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A BRYOPHYTE-LIKE PLANT FROM THE LOWER CARBONIFEROUS OF THE MOSCOW COAL BASIN

МОХОПОДОБНОЕ РАСТЕНИЕ ИЗ НИЖНЕГО КАРБОНА ПОДМОСКОВНОГО УГОЛЬНОГО БАССЕЙНА

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Abstract

A small thalloid plant *Mstikhinia duranteae* gen. et sp. nov. from the Lower Carboniferous deposits of the Moscow Coal Basin is described. The most remarkable feature of *Mstikhinia* is the numerous pores. These pores are variable in size and shape, ranging from simple circular holes to structures similar to immersed stomata with guard-cells. We consider these pores served for mucilage release and probably are not homologous to stomata of tracheophytes. On the whole, *Mstikhinia* combines the characters of several plant divisions, e.g. Anthocerotae, Hepaticae, Pteridophyta (gametophytes), but it cannot be attributed to any of them. For such combined forms, Meyen (1987) introduced the concept of “synthetic type”. It seems probable that *Mstikhinia* belongs to one of such ancient “synthetic” groups, not recognized yet.

Резюме

Из нижнекаменноугольных отложений Подмосковного угольного бассейна описано мелкое талломное растение *Mstikhinia duranteae* gen. et sp. nov. Наиболее своеобразной чертой *Mstikhinia* являются многочисленные поры. Они имеют различную форму и размеры, от простых округлых отверстий до структур, сходных с погруженными устьицами с замыкающими клетками. Предполагается, что эти поры могли служить для выделения слизи и, вероятно, не гомологичны устьицам сосудистых растений. В целом *Mstikhinia* обладает признаками нескольких отделов растений, в том числе, Anthocerotae, Hepaticae и гаметофитов Pteridophyta, но не может быть отнесена ни к одному из них. Для таких комбинированных форм С.В. Мейен (1987) ввел понятие «синтетического типа». Представляется вероятным, что *Mstikhinia* принадлежит к одной из таких древних «синтетических» групп, до сих пор не распознанных.

INTRODUCTION

Bryophytes were often considered to be the oldest land plants but according to molecular phylogenetic data the moss, liverwort, hornwort and vascular plant lineages probably diversified from a common ancestor between the Silurian or Early Devonian (Newton et al., 2007). At the same time, available palaeontological data are not in a full agreement with this statement. The oldest unequivocal hepatics, *Metzgeriothallus sharonae* (Hernick et al., 2008) and *Hepaticites devonicus* (Hueber, 1961), were found as late as the Middle and Upper Devonian respectively, while the oldest moss was found only in the Upper Carboniferous (cf. Jovet-Ast, 1967; Meyen, 1987; Oostendorp, 1987; Krassilov & Schuster, 1984). The Anthocerotae are definitely known in macrofossils from Dominican Amber of Eocene-Oligocene age (Frahm, 2005) and in spores from the Cretaceous. The Cretaceous *Notothylacites filiformis,* described as a member of Anthocerotae, is now usually considered to be a hepatic (Krassilov &

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Fig. 1. Geographic position of the Moscow Coal Basin (heavy line).

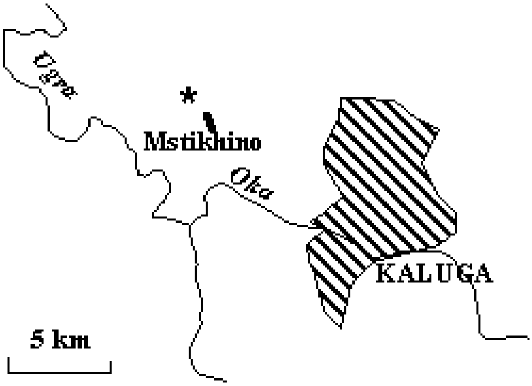


Fig. 2. Geographic position of the locality (asterisk) yielding *Mstikhinia duranteae* gen. et sp. nov. remains.

Schuster, 1984; Oostendorp, 1987). This incompleteness of the fossil record depends, among other factors, on the absence of lignification of bryophyte tissues, which decreases their chance for fossilization, as well as on the small plant size, which makes it difficult to find them in the bedding planes.

Therefore, all the data on Palaeozoic bryophytes are important and we do not hesitate to present here a new finding of a bryophyte-like plant even though its morphology is incompletely known and the affinity to Bryophytes is far from certain.

Neither bryophytes, nor other similar plants, were recorded previously in the Moscow Coal Basin Lower Carboniferous.

MATERIAL AND METHODS

The studied material comes from a limestone quarry situated 8 km NW from Kaluga city near the village Mstikhino (Fig. 1, 2; abbreviation "Mstikhino" for ease of reference).

The plant remains were collected from a small lens of terrigenous sediments at the base of the limestones of Mikhailovsky Horizon of the Upper Viséan. The stratigraphy of these deposits is shown on the Table 1 (p. 116). The lens occurs in a shallow depression on the eroded surface of the limestones of Aleksinian Horizon (Fig. 87, p. 115).

The sedimentary environments during the lens formation are reconstructed as an alluvial plain submerged under shallow sea water. The relief of the sea bottom was so flattened that even the slightest regressive oscillations caused the barring of its large parts, there the processes of terrigenous sedimentation and vegetation settlement began (Shvetsov, 1938; Mosseichik et al., 2003; Mosseichik, Ignatiev, 2004).

The rose-colored, microcrystalline, massive limestones, which underlie the lens, are commonly interpreted as sediments of an open sea. At the same time, judging by the findings of *in situ* rhizophores of arborescent lycopods (see below), these limestones were deposited near the mainland or an island shore inhabited by these plants. The eroded top of the limestones indicates a break in marine sedimentation and the beginning of formation of continental deposits including a small shallow fresh-water, relic lake basin, where the lens with plant remains was formed.

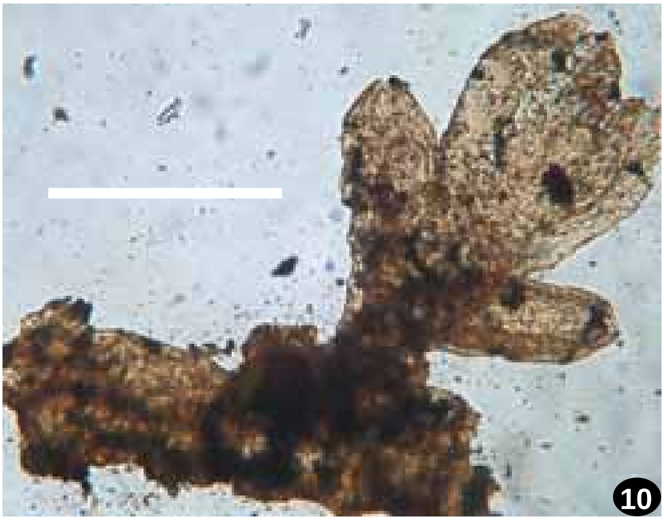
The base of the lens consists of a disturbed fine horizontal bedding enriched by organic matter dark-grey clays. The accumulations of plant detritus occur across the bedding planes. The roof of clays is highly ferruginated (Fig. 87). The abundance of organic matter and the ferruginization emphasize the eutrophic state of the lake basin at the early stages of its existence. Recent lakes of this type have a well-illuminated and warmed epilimnion, where phytoplankton develops well and the gradual depth increase helps development of coastal vegetation of all ecological groups (Sadchikov & Kudryashov, 2005).

The higher level of lens body consists of the grey and light-grey color clays similar to that in bottom of lens; they have lump structure, which

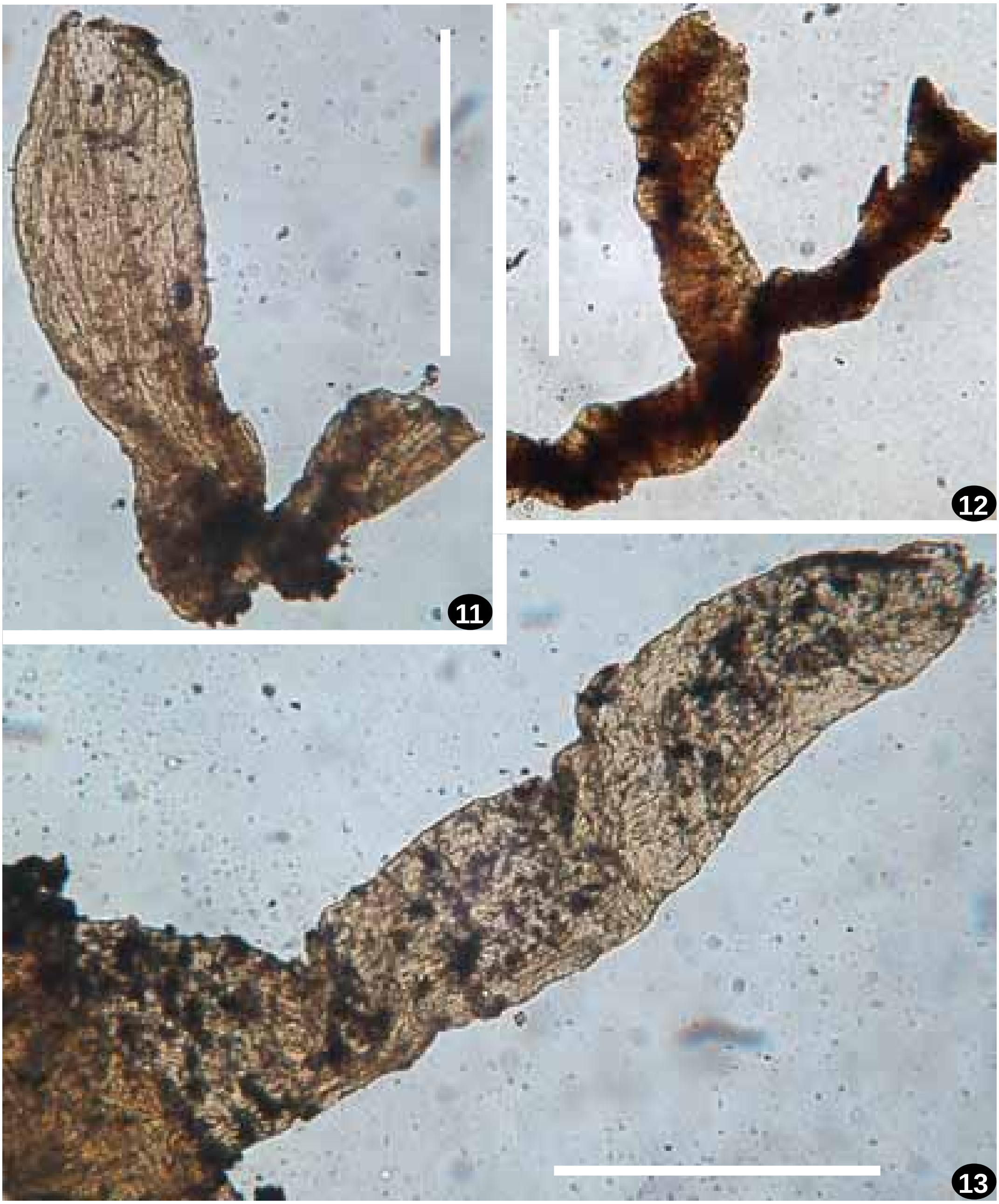
cont. on p. 115

Figs. 3-6. *Mstikhinia duranteae*, habit.

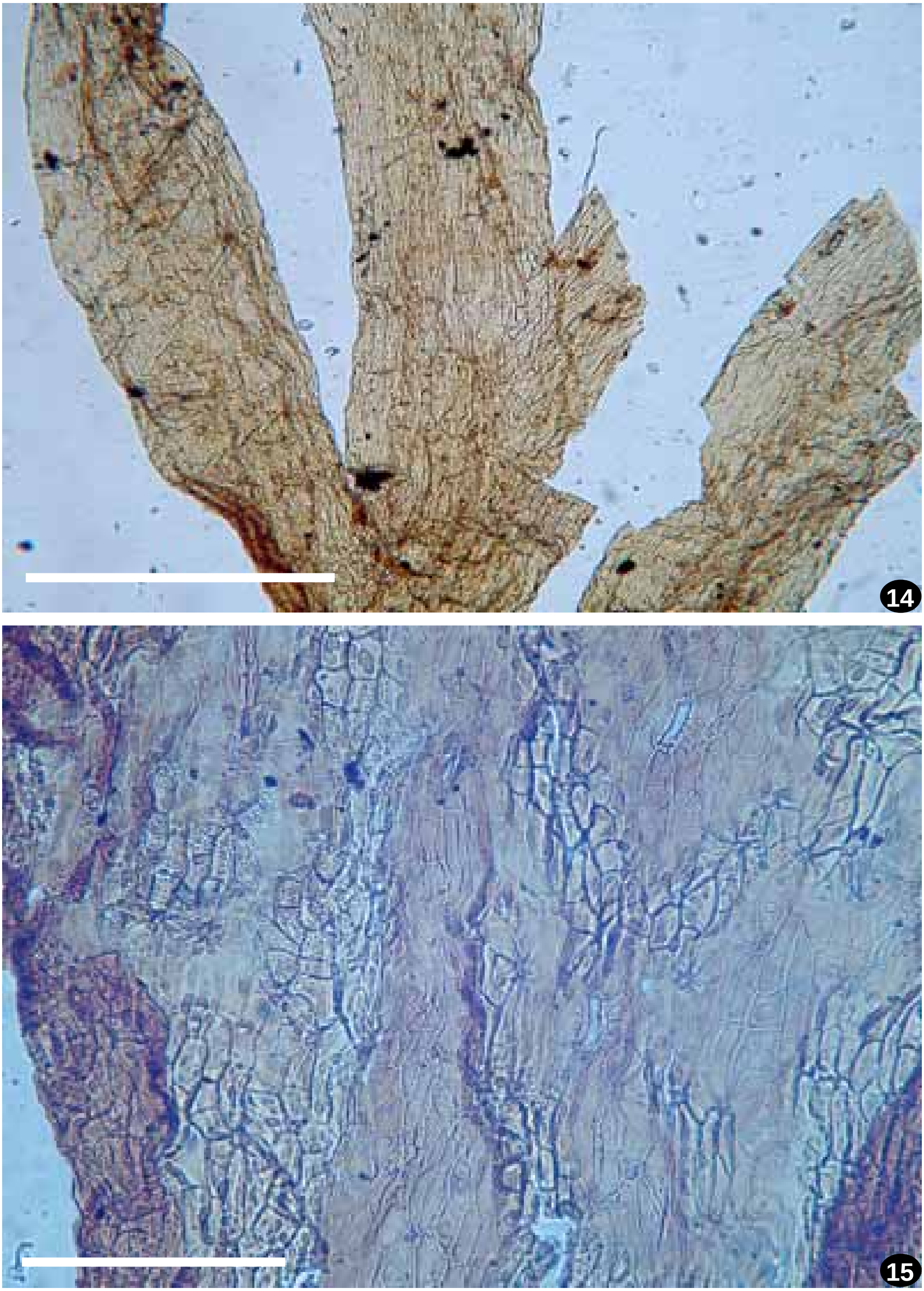
3 – 4865/182-1-8; 4 – 4865/182-1-9; 5 – 4865/182-1-2; 6 – 4865/182-1-7.
Scales 1 mm.



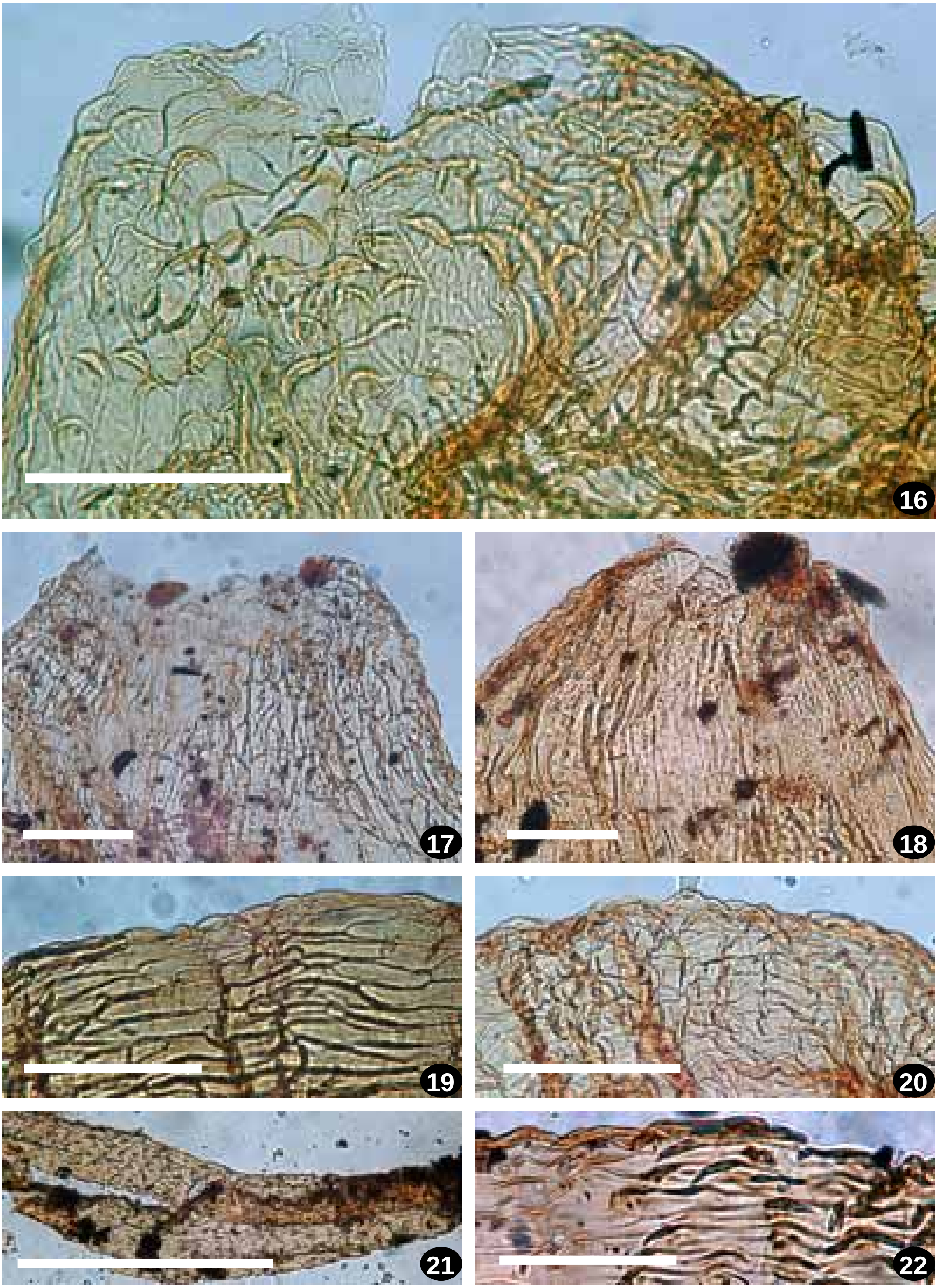
Figs. 7-10. *Mstikhinia duranteae*, habit. 7 – 4865/182-6-3; 8 – 4865/182-1-4 (holotype); 9 – 4865/182-6-5; 10 – 4865/182-6-4. Scales 1 mm.



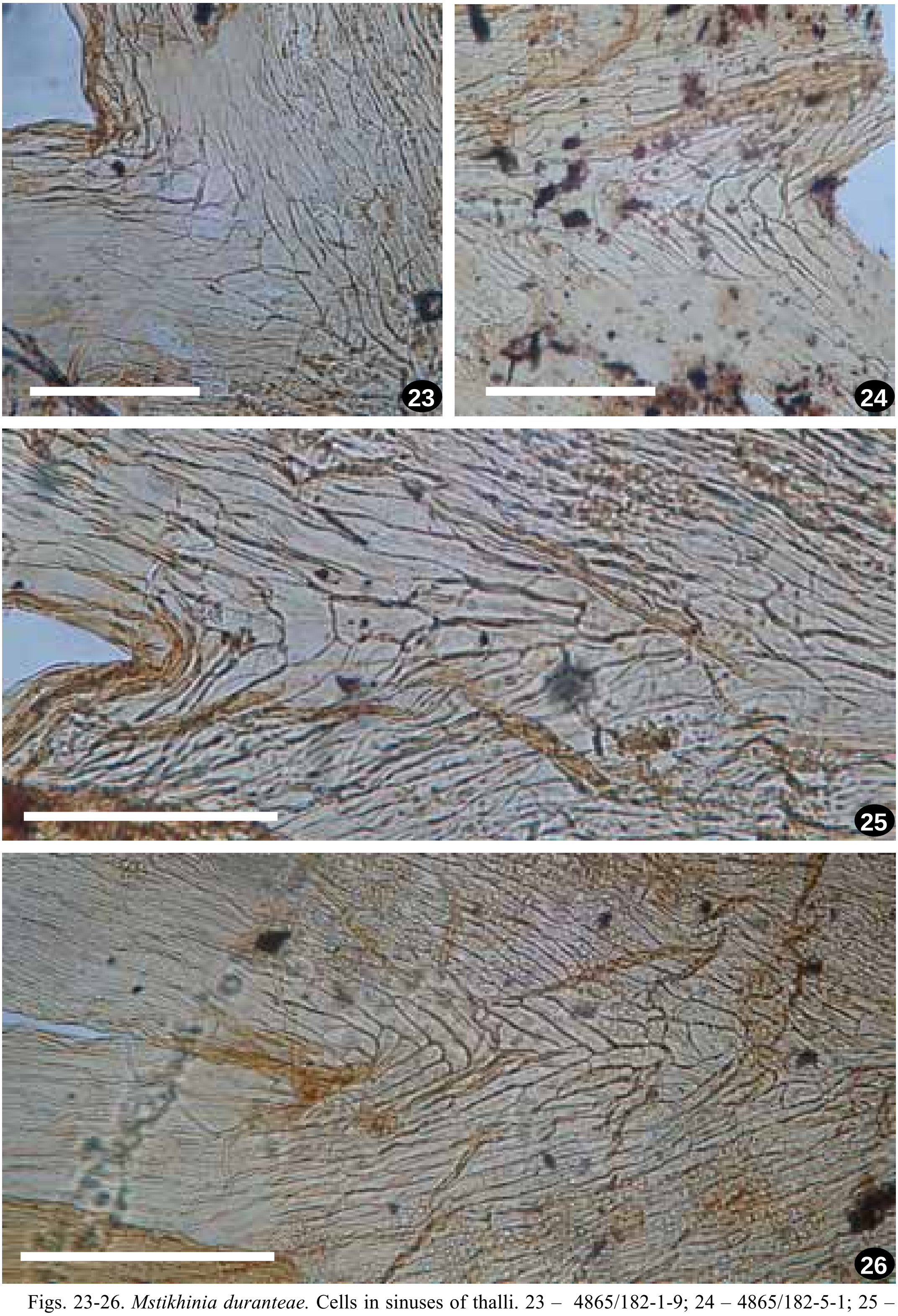
Figs. 11-13. *Mstikhinia duranteae*, habit. 11 – 4865/182-5-2; 12 – 4865/180-1-1; 13 – 4865/182-5-6. Scales 1 mm.



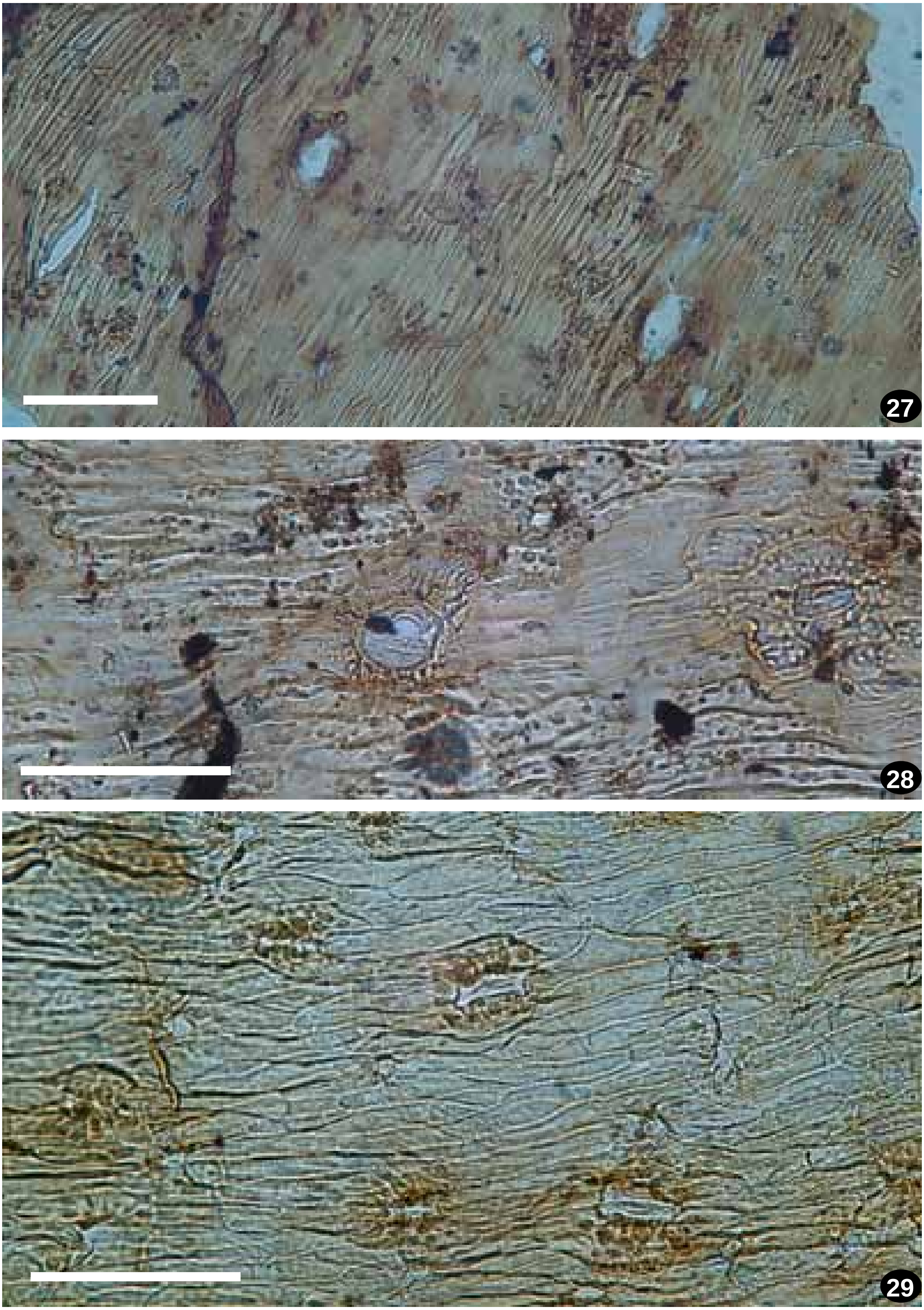
Figs. 14-15. *Mstikhinia duranteae*, holotype, 4865/182-1-4. 14 – habit; 15 – cells of proximal part of thallus. Scale bar for 14 – 1 mm, for 15 – 100 µm.



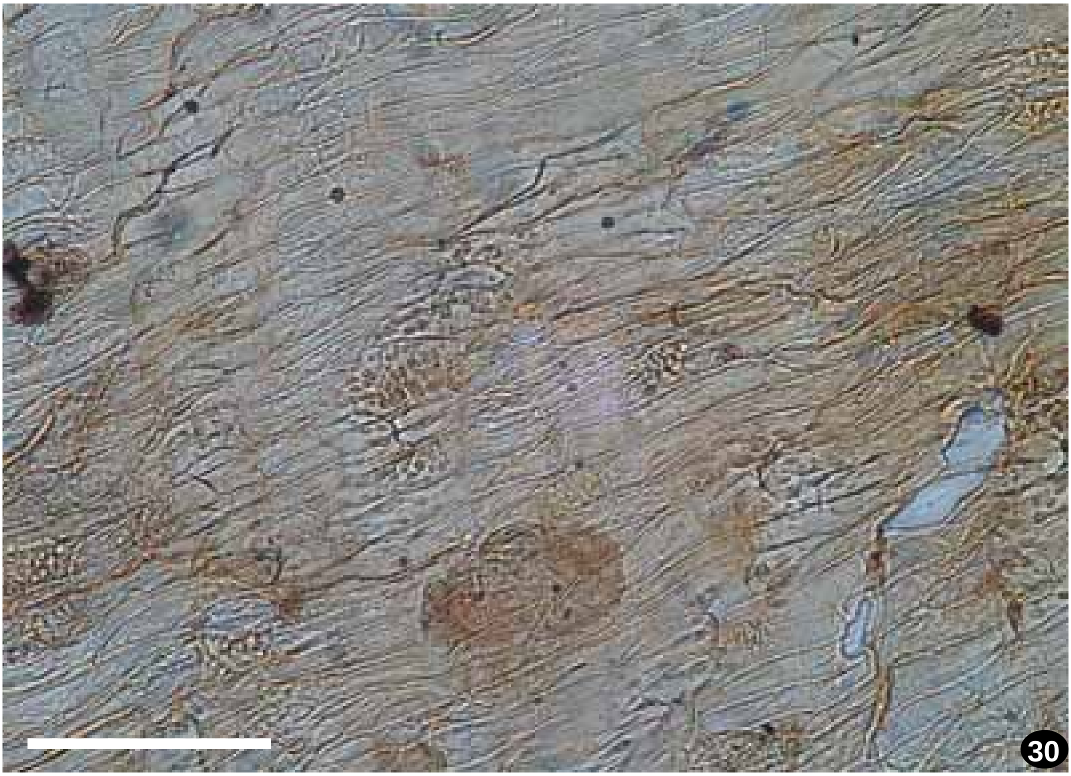
Figs. 16-22. *Mstikhinia duranteae.* 16-18 – distal portion of thalli (near growing point?), showing short convex cells; 19-20 – parts somewhat below distal ends of thalli; 21-22 - convex-wavy cells in the middle part of thallus, i.e. not in its apical part. 16 – 4865/182-2-6; 17 – 4865/182-6-1; 18 – 4865/182-6-2; 19 – 4865/182-1-9; 20 – 4865/182-2-6; 21&22 – 4865/182-5-9. Scale bars for 16-20 & 22 – 50 µm; for 21 – 1 mm.



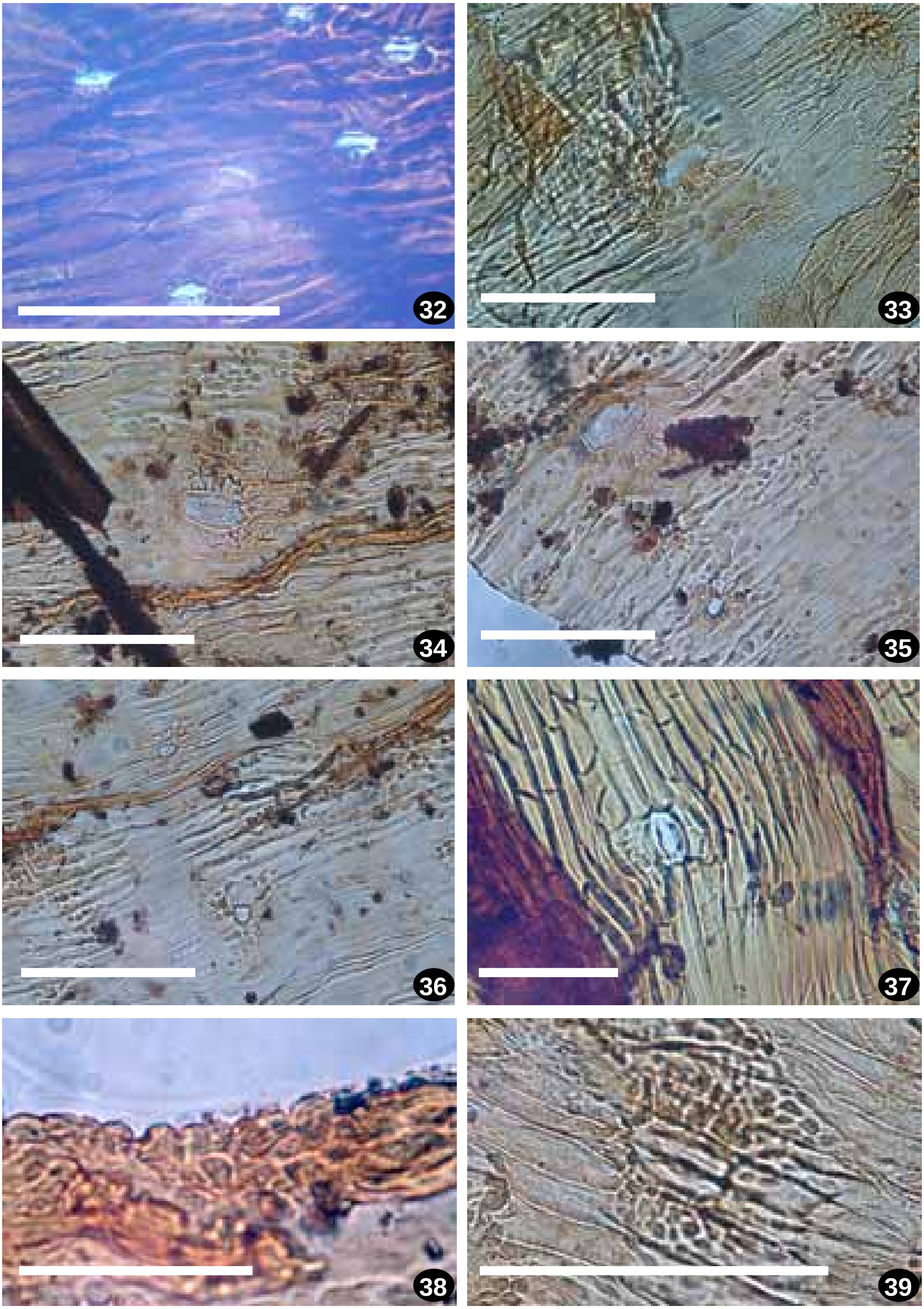
Figs. 23-26. *Mstikhinia duranteae.* Cells in sinuses of thalli. 23 – 4865/182-1-9; 24 – 4865/182-5-1; 25 – 4865/182-2-1; 26 – 4865/182-1-7. Scale bars for 23-26 – 50 µm.



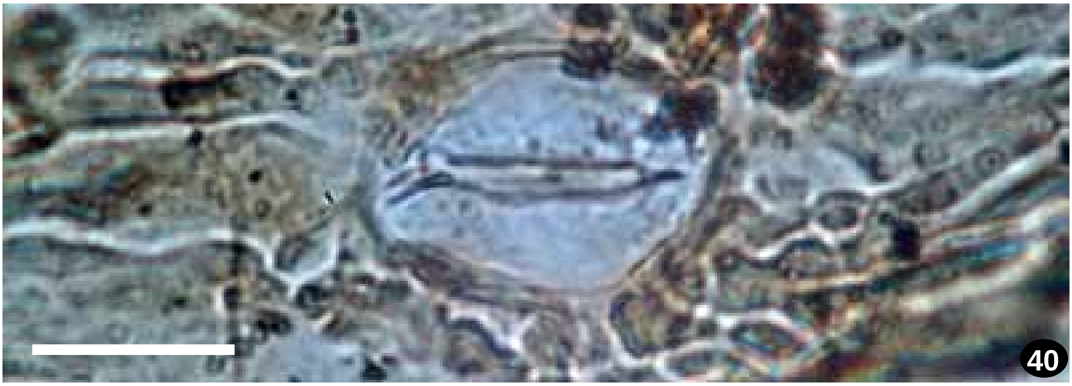
Figs. 27-29. *Mstikhinia duranteae.* Areolation of thalli, showing pores of different size. 27 – 4865/182-2-3, 28 – 4865/182-6-8; 29 - 4865/182-1-8. Scale bars for 27-29 – 50 µm.



Figs. 30-31. *Mstikhinia duranteae*, from holotype, 4865/182-1-4. Areolation of thalli, showing pores of different size. Scale bars for 30-31 – 50 μm.



Figs. 32-39. *Mstikhinia duranteae*. Stomata-like pores (#38 – view from acute angle); various specimens of collection 4865/182. Scale bars for 32-39 – 50 µm.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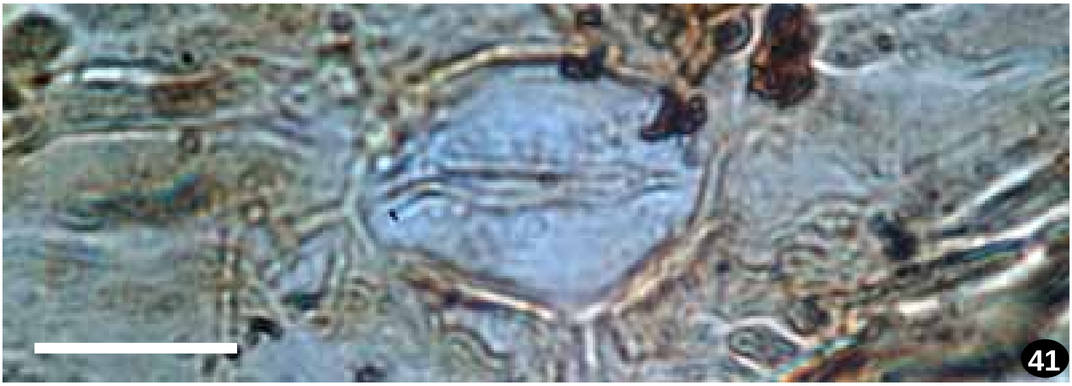
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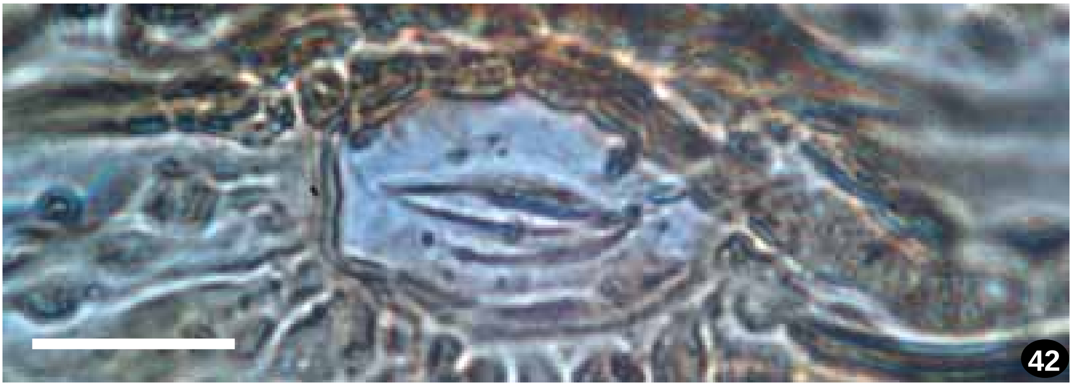
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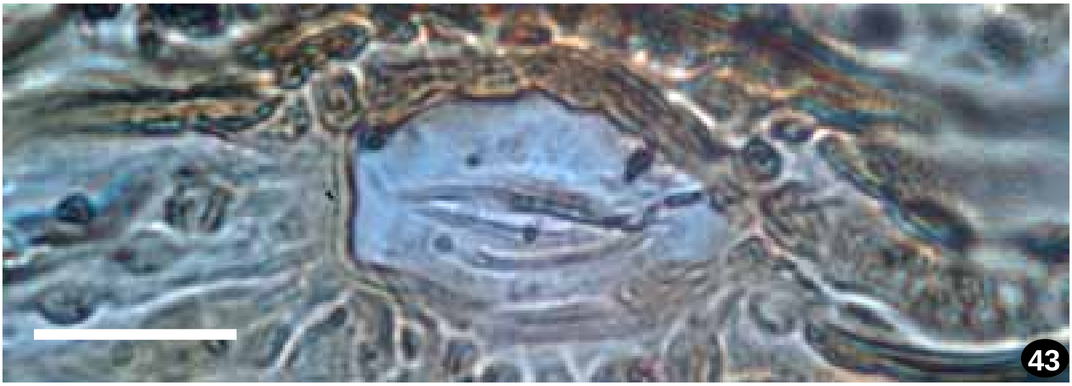
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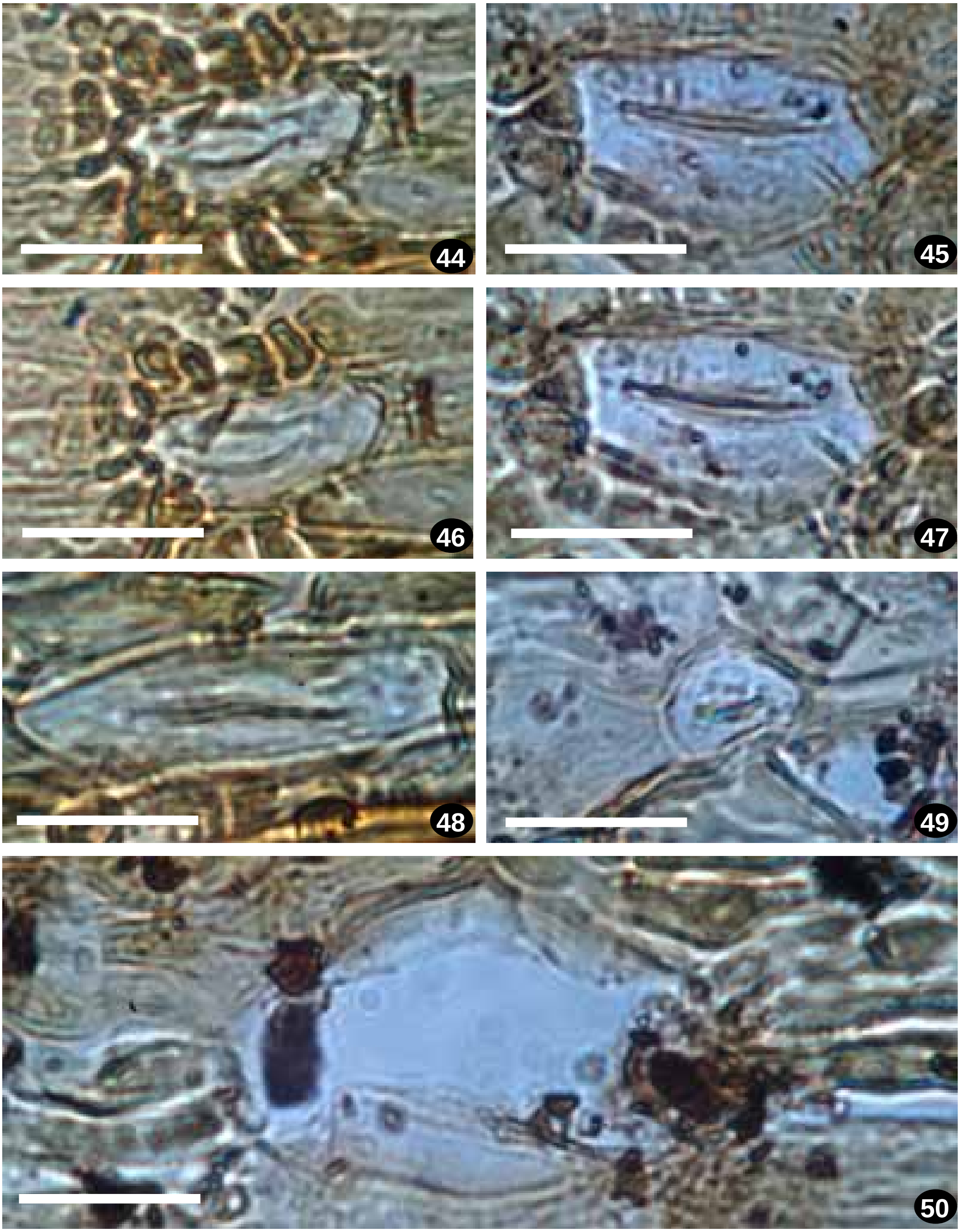
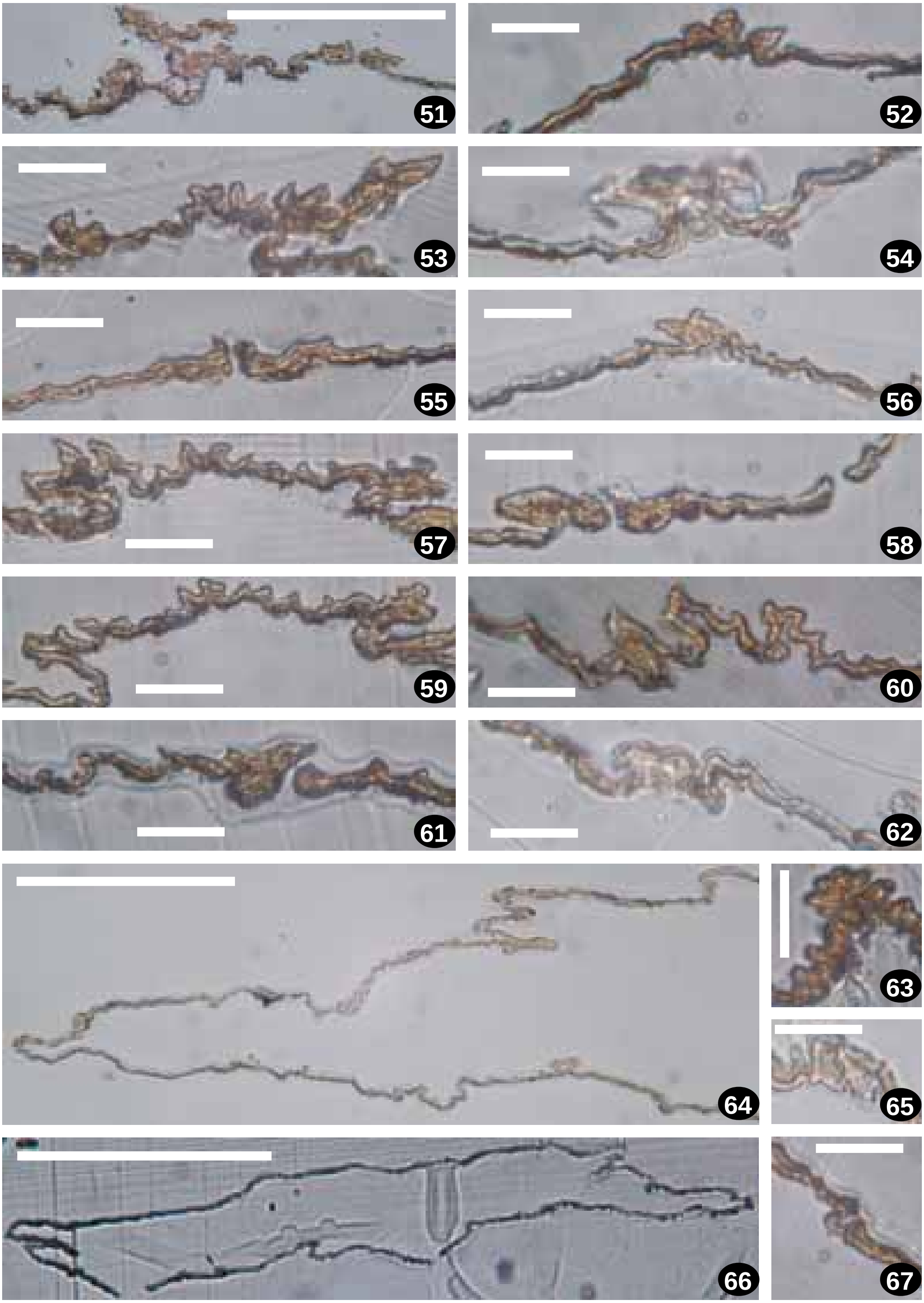
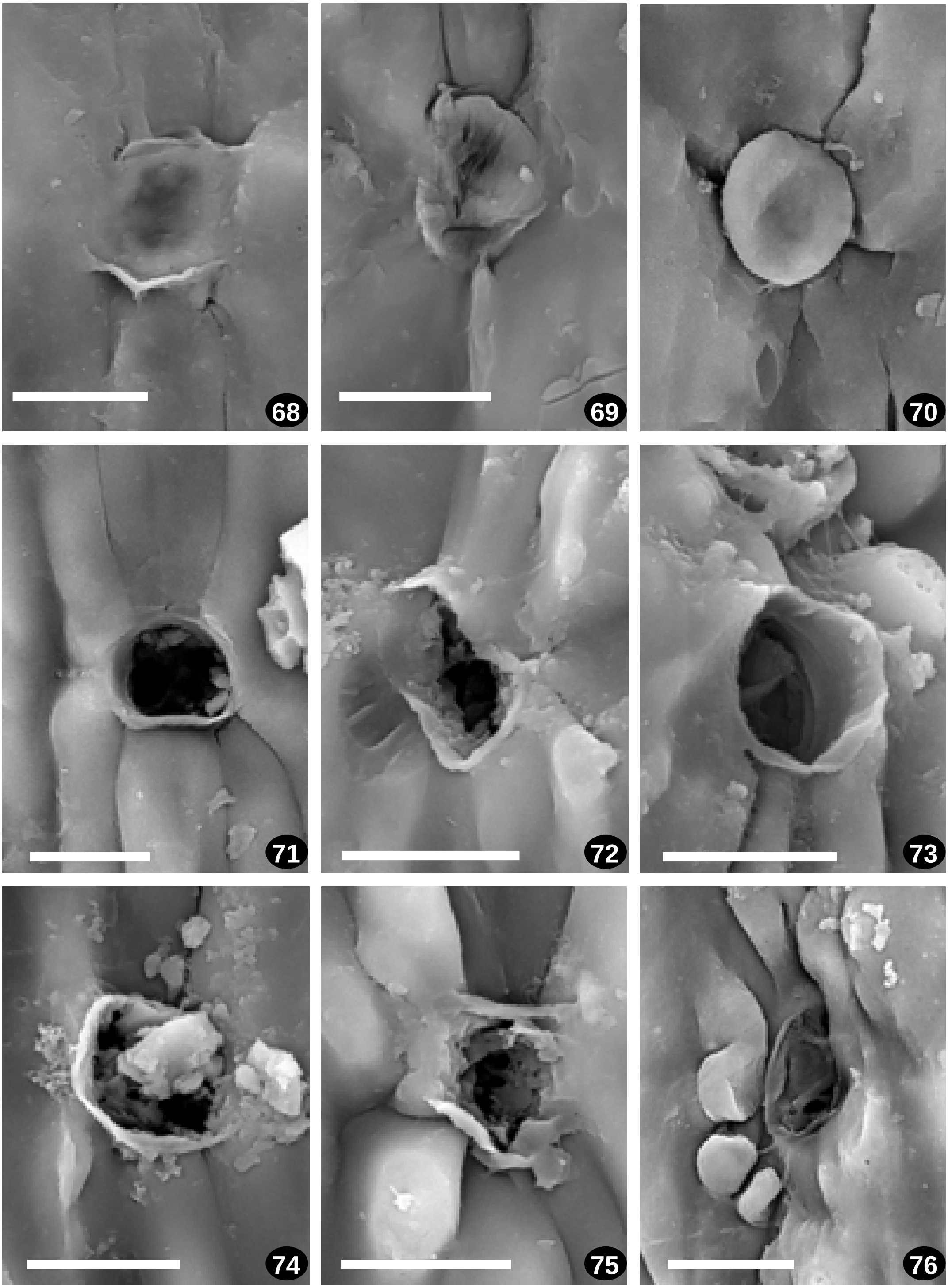


Figs. 44-50. *Mstikhinia duranteae*. Stomata-like pores. 44, 46, 48 from 4865/182-1; 45, 47, 49-50 from 4865/182-6. Pictures 44 & 46 and 45 & 47 are taken from the same pores with slightly different focus. Scale bars for 44-50 – 10 µm.

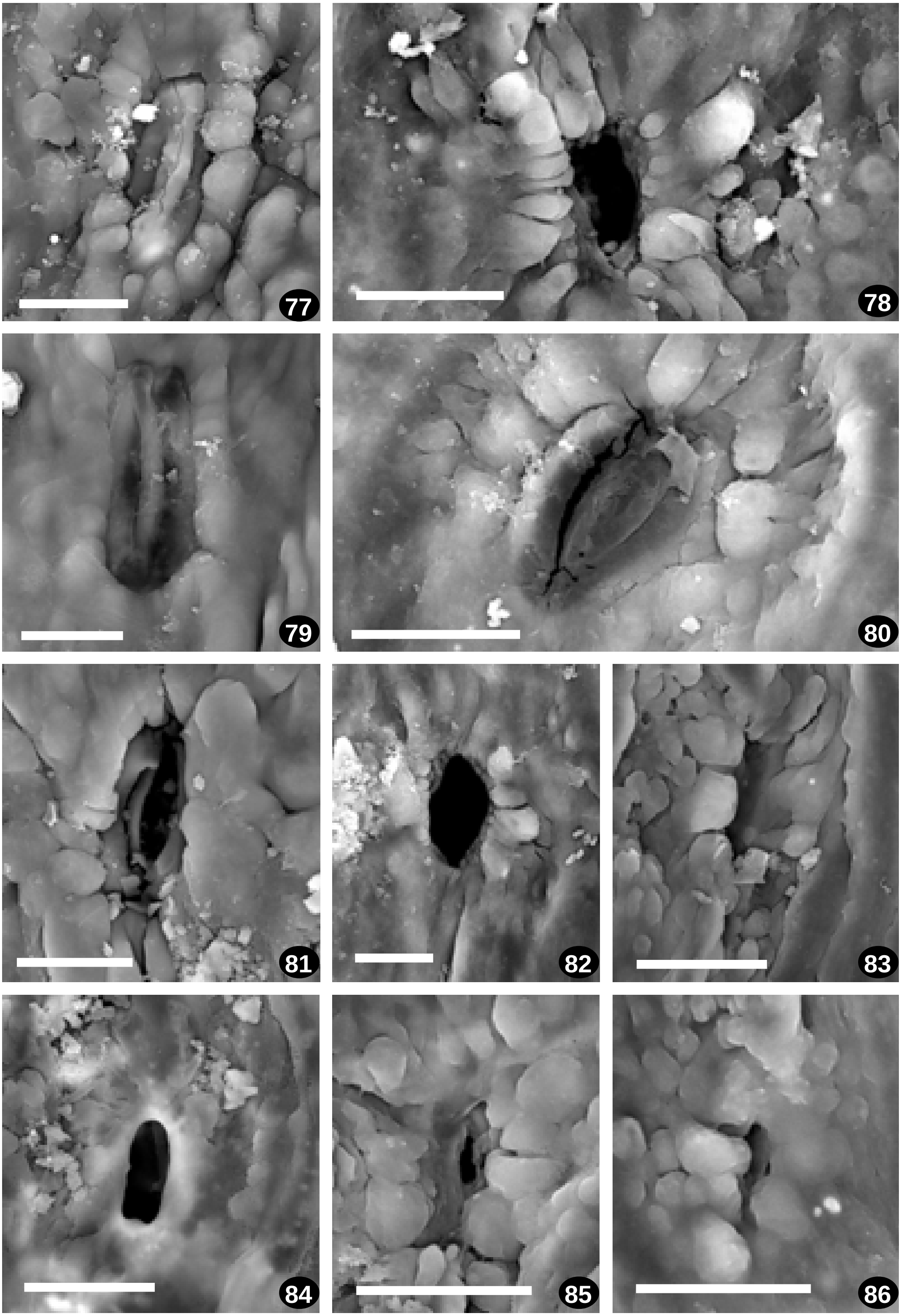
Figs. 40-43 (opposite page). *Mstikhinia duranteae*. Stomata-like pores; 4865/182-6. Pictures 40 & 41 and 42 & 43 are taken from the same pores with slightly different focus. Scale bars for 40-43 – 10 µm.



Figs. 51-67. *Mstikhinia duranteae*. Transverse section of thallus, 4865/182-TS. Scale bars for 51-63, 65, 67 – 10 µm; for 64 – 50 µm; for 66 – 0.2 mm. In all pictures (except 62, 64) outer surface of cuticle is below.



Figs. 68-76. *Mstikhinia duranteae*. SEM pictures of smaller pores. Note that the smallest ones (#68-69) are filled (? by dried mucilage-like substance). From 4865/182. Scale bars 10 µm.



Figs. 77-86. *Mstikhinia duranteae*. SEM pictures of larger pores. From 4865/182. Scale bars 20 μm.

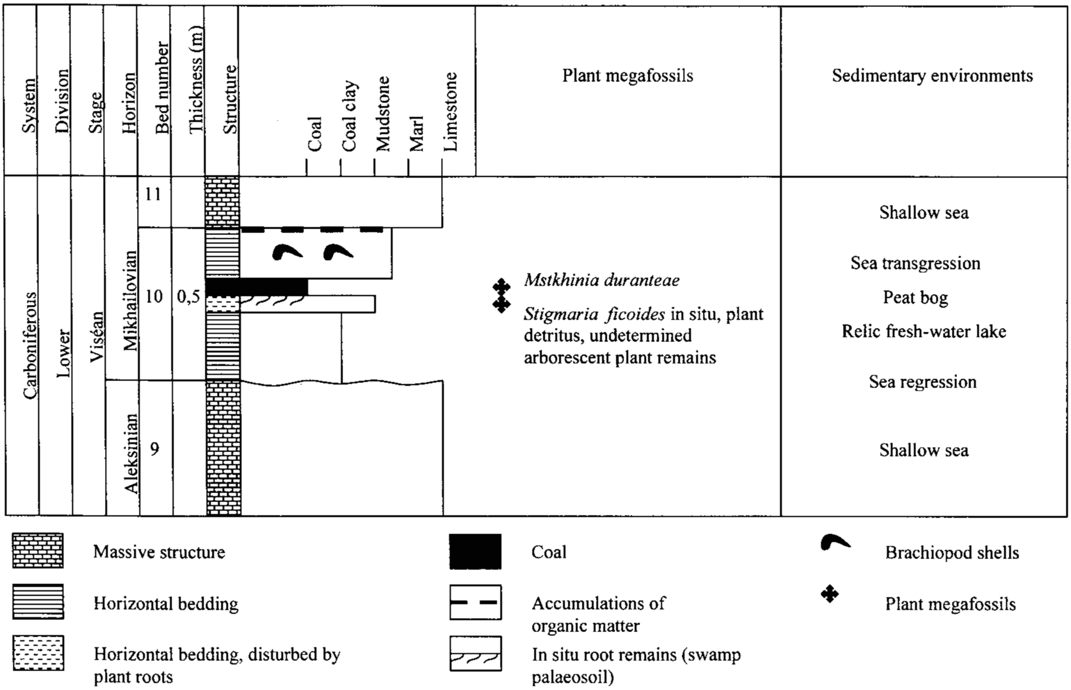


Fig. 87. Lithological log for the locality “Mstikhino”.

is apparently caused by the action of plant roots, first by those of *Stigmaria ficoides* buried *in situ*. This shows that the process of lake overgrowing began with the colonization of its margins by arborescent lycopods with rhizophores of *Stigmaria* type. According to the classification of Papchenkov (1983; cited from: Sadchikov & Kudryashov, 2005) these plants, whose reproduction cycle was strongly connected with water, probably belong to the ecological groups of helophytes and near-water plants (arborescent hygrophytes).

The top of the lens is covered by a thin coal layer (5 cm thick) that indicates the full overgrowing of the lake and its transformation into a high bog, supplied by atmospheric precipitation and land water.

The development of the peat bog was interrupted by a sea transgression. The coal is covered by a layer of rust-color marl with large brachiopod shells and local accumulation of plant debris on the bedding planes. At the top of the marl a mass accumulation of allochtonous organic matters occurs.

The marl is overlaid by the thick series of massive microcrystalline limestones, analogous to that which underlies the lens bottom.

The coal and dark-grey clays contain numerous coalified compressions of fragments, pieces of plant inner tissues, dispersed spores, and some other remains. Among them the thallus fragments of *Mstikhinia duranteae* gen. et sp. nov. predominate.

The material consists of slightly metamorphosed or naturally macerated compressions. They were oxidized using Schulze’s solution ($HNO_{3\ \text{conc.}} + KClO_3$). To study the cuticles scanning electron and light microscopy were used. For SEM, cuticles after maceration were coated with gold and studied under CamScan MV 2300. Light microscopy used material mounted on slides in glycerin-gelatine. One piece of thallus was embedded in Araldite 6005 medium (according to the protocol of the manufacturer) and then cut at sections 2–3 mkm thick, put on a glass slide and photographed without mounting in any medium.

No inner tissues were clearly detected within the thallus remains of *Mstikhinia*. At the same time, several dispersed pieces of peculiar “conducting tissue” were found with the remains during bulk maceration. They are not formally described and discussed here, but their brief characteristics and illustrations are given at the end of the paper.

Table 1 Biostratigraphy of the Visean deposits of Moscow coal Basin

Stage	Horizons	Megafloral zones (Mosseichik, 2005)	Foraminifera zones (Alekseev et al., 2004)	Conodont zones (Alekseev et al., 2004)
Visean	Venevian	*Sublepidodendron shvetzovii*	*Eostaffella tenebrosa–Endothyranopsis sphaerica*	*Lochriea ziegleri*
	Mikhailovian		*Eostaffella ikensis*	*Lochriea nodosa*
	Aleksinian		*Eostaffella proikensis–Archaediscus gigas*	*Gnathodus bilineatus*
	Tulian		*Endothyranopsis compressa*	
	Bobrikian	*Gryzlovia meyenii*	No fauna	

PLANT DESCRIPTION

Mstikhinia, gen. nov.

Diagnosis: Plant thalloid, multistratose, monopodially and dichotomously branched. Epidermis with pores that are relatively evenly arranged and variable in shape and size, ranging from simple circular holes to stomata-like structures with paired "guard" cells. Most pores surrounded by cells with large gently rounded papillae. Epidermal cells short and slightly convex in distal parts of thallus, elongate to linear in more proximal parts; cell in sinuses of thallus branches forming parquet-like pattern. Scales and rhizoids absent.

Type species: Mstikhinia duranteae, sp. nov.; Lower Carboniferous (Mississippian), Upper Viséan, Moscow Coal Basin.

Ethymology: generic name after "Mstikhino", type locality of the plant.

Comparison: Mstikhinia differs from *Hepaticites* Walton by non-lobate thallus, absence of rhizoids and presence of pores. The genus *Thallites* Walton was established for thalloid plant megafossils, which have no characters that can be attributed to algae, bryophytes or tracheophytes with certainty (Jovet-Ast, 1967). The pores of *Mstikhinia* distinguish it from trachaeophyte sporophytes. *Mstikhinia* differs from both sporophytes and gametophytes of rhyniophytes (Edwards et al., 1998; Kerp et al., 2004) by the absence of regular stomata. The rhyniophytes as well as other tracheophytes have also rather well developed conductive tissues and branching systems. The Devonian *Orestovia* (Krassilov, 1982) has stomata-like structures, but, unlike *Mstikhinia,* they have circular raisings of smooth subsidiary cells. *Nematothallus* (Edwards & Rose, 1984) sometimes has pores similar to that of *Mstikhinia.*

Mstikhinia duranteae, sp. nov.

Ethymology: species name after Marina V. Durante, Russian palaeobotanist.

Figs. 3-86.

Holotype: Geological Institute of the Russian Academy of Science, spec. 4865/182-1-4 (Figs. 8, 14, 15, 30, 31); "Mstikhino", Lower Carboniferous (Mississippian), Viséan, Mikhailovian Horizon.

Diagnosis: Main part of thallus broadly linear, up to 5 mm long and 0.6 mm wide; lateral parts of thallus oblong-linear, dichotomously branched, 2-5 mm long, 0.2-0.5 mm wide, towards obtuse apex narrowed or otherwise broadened. Midrib absent. Epidermal structure on all sides of thallus similar; cells shortly elongate or subisodiametric, ca. 30 μm, to linear, up to 130 x 10 μm, in sinuses enlarged and forming parquet-like pattern. Cells near apices short, slightly protruding, making the outline of the subapical part of the thallus wavy. Pores variable, from small circular pores, 7-20 μm, to complex stomata-like structures with paired "guard" cells, 30-50 mkm long and 7-10 mkm wide, slightly immersed, with long axes oriented along the thallus length. "Subsidiary" cells of stomata-like structures with papillae.

Description: We studied ca. 50 fragments of thalli, ca. 20 of them big enough to characterize the plant shape.

Apical (young) parts of the thallus are represented by rather pale and transparent cuticle "sacs" (Figs. 3–22). Judging by these cuticles *Mstikhinia* was a multistratose thalloid plant, dichotomously branched in various planes (Figs. 3–13). The lobes are 0.5-0.8 mm wide in compressed state (as seen in slides, cf. also transverse section in Fig. 66), with maximum width up to ca. 1.3 mm near the furcation point (Figs. 8–9). Subapical cells are short and characteristically inflated (Figs. 16-18); shortly below the cells become elongate to linear (Figs. 27-37), except at sinuses just below the furcation point (Figs. 23–26) and in proximal areas of the thallus (Fig. 15).

Some cuticle fragments are darker with more thick-walled cells (cf. Fig. 32). They were not found in organic connection with the above cited apical parts and probably belonged to older individuals. We suppose both types of cuticles belong to the same species, because of their close association in the same locality, as well as similar cellular structure and pore patterns.

Mstikhinia has no indications of dorsiventrality: the epidermal structure on all sides of the thallus is uniform. Transverse sections exhibit various folds of cuticle (Figs. 51-67), but otherwise the cuticular structure looks identical all around the plant.

The epidermal cells (more precisely their imprints on the cuticle) are clearly seen in all the specimens. Papillose cells are disposed around all pores except the smallest circular ones. Although the surface view often does not allow to say if the raisings are solid and should be classified as papillae, or empty and are in fact mamillae, we interpret them as the former because they are usually several per one cell whereas mamillae are usually single per cell. In most cases the surface of the thallus is smooth, this is especially obvious at the edges of the thallus. However, in several places (cf. Figs. 21–22) the cells are wavy-bulging. Note that in this latter case the bulging cells are located far from the apical zone, where cells are commonly bulging or inflated (Figs. 16, 20).

The numerous pores occur all along the thallus except on its apical parts (and probably also at its sinusal portions). There is no obvious regularity in pore arrangement, although the average distance between them is rather even (Figs. 27–31). The pores vary in size (cf. Figs. 32–39 and 58–86). The smallest ones are round; the cells around them are usually smooth. Small pores often possess a thin "collar" around their perimeter, quite distinct under SEM (Figs. 71-74), although not so strongly marked under the light microscope. Some of the smallest round pores have round plugs. It is unclear if such a plug was formed by a small intact cell, or if this was a drop of mucilage-like substance dried up in the opening of an internal reservoir. The latter idea is supported by Fig. 67 that demonstrates a cross-section with a drop-like structure near a pore.

The larger (although not the largest) pores are elongate in outline, slightly immersed. The better preserved ones resemble stomata with two guard cells (Figs. 28-31, 34–35, 39, etc.). The cuticle of the "guard cells" demonstrates a thin lip-shaped thickening along the stomatal cleft (Figs 40–48). In this paper these openings are called "stomata-like structures". However many of these stomata-like structures look like a hole (Fig. 28), and we assume the "guard cells" were destroyed in the course of preservation processes or laboratory treatment.

The largest openings look like much enlarged stomata-like ones with broken "guard cells" (Figs. 27, 30, 32, 50).

Although these types of openings differ, there are transitions between them.

Cells in the sinus area are long rectangular in shape and arranged in an interlocking pattern reminiscent of "parquet" flooring.

* * *

The bulk includes some pieces of internal plant tissue (Figs. 88–99). They are composed by elongate cells with largely smooth walls (Figs. 89–91), or with sparse circular thickenings (Fig. 93), and occasionally with ovate perforations at the oblique ends of cells (Figs. 94–96). Smooth conductive cells are considered to be characteristic of bryophytes (Ligrone et al., 2000). The unusual characters of the described tissue are the rather regular intercellular channels. A somewhat similar pattern is known in *Prototaxites*, a genus now referred to the Fungi, where macro- and microhyphae form peculiar masses (Hueber, 2001). The presence of ovate perforations, however, excludes the attribution of these remains to *Prototaxites* (unless its interpretation as a fungus is incorrect or not applicable to all so-classified fossils).

These remains were not found in organic connection with *Mstikhinia*. However their close association in the same burial may indicate that they are derived from the same plant. For this reason we provide here the illustrations of these internal tissues without expanded description and discussion.

DISCUSSION

There is a series of problems with the interpretation of *Mstikhinia*:

1) Was it an alga or an embryophyte?

2) And if the latter, does it belong to the gametophytic or sporophytic generation?

3) And in both cases, is it a liverwort or hornwort or tracheophyte or rhyniophyte or something else?

Obviously, the available material does not allow us to give any certain answer. It is particularly difficult to exclude an algal interpretation of *Mstikhinia* because the taxonomy of algae is based on characters mainly unavailable in the fossil state. The external habit of *Mstikhinia* resembles that of some red and brown algae. However, due to the absence of tetrasporangia and trichomes, branching at very narrow angle, elongate epidermal cells, quite small size of plants and enigmatic pores, *Mstikhinia* can hardly be placed in the red algae.

The small size of the plants, dichotomous branching, and the absence of true stomata are evidence for the gametophytic nature of *Mstikhinia*. Although the ultimate lobes of tracheophyte leaves could have the same dimensions, the absence of venation, true stomata, and tracheids, does not allow *Mstikhinia* to be attributed to sporophytic generation of a vascular plant, while the general morphology excludes the sporophytic generation of extant bryophyte lineages.

The branched *Mstikhinia* is different from the almost unbranched gametophytes (*Langiophyton, Lyonophyton* and *Remiophyton,* Kerp et al., 2004) and the little branched sporophytes (*Horneophyton*, Edwards, 2004) of Rhyniophyta. Rhyniophytes are characterized also by the true stomata and by the presence of tracheids.

The assumption that *Mstikhinia* does not belong to the pinnules of a fern is based on the absence of any corresponding fronds in the same deposits. The highly dissected fronds of putative ferns and pteridosperms from the Late Viséan deposits of Moscow Coal Basin are attributed to several morphological genera, among which the dispersed pinnules of *Rhodeopteridium* are most similar to *Mstikhinia*. At the same time, in contrast to *Mstikhinia* those pinnules are two or three times dichotomized into linear segments disposed in one plane and have a distinct vein in each segment.

Among the gametophytes, *Mstikhinia* has a certain similarity in habit to liverworts, horsetails and hornworts. The representatives of all these groups normally have rhizoids, which are absent in *Mstikhinia*. However, aquatic liverworts often lack rhizoids. Thus, the taxonomic value of this character should not be overestimated. Also the lamellae of horsetail gametophytes always lack rhizoids (Duckett, 1973, 1979).

The more precise definition of *Mstikhinia* affinities depends on the better understanding of the pore structure, and, ideallly, on the understanding of their function. In front view under moderate magnification, many pores are very similar to stomata. They are partly immersed as in many mosses (albeit in sporophytes only, namely on the capsule walls). The area inside the surrounding cells shows thinner cuticle with a longitudinal slit, which in some cases does not reach the edges of the "inside area" ("single guard cell"). This is unlike most stomata, but in the moss family Funariaceae the guard cell is also single (Loeske, 1914). Namely, at the early stages of development in Funariaceae, there are two guard cells, but later they fuse and form a unique cell with the channel in its central part. However, in some *Mstikhinia* "stomata", the slit also does not reach the edges of the opening (Fig. 49). Available cross sections of *Mstikhinia* cuticle do not show distinct guard cells. Therefore, the interpretation of *Mstikhinia* "stomata" cannot be proved. However, if these structures of *Mstikhinia* are not stomata, what are they?

Pores other than stomata are used for air exchange (Marchantiopsida), for the release of reproductive cells from internal gametangia (some Hepaticae, Anthocerotae, gametophytes of Lycophyta and Pteridophyta, including *Equisetum,* and some algae), and for the release of mucilage (Anthocerotae, and *Treubia* and some other Hepaticae). Our knowledge of the structure of *Mstikhinia* is not sufficient to choose among these functions. Only highly hypothetical considerations are possible now. Air exchange does not seem to be a critical factor for a plant with a thallus less than 1 mm wide. In the extant hepatics air pores are known mostly in the relatively large plants like *Marchantia*, and lacking in the small complex thalloid plants, like *Riccia fluitans*. Also the air pores in hepatics are quite uniform. The uniformity is also characteristic of the surface cells around gametangia or the mouth of gametangial necks in Anthocerotae, ferns, *Equisetum*, etc.

The mucilage clefts known in Anthocerotae are worth discussing, because they are quite irregular in shape and sometimes are surrounded by distinctive cells comparable with stomata guard cells. Schuster (1984) and Proskauer (1951) called them just stomata. Proskauer (1951, p. 333) noted that in Anthocerotae "... stomata in the sporophyte, considered by me as genetically homologous with the slime-pores present, as far as is known, in the gametophytes of all members of the order...". Schuster (1984) supported this statement and mentioned that ventral "stomata"' in hornworts occur in all species, being elliptical to fusiform openings, and guard cells are sometimes regularly sausage-shaped (Goebel, 1915). Illustrations of "stomata" in the literature are too scanty. Our own limited observations reveal the great variation in size, but we found nothing comparable with the guard cells in shape.

The presence of "plugs" above the smallest pores of *Mstikhinia* (Figs. 68-70), as well as paler material seen near pores on the cross sections (Fig. 67) can be explained by the mucilage producing function of pores. At the same time, mucilage-rich plants, such as hornworts and some basal liverworts, e.g. *Treubia* and *Haplomitrium,* are mostly delicate organisms with thin-walled epidermal cells, whereas *Mstikhinia* has well-developed cuticle. Also, the recent Anthocerotae have large, isodiametric to short polygonal surface cells, distinct from the elongate and moderately thick-walled epidermal cells of *Mstikhinia*.

The comparison with fossil Palaeozoic plant groups is also not much more promising.

Krassilov (1982) demonstrated the quite peculiar structure of guard cells in the Devonian *Orestovia*: they are attached to subsidiary cells by just a small surface, and mostly covered by the epidermis raised in the shape of a truncated cone. The latter makes them immersed, poorly seen from the outer surface, but clearly seen from the inner surface. Krassilov (1982) considered them as stomata. Edwards et al. (1998) did not agree with this interpretation and left *Orestovia* outside of the unequivocal Embryophytes. Gomankov (2006) recently re-visited *Orestovia* material and concluded that the stomata-like structures are probably referrable to stomata, but they are quite distinct from that of any known embryophyte. The pores of *Mstikhinia* are different from the stomata-like structures of *Orestovia* in the absence of apparent guard cells, in the greater size variation, in the papillose (vs. smooth) surrounding cells, etc.

The pores of *Nematothallus* (Edwards, 1982; Edwards & Rose, 1984) are sometimes surrounded by papillae quite similar to that of *Mstikhinia*. However, in *Nematothallus* the cellular organization itself has not been proven yet. At the same time, it is necessary to underline that pores and stomata of different organisms may affect the adjacent cells in a similar way, resulting in specific "crowding" and sometimes, raisings, thickenings and papillosity. A similar pattern can be found around immersed stomata of extant mosses (Lewinsky-Haapasaari, 1995; Wilbraham & Long, 2005); around the secretory organ of the sporophyte of *Horneophyton* (Edwards, 2004, Fig. 2g), around the oil-cells of complex thalloid liverworts (Malcolm & Malcolm, 2000, p. 138), around the stomata of many tracheophytes, etc. For this reason, a certain similarity with pores of *Bitelaria* from the Devonian of Ukraine (Krassilov et al., 1987) can be misleading as well. *Bitelaria* is also characterized by the presence of cap-like organs interpreted as sporangia.

* * *

We can conclude that *Mstikhinia* combines the characters of several plant divisions, but cannot be attributed to any of them. For such combined forms, Meyen (1987) introduced the concept of "synthetic type". He noted that the earlier the geological record, the higher are the ranks of taxa whose characters are combined in these "synthetic types". It seems probable that *Mstikhinia* belongs to one such ancient "synthetic" groups, not recognized yet.

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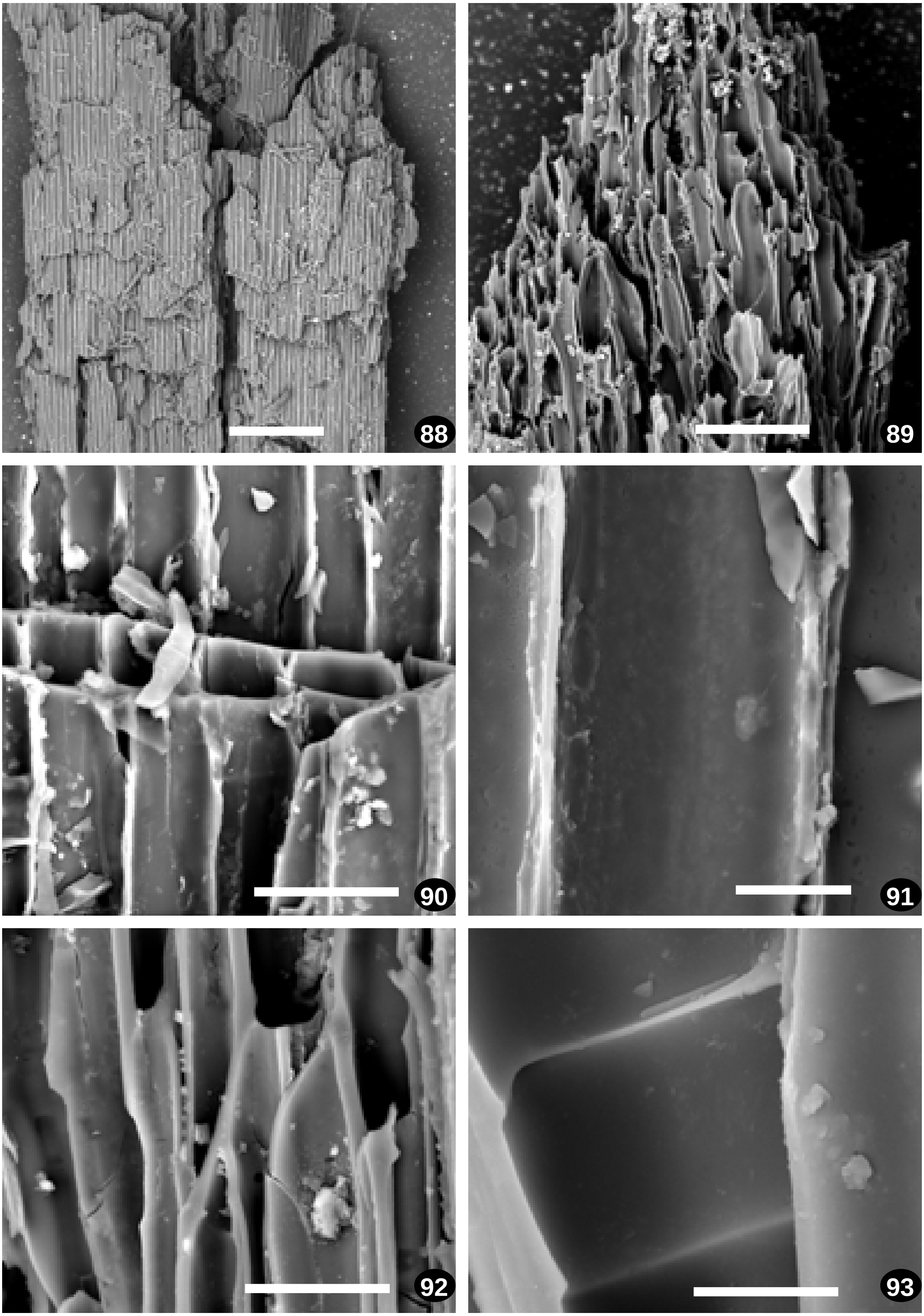
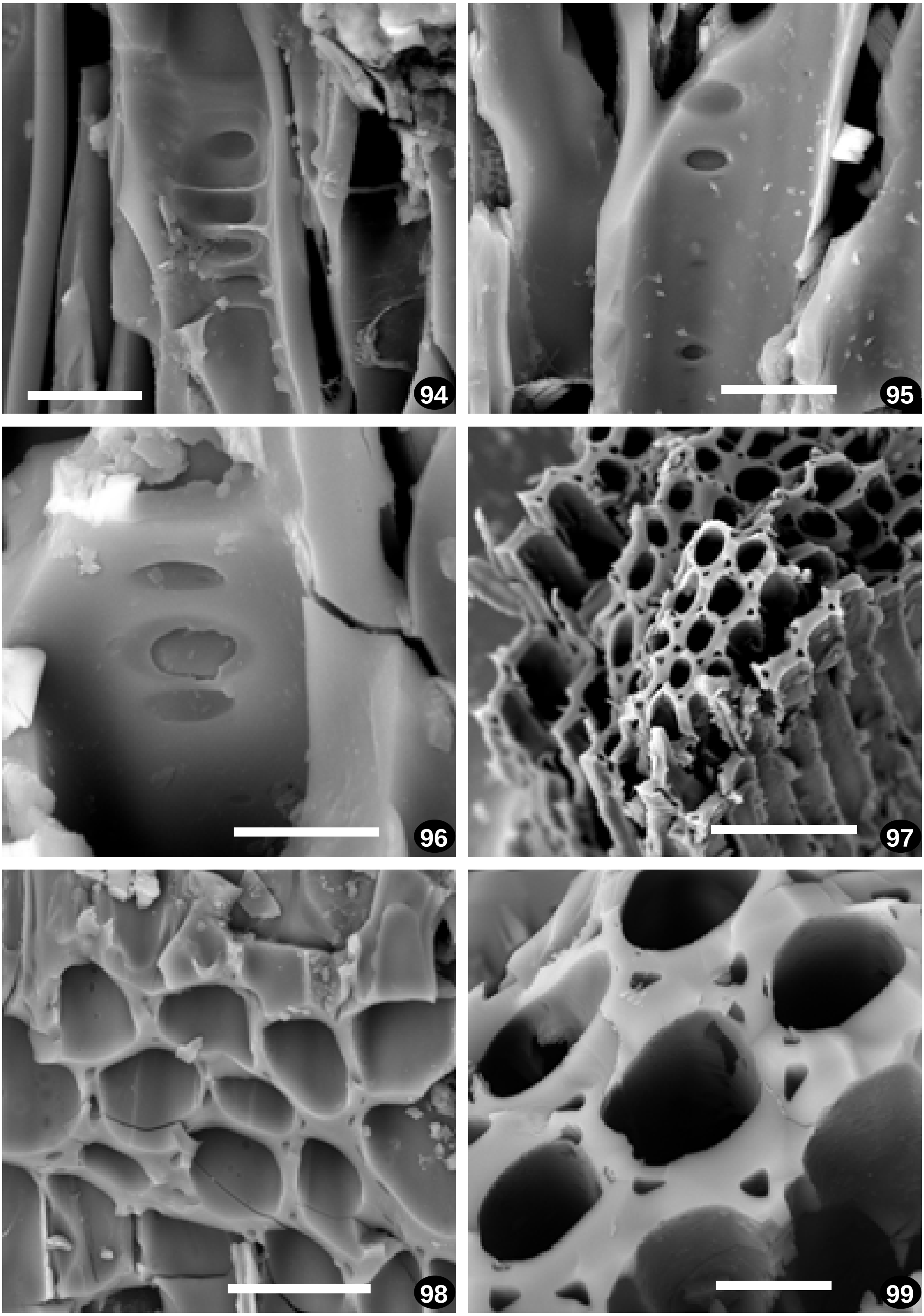


APPENDIX. Figs. 88-93. SEM pictures of the putatively conducting tissues found with cuticles of *Mstikhinia duranteae*. From 4865/182. Scale bars for 88 – 0.5 mm; 89 – 200 µm; 90, 92 – 50 µm; 91 – 20 µm; 93 – 10 µm.



APPENDIX. Figs. 94-99. SEM pictures of the pupatively conducting tissues found with cuticles of *Mstikhinia duranteae*. From 4865/182. Scale bars for 97 – 100 μm; 98 – 50 μm; 94-95, 99 – 20 μm; 96 – 10 μm.