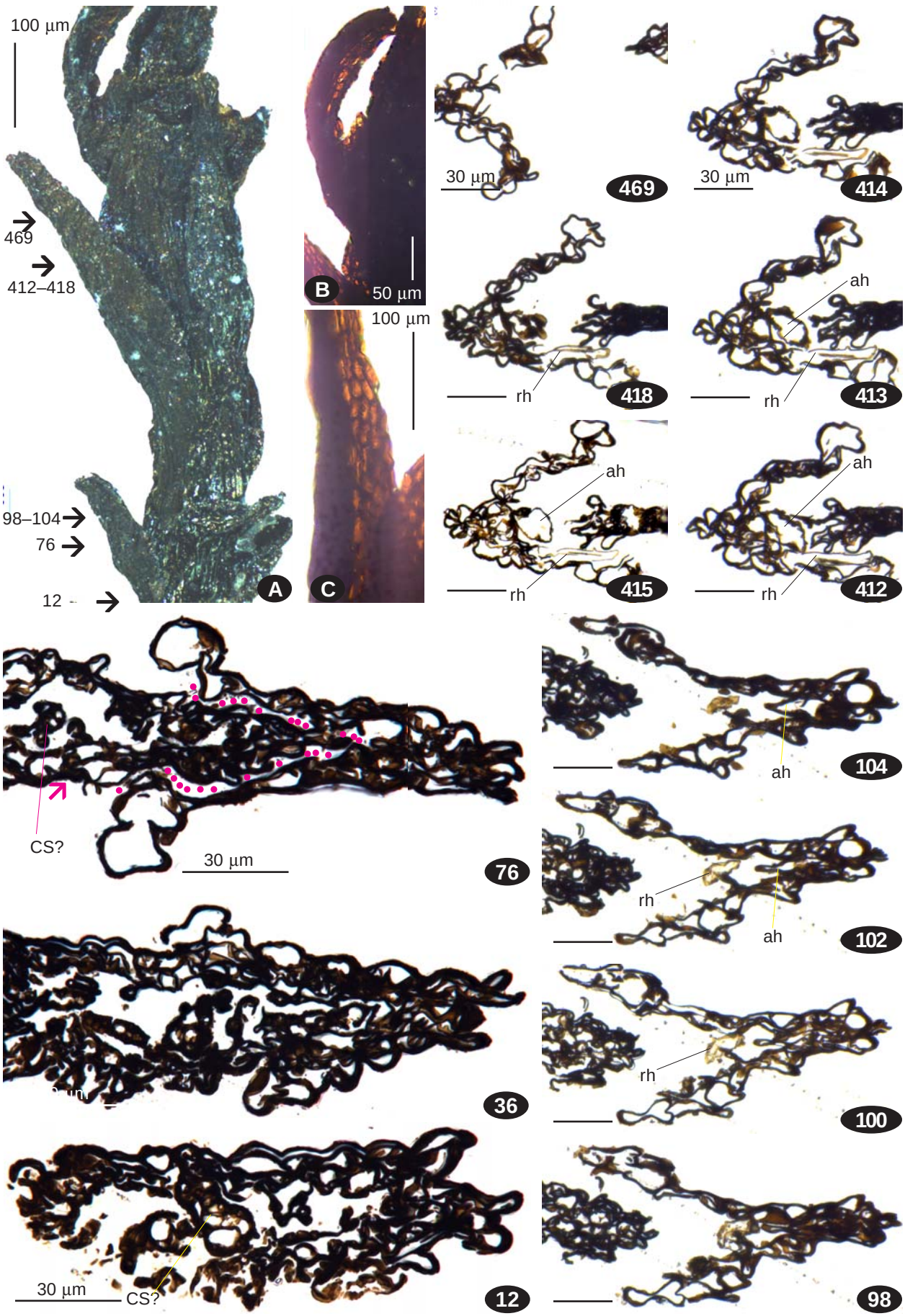
The stem in the lowest part of this fragment, in '12', and to a certain extent in '36' and '76', is only moderately compressed, while in more distal part, in '412' and further up, its cells are pressed, so individual cells are indiscernible.

Epidermal stem cells seen in lower sections are thick-walled and partly retaining their original shape (Fig. 11, '76'), being ca. 20 μm wide, i.e. similar to those found in shoots shown above (Figs. 1–2). Inner cortical cells are mostly not observed, apparently disappeared during fossilization because of their too thin cell walls. The presence of the central strand is questionable: there are cells in the central positions of sections with smaller lumina,

Fig. 11 (page 257). *Arvildia elenae,* Aristovo_CUT2 series; LM images. A–C: shoot; '12'–'469': section images numbered by a distance from the lower part of the shoot. Scale bars for all sections are 30 μm and are equal, except for '12', '36' and '76', where magnification is slightly higher). Shoot photos were taken for plant embedded in resin (A), with epi-illumination, and before embedding, in transmitted light. Note relatively less damage of the leaf marginal cells. Sections position is shown in A.

Sections are showing part of stem (severely compressed and with strongly distorted and compressed cells) and basal parts of leaves, mostly adjoining to stem by their base. Epidermal stem cells were relatively thick-walled and therefore some of them probably retained original shape (e.g. '76' arrowed), although most of them are strongly distorted. Inner cortical cells dissappeared during fossilization, probably because of their too thin-walled structure. The presence of the central strand is questionable (CS?): there are cells with smaller lumina in the central position of sections, but their structure is not distinct and they might be simply a part of cortex.

Two groups of the shoot transverse sections in the interval '98' to '469' are selected to show parts of stem and basal parts of leaves with additional structures in leaf axils. In addition to leaf and stem cells, the leaf axils possess brownish structures interpreted as rhizoid (rh), and colorless structures interpreted as axillary hair (ah).


100 µm
469
412–418
98–104
76
12
A
B
50 µm
C
100 µm
30 µm
469
30 µm
414
rh
418
ah
rh
413
ah
rh
415
ah
rh
412
CS?
30 µm
76
ah
104
rh
ah
102
36
rh
100
30 µm
CS?
12
98

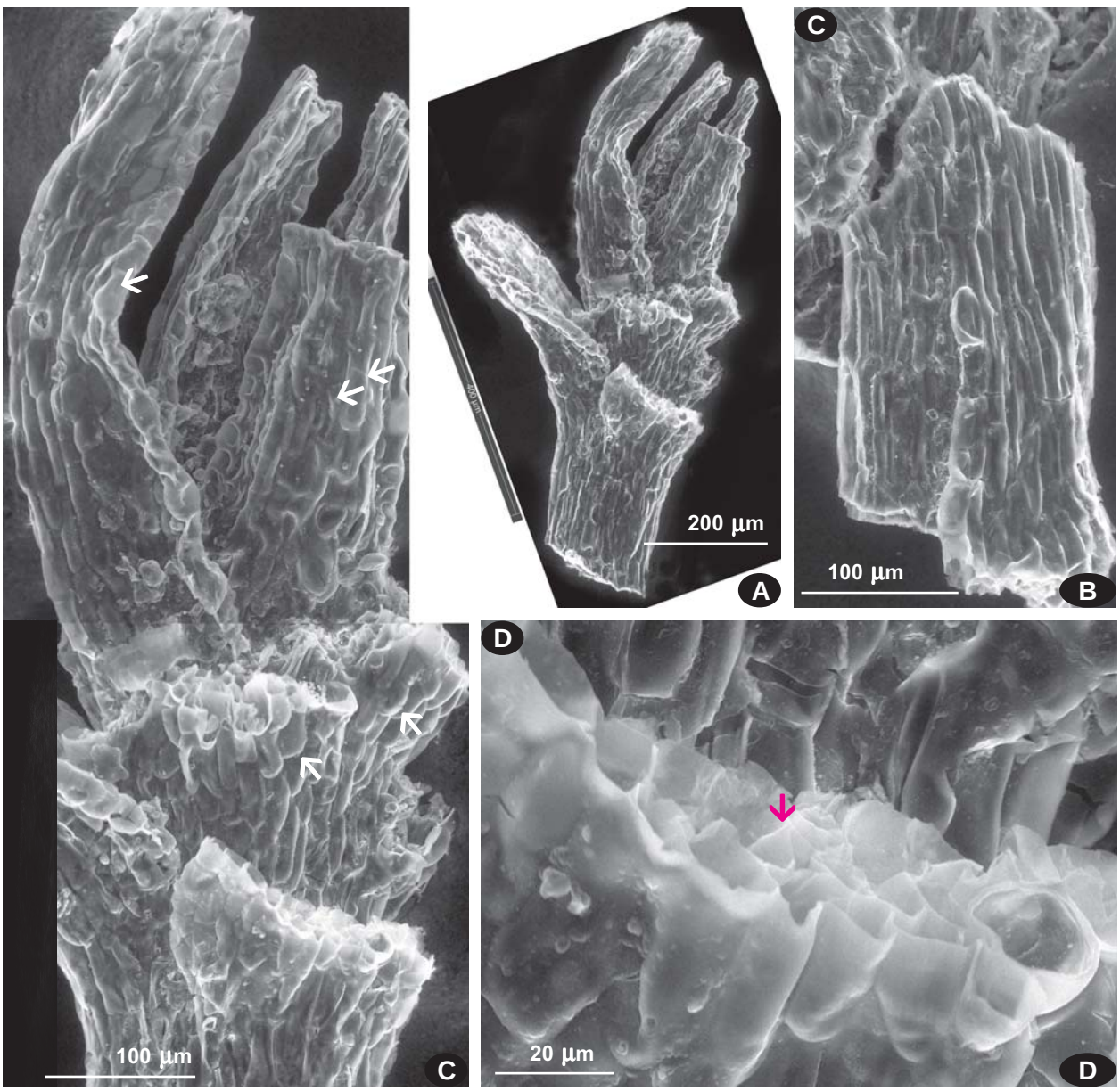


Fig. 12. *Arvildia elenae* shoot (Aristovo_113_10; SEM-Quattro images). When mounted, the specimen was broken off into two parts, the upper fragment shown in A, C, D, and the lower one on B. The former images illustrate shoot tips with small leaves. Four leaves (in front and right) are broken off, showing multistratose costa (cf. close up in 'D'), with only slightly smaller cells in its middle (red arrow). Image 'B' illustrates a structure of elongate cells in one row, interpreted as axillary hair in the axil of a leaf that was below (absent in the original sample). In a number of places (arrowed), the cell walls are bulging on the dorsal surface.

but their structure and grouping are not distinct enough to ensure the presence of the stem central strand.

The transverse section in Fig. 11, '76' includes both the stem and the leaf base: the space between them is partly marked by dots for clearer delimitation. Leaf cells are also strongly compressed, but the marginal cells are almost round, probably due to firmer cell walls, which, however, do not associate with thicker cell walls in this case. A somewhat or distinctly bigger marginal cells are seen in other sections as well, although they are not as round as in Fig. 11, '76'.

The section '469' shows an already mentioned rule that the distal laminal cells likely possess firmer cell walls and better retain their original shape compared to more proximal ones.

Among the shoot transverse sections, we selected two groups, from '98' to '104' and from '412' to '418', which show parts of stem and basal parts of leaves with additional structures in leaf axils. In addition to leaf and stem cells, the leaf axils possess brownish structures interpreted as rhizoids (rh), and colorless structures interpreted as axillary hairs (ah).

Rhizoids interpretation is tentative, considering the observation of true rhizoids with oblique cell walls in the previous study of Ignatov (1990). Thus, the brown elongate axillary structures are referred to rhizoids based

mainly on their elongate shape and brown color, different from the color of other parts of the specimen. Additionally, a line inside such structure can be assumed as an oblique cell wall. The brown color in sections of the series '98' to '104' occurs in elongate structure, which may be a part of rhizoid, but also a distal part axillary hair. Axillary hair interpretation is more definite due to its position, and in series '98'–'104' the basal cell differentiation is also apparent. The broader shape of the axillary hair in '412' to '418' (ca 14 μm wide) compared to that in '98'–'104' (10–12 μm wide) can be explained by the pressure from neighboring cells.

Axillary hair was rather unexpectedly found during the observation of one shoot of *Arvildia* (Fig. 12) in low-vacuum SEM Quattro. This shoot is similar to one used for the third series of transverse sections (Fig. 11) and also to the shoot shown in Fig. 2: it has small leaves with short rectangular laminal cells. A slightly bulging cells and weakly differentiated costa with thick-walled dorsal epidermis confirm the placement of the specimen in *Arvildia elenae*.

A putative axillary hair has been found in the lower part of the specimen, apparently in axil of leaf which has been broken off. It is formed of five elongate cells in one row: from base to apex 35×18 μm, 35×19 μm, 50×21 μm, 33×17 μm, and 37×17 μm. Axillary hairs are usually narrower, with more clearly differentiated basal cell, though a structure similar to the observed here is known in the axillary hairs of *Oedipodium* (Ignatov *et al*., 2022). The only other possibility for this structure would be a paraphysis. It better agrees with paraphyses in size, but the position in the middle of the stem among leaves is unusual. But when in *Andreaea* the archegonia are scattered along the stem, the paraphyses sometimes are also scattered.

Discussion

Among the various types of preservation, the permineralized fossils have in a whole an undoubtful priority, because the plant shape in this case remains intact (Tomescu *et al.*, 2016, 2018). However, the potential of bryophyte fossil compressions is also great, as it was recently demonstrated by Bomfleur *et al.* (2023). The present study of *Arvildia* also shows that the study of compression may markedly expand the circumscription of this genus.

The serial sections allowed us to study the structure of costa, estimate cell wall decomposition during fossilization, describe cell surface structures, and measure cellular characters with a precision of transmission electron microscopy. The latter opens a way to estimate biomechanical properties of bryophytes. The differential resistance of the cell walls to pressure might characterize the structural morphology of moss body, which usually remains out of scope of reseraches. Moss biomechanical studies are few and usually address to the largest species (During *et al*., 2015). A firmer cells walls in distal part of leaf and along the margins, which were revealed in *Arvildia* in a serial section studies, intuitively agree with what we should expect in moss leaves for proper mantainance of their shape, but, as a whole, this is rather a white spot in our current knowledge.

Taxonomy

Based on the general microscopical observations, in the original description *Arvildia* was compared mainly with Pottiaceae and, to some extent, with Grimmiaceae, Seligeriaceae, and Orthotrichaceae. The new data on its structure change this idea about *Arvildia* relationshhips.

The costa structure, as it was found in two series of sections studied under LM and TEM (Figs. 6–10), and two specimens observed under SEM (Figs. 5, 12), is too weakly differentiated compared to the Pottiaceae. Only solitary substereids occur in the costa of *Arvildia*.

The quite large, thick-walled and often bulging cells of *Arvildia* are similar to those of *Andreaea* and *Andreaeobryum*. In these genera the costa is also poorly differentiated and includes at best only few cells with narrower lumina. A similarity with *Andreaea* is especially apparent in one large leaf, called here *Arvildia* sp. (Fig. 4D–H). The latter is drastically similar to *A. elenae* in the laminal cell structure and very likely has to be referred to the same genus. At the same time, such great leaf dimorphism calls to a comparison with *Andreaea,* where perichaetial leaves differ from stem leaves both in size and shape in a way very similar to the difference between most leaves of *Arvildia* and the leaf of *A.* sp.

The crucial support of the affinity of *Arvildia* with Andreaeopsida would be the *Andreaea*-pattern of areolation in the subapical part of leaf, where the apical cell experiences unifacial divisions, making subapical cell uniseriate, and then biseriate (Ruhland, 1924). Unfortunately, apices of *Arvildia* are mostly broken off or formed by strongly bulging cells. A clear view obtained for apical part of leaf is shown for the large leaf, in which the cell arrangment does not fit *Andreaea*-pattern (Fig. 3D), as the divisions of apical cell are bifacial. A putative *Andreaea* pattern is found only once in a very fragile leaf (Fig. 9A), which we decided to use for cutting and enbedded in the resine; we have taken its photos through the resin, so the image is only moderately convincing. If our interpretation of this '9A' specimens is correct, then *Andreaea* is undoubtly a closest relative of *Arvildia*. Even if the evaluation of this specimenis is not correct, the unifacial division of the apical cell in *Andreaea* is common but not obligatory, and in some very young leaves the apical cell divisions may turn to oblique, while in developed leaves the turn of apical cell to bifacial division is well known (Ruhland, 1924).

According to the recent phylogenetic studies (Liu *et al*., 2019; Bechteler *et al.*, 2023), *Andreaeobryum* is the earliest divergent lineage in the clade of *Andreaeobryum+Andreaea*, and since *Andreaeobryum* has bifacial apical leaf cell, it is very likely that the ancient *Andreaea* aquired unifacial mode of apical cell division.

Andreaeobryum is a very peculiar in its axillary hairs, which are beaked, unlike those of *Andreaea*. So if the structure in Fig. 12B is an axillary hair, the conclusion that *Arvildia* is closer to the latter than to the former is straightforvard. But even it is not, the upper cell of a more definite axillary hair in Fig. 11 '98'–'104' is narrowly tapered to its apex, whereas in *Andreaeobryum* the upper cell of axillary hair is inflated (Ignatov *et al*., 2022).

Weak differentiation of costa is known in the modern flora in Grimmiaceae, Seligeriaceae, Orthotrichaceae, and Meesiaceae, but its combination with large, round, strongly bulging cells and stout costa is not known in these families.

The further discussion on relationships of *Arvildia* has to be postponed. There are still many gaps in the knowledge of this genus, as the material used for our observation was limited. Moreover, we necessarily accepted several assumptions that (1) all discussed species comprise a single genus; (2) *Arvildia* sp. is a perichaetial leaf of *A. elenae* or *A. obtusifolia*.

However, what seems unquestionable is that the applied approach of serial sectioning and more thorough preparation will be helpful for the interpretation of fossil mosses.

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