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A new *Rhaphidopteris* from the Lower Liassic of Bavaria, Germany*

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ABSTRACT. A new species of the genus *Rhaphidopteris* Barale, *Rhaphidopteris duetschii* (created by the first author), is described from a clay lens in a sandpit ('Grube Dietz') near the village of Pechgraben, northern Bavaria. As good cuticle preparations could be made, the specimen is described in detail and compared to other species of the genus *Rhaphidopteris* (including species that were formerly described under *Stenopteris* Saporta). It is for the first time that a species of *Rhaphidopteris* has been recorded from Germany. So far, well-known species have been recorded from Greenland, Yorkshire (UK), France and China and vary in age between Rhaetian (latest Triassic) and Kimmeridgian (late Jurassic).

KEY WORDS: *Rhaphidopteris*, cuticle, Lower Liassic, Germany

INTRODUCTION

The Lower Liassic (Hettangian) sediments in Bavaria (Germany) contain a diverse fossil flora, mainly preserved in clay lenses in sandy sediments. Many of the old localities are inaccessible nowadays but new sandpits provide often important new localities. In the last decade, many specimens have been found in various clay lenses in two sand pits near the village of Pechgraben (district Kulmbach) including some interesting material and some new species. For an up to date review, see Van Konijnenburg-van Cittert et al. (1998) and Van Konijnenburg-van Cittert & Schmeißner (1999).

From one of these sand pits, a specimen resembling the Mesozoic genus *Rhaphidopteris* was collected. Cuticular analysis indicates that the specimen indeed belongs to this genus, and comparison with other well-known species learns that we are dealing with a new species of this relatively rare genus. It is described here in detail.

MATERIAL AND METHODS

The holotype originates from the sand pit ('Grube') Dietz, south of Pechgraben (district Kulmbach); TK 1:25.000, Blatt 5935 Marktschorgast, R ^{44}67250, H ^{55}41250. In sand pit Dietz an up to 10 m thick Lower Liassic (Hettangian) fluviatile deltaic succession is exposed. Clay lenses in various sizes are present in the so-called 'Pflanzensandstein' (Weber 1968). They represent among others deposits of old watercourses. When the sand is dug from the pit, the clay lenses disappear as well, so often they are only exposed for a short period. In the lowermost of the recently exposed clay lenses in sand pit Dietz the *Rhaphidopteris* specimen was found by Mr. Dütsch. It has been deposited at the Staatliches Museum für Naturkunde Stuttgart (SMNS no. P.1879). The later found similar, smaller specimen from the same sand pit is kept in his private collection.

The morphology of the type specimen was studied under a dissecting microscope and its cuticle was prepared by macerating in Schulze's reagent (a saturated mixture of $KClO_3$ and 33% HNO_3), followed by neutralisation in 5% ammonia. After rinsing thoroughly in

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water, the upper and lower cuticles were separated with needles and transferred to slides for LM study (Leitz Ortholux). There was too little material to do a SEM study as well.

SYSTEMATIC PART

Pteridospermae

Rhaphidopteris Barale 1972a

Material of this particular type of leaf is for the first time described from the Liassic of Bavaria (Germany). The genus *Rhaphidopteris* is characterized by usually bi-tripinnate, coriaceous leaves with narrow segments (pinnules). The ultimate segments possess only one vein extending (almost) to the rounded apex. The leaves are usually amphistomatic (stomata on both the upper and lower cuticle), but sometimes the number of stomata on the upper cuticle is considerably less than on the lower one. The haplocheilic stomata are typically sparsely scattered and longitudinally oriented. The number of subsidiary cells is around 4–6 but they are often uneven in size and shape, and usually carry papillae. The guard cells are situated at the bottom of a small rectangular pit, thinly cutinised. Trichomes are usually present.

Harris (1932, 1964) described similar seed ferns from the Rhaeto-Liassic of Greenland and the Middle Jurassic of Yorkshire in the genus *Stenopteris* Saporta 1873. This genus, however, does not exist anymore as its type species, *Stenopteris desmomera*, was attributed to the genus *Pachypteris* Brongniart. Therefore, Barale (1972a) created the new genus *Rhaphidopteris* for the material of *Stenopteris* that was clearly different from *Pachypteris*. He choose *Rhaphidopteris astartensis* (Harris)Barale from the Jurassic of Greenland as the type species for the new genus, and made five new combinations in *Rhaphidopteris* (two from the Rhaeto-Liassic of Greenland and three from the Middle Jurassic of Yorkshire). Harris (1981) agreed with this. In the same year Barale (1972b) described a new species of *Rhaphidopteris*, *R. fragilis*, from the Kimmeridgian of France. He also considered the three Southern Hemisphere species of *Stenopteris* (see Jones & De Jersey 1947) as being different and rather belonging to the genus *Dicroidium* because of the basal forking of the rachis.

Zhou and Zhang (2000) divided the genus *Rhaphidopteris* into five morphological groups, in the same time describing two new species from the Jurassic of China:

Group 1, the *R. astartensis*-group (with the type species *R. astartensis*, *R. nitida*, *R. nana*, *R. gracilis* and *R. shaohuae*, the latter two from the Jurassic of China) is characterized by pinnate or dichotomous leaves with segments of the different orders with more or less the same width, containing one vein dividing only below the division of the lamina. Cuticle thin with sparse stomata.

Group 2, the *R. williamsonis*-group (*R. williamsonis*, *R. fragilis* and *R. cornuta*, the latter from China) differs from group 1 in having more slender ultimate segments than the other segments, and in the fact that only the ultimate segments have only one vein.

Group 3, the *R. rhipidoides*-group (with *R. rhipidoides* from China) with wide, lobate segments and a flabellate venation. Cuticle is again thin with sparse stomata.

Group 4, the *R. praecursoria*-group encompasses some Russian, Chinese and a Japanese species, and is characterized by pinnate leaves with wide segments, a pinnate venation and a thick cuticle with numerous actinocytic stomata.

Group 5, the *R. dinosaurensis*-group (*R. dinosaurensis* and *Stenopteris spectabilis* from the Liassic of China) has dorsiventral organs with sessile, mostly bifurcating leaves. The cuticle is rather thick with usually numerous stomata.

Zhou and Zhang (op. cit.) considered that group 4 with its thick cuticle and numerous actinocytic stomata had little in common with *R. astartensis* and might rather belong to the genus *Pachypteris*. Group 5 is completely different in leaf organisation from the type species and was placed as the type species in the genus *Tharrisia* Zhou, Wu & Zhang (Zhou et al. 2001). Thus they restricted the genus *Rhaphidopteris* to the groups 1 to 3.

As to the affinities of this genus, both Harris (1932, 1964) and Barale (1972a, b) believed that it is related to the Mesozoic pteridosperms. Unfortunately, no fructification has ever been found in connection with any of the species. The only reason for this assumption is the pinnate leaf morphology in combination with the presence of a resistant cuticle. How-

ever, *Rhaphidopteris* differs from e.g. the Corystospermales and Peltaspermales in cuticular structure and especially in the configuration of the stomata. According to Harris (1932, 1935, 1964) the cuticle even resembles that of *Czekanowskia* and narrow leaves of *Baiera*. So, the relationship of the form genus *Rhaphidopteris* remains unclear.

Rhaphidopteris duetschii van Konijnenburg-van Cittert **sp. nov.**

Pl. 1 figs 1–8

Holotype. Pl. 1 figs 1, 2.

Repository. Staatliches Museum für Naturkunde Stuttgart (SMNS no. P.1879).

Type locality. Sand pit Dietz, Pechgraben, Bavaria, Germany.

Stratigraphy and age. Early Liassic, Hettangian.

Etymology. After Mr. G. Dütsch who found the holotype.

Diagnosis. Leaves bi- or tripinnate; petiole unknown. Pinnae suboppositely inserted at ca. 45°. Lowermost basiscopic pinnules arising either from the main rachis or from the lowermost part of the pinna rachis; following pinnules arising more or less alternately with a long decurrent base along the rachis and a lamina that then curves outwards at 30–45°; basal pinnules slightly lobed, more apical ones entire; apices obtuse, no veins visible macroscopically.

Cuticle thin, amphistomatic, majority of stomata occurring on the lower cuticle; midrib clearly indicated by longitudinal epidermal cells on both cuticles, secondary veins only vaguely indicated by a few rows of slightly elongated cells; other epidermal cells more or less isodiametric; stomata simple, consisting of 2 not sunken guard cells surrounded by 5–6 subsidiary cells; large number of trichomes present, especially on the lower cuticle.

DESCRIPTION

It is only a small leaf fragment, 4.2 cm long and 3.7 cm wide (Pl. 1 figs 1, 2). The rachis is just over 1 mm wide with a faint longitudinal, median depression. The pinnae are suboppositely inserted at ca. 45° with a distances of 7–9 mm between them. The lowermost basiscopic pinnules arise either from the main rachis or from the lowermost part of the pinna rachis. The following pinnules arise more or less alternating with a long (up to 3 mm) decurrent base along the rachis and a lamina that then curves outwards at 30–45°. The basal pinnules (ca. 5 mm long and 1–2 mm wide) are slightly lobed, the more apical ones (3 mm long, 1 mm wide) are entire. The apices are obtuse and there are no veins visible.

Next to the here described leaf fragment, some apical parts of another fragment are visible that might have belonged to the same leaf. If this was the case, then the leaf was tripinnate at least.

The relatively thin cuticle is amphistomatic (ca. 2 μm thick) but the majority of stomata occurs on the lower cuticle (compare Pl. 1 figs 5 and 8). The midrib is clearly indicated by longitudinal epidermal cells on both cuticles, secondary veins are only vaguely indicated by a few rows of slightly elongated cells. All other epidermal cells are more or less isodiametric. The stomata are simple, consisting of 2 unsunken guard cells surrounded by 5–6 subsidiary cells that are not very specialised (Pl. 1 figs 3, 4, 7). A large number of trichomes is present, especially on the lower cuticle (Pl. 1 fig. 6).

COMPARISON WITH OTHER *RHAPHIDOPTERIS* SPECIES

For the comparison with various other *Rhaphidopteris* species, we will restrict ourselves to the groups 1–3 from Zhou and Zhang (2000). Comparing the present specimen with the Rhaeto-Liassic type species *R. astartensis* from Greenland (Harris 1932), the differences can be easily spotted; the pinnules are much longer than in *R. duetschii* and it has a thicker cuticle that are more or less the same on both sides (completely amphistomatic).

The three Middle Jurassic species from Yorkshire (*R. williamsonis*, *R. nitida* and *R. nana*) are more similar in being tripinnate with short pinnules (see Harris 1964). *R. williamsonis* with leaves over 10 cm long, differs in having very crowded, larger pinnules that sometimes overlap. The cuticle is completely amphistomatic with numerous trichome bases. The leaves of *R. nana* and *R. nitida* are both under 10 cm (as is probably also the case in *R. duetschii*); the leaves are coarsely branched in *R. nana* which resembles in this respect *R. duetschii*, but the ultimate leaf segments (pin-

nules) are usually longer and moreover, the cuticle is completely amphistomatic with stomata more or less in rows and lacking trichomes (other than papilla on subsidiary cells). The leaves are finely branched in *R. nitida* with often overlapping leaf segments and a rather thin hypostomatic cuticle that lacks trichomes. This species is most similar to *R. duetschii*.

The Late Jurassic *R. fragilis* from France (Barale 1972b) is macromorphologically quite similar to our material but there are resin bodies and the cuticle presents some differences; the leaves are completely amphistomatic, and although each lobe demonstrates a single vein, no veins are visible in the cuticles. The subsidiary cells are papillate just as most normal epidermal cells. No normal trichomes have been recorded, but roundish "secretorial elements" that are 150–300 μm in diameter.

As to the Chinese species *R. gracilis* (Middle Jurassic of Qinghai), *R. cornuta*, *R. shaohuae* and *R. rhipidoides* (all from the Yima Formation, Henan, earliest Middle Jurassic), the original literature on *R. gracilis* was not available. According to Zhou and Zhang (2000), the species falls in their group 1, has dichotomously branched primary segments and a thick rachis. However, details of the shape of the leaf segments and the cuticle are unknown. *R. cornuta* Zhang & Zhou (Zhang & Zhou 1996) is also characterized by a primary dichotomous branching; the pinnae and pinnules are asymmetrical, alternate and branch in a katadromic way and are basally strongly contracted forming a more or less cuneate base, often with a short petiole. The broader segments (pinnae) contain up to 5 veins, but only one vein enters each ultimate segment (pinnule); apex of each ultimate segment acute to even acuminate. The cuticle is amphistomatic, stomata sparsely distributed, mainly longitudinally oriented. Guard cells

Table 1. Comparison between the various *Rhaphidopteris* species

	R.duetschii	*R.astartensis*	*R.williamsonis*	*R.nana*	*R.nitida*
branching	tripinnate	bipinnate	tripinnate	tripinnate	tripinnate
pinnule length	3–5 mm	up to 6 cm	up to 5 mm	3–7 mm	2–4 mm
pinnule overlap	no	no	yes	no	yes
cuticle thickness	ca. 1 μm	thick	ca. 2 μm	ca. 2–3 μm	ca. 1 μm
distribution of stomata	amphistomatic, but majority on lower cuticle	amphistomatic	amphistomatic	amphistomatic	hypostomatic
veins visible in cuticle	clearly indicated	no	visible	no	clearly indicated
papillae on subsidiary cells	no	slight thickening	yes	slight thickening	no
papillae on epidermal cells	no	no	no	no	no
trichomes	common	absent	numerous	occasional	absent
	R.fragilis	*R.gracilis*	*R.cornuta*	*R.shaohuae*	*R.rhipidoides*
branching	tripinnate	dichotomous primary segments	dichotomous primary segments, further bipinnate	once pinnate, primary segments dichotomously divided	once pinnate pinnae wedge-shaped (*Ginkgo*-like)
pinnule length	1–4 mm	?	up to 5 mm	ca. 1 mm	ca. 5 mm
pinnule overlap	no	no	no	no	no
cuticle thickness	2 μm	ca. 1 μm?	1–1.5 μm	less than 1 μm	1.5–2 μm
distribution of stomata	amphistomatic	?	amphistomatic, but majority on lower cuticle	unknown	amphistomatic
veins visible in cuticle	no	?	indicated	unknown	no
papillae on subsidiary cells	yes	?	yes	unknown	no
papillae on epidermal cells	yes	?	no	no	no
trichomes	absent	?	no	unknown	no

sunken, with ca. 5 subsidiary cells surrounding them, each carrying a hollow papilla.

R. shaohuae Zhou & Zhang (Zhou & Zhang 2000) resembles *R. cornuta* in cuticle structure but *R. nitida* in gross morphology; the ultimate segments are less crowded and never overlap, and the first branching is dichotomous. The ultimate segments have an acute apex.

R. rhipidoides Zhou & Zhang (Zhou & Zhang 2000) resembles more a *Ginkgo*-like fossil than a typical *Rhaphidopteris* species. The leaf is pinnate, the pinnae alternate, with a long petiole-like base and a fan-shaped upper part widening upwards and 2–3 times dichotomously branched. The ultimate segments are wedge-shaped, with a truncate apex. Venation flabellate, 2–4 veins in each ultimate segment. Cuticle clearly amphistomatic, stomata sparsely distributed, with slightly sunken guard cells and 5–6 subsidiary cells without papillae.

The differences between the various species are summarized in Table 1.

It also has to be mentioned that Hartmann (1967) described a new species of *Thinnfeldia* (*T. minima*) from the Lower Liassic of Grossbellhofen, Bavaria that resembles *Rhaphidopteri duetschii* in gross morphology. The only specimen is bipinnate with 1.0–1.3 cm long pinnae and 1–2 mm long pinnules. However, the cuticle morphology is completely different as the amphistomatic leaves have moderately thick cuticles with stomata of the type generally found in the genus *Pachypteris* and without any trichomes.

CONCLUSIONS

Rhaphidopteris duetschii is a new species of *Rhaphidopteris* Barale, belonging to group 1 (*Astartensis*-group) in the genus *Rhaphidopteris* as defined by Zhou and Zhang (2000).

Even after removal of the groups 4 and 5 (with their thick cuticles) from the genus *Rhaphidopteris*, the genus remains rather heteromorph, as is also stated by Zhou and Zhang (2000).

We believe that the typically bi–tripinnate species with clear pinnules and a pinnate venation (occurring in groups 1 and 2 and including *R. duetschii*) may belong to a different genus than the species with wide, wedge- or fan-shaped leaves with flabellate venation (*R. rhipidoides*).

Even within groups 1 and 2, the species in which the first branching is dichotomous (*R. gracilis, R. cornuta* and *R. shaohuae*), may belong to a different genus than the species in which all branching is pinnate.

Therefore, the assumption of Zhou and Zhang (2000) that the genus *Rhaphidopteris* is more closely related to the Ginkgoales than the Pteridospermae, may only hold for part of the genus. Certainly *R. duetschii* looks like a pteridosperm in its gross morphology.

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PLATE

Plate 1

1. *Rhaphidopteris duetschii* sp. nov., holotype × 1
2. *Rhaphidopteris duetschii* sp. nov., holotype × 2
3. Stoma from upper cuticle of *Rhaphidopteris duetschii* sp. nov. × 400
4. Stoma from upper cuticle of *Rhaphidopteris duetschii* sp. nov. × 400
5. General view of upper cuticle of *Rhaphidopteris duetschii* sp. nov. × 250
6. Two trichomes on lower cuticle of *Rhaphidopteris duetschii* sp. nov. × 400
7. Stomata on lower cuticle of *Rhaphidopteris duetschii* sp. nov. × 400
8. General view of lower cuticle of *Rhaphidopteris duetschii* sp. nov. × 250


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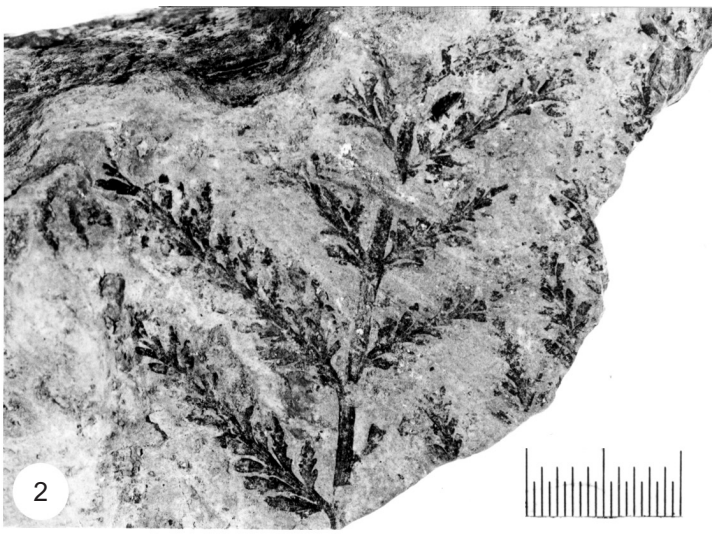
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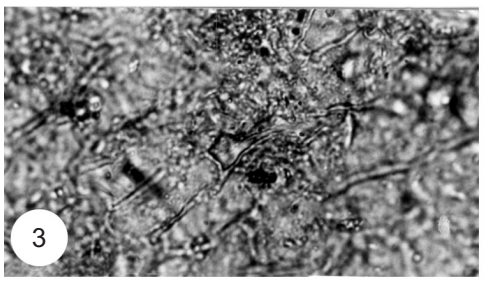
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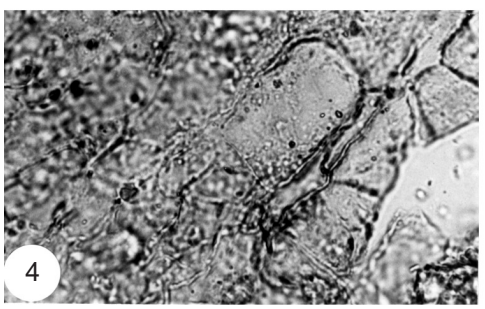
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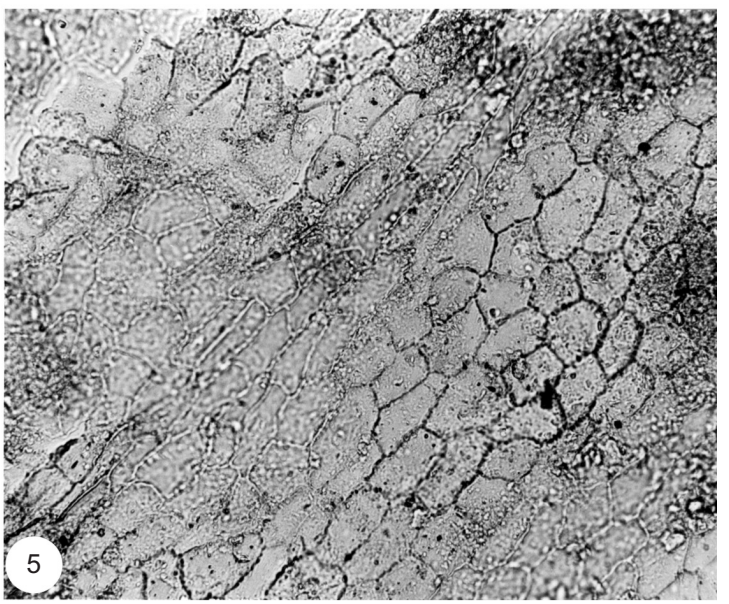
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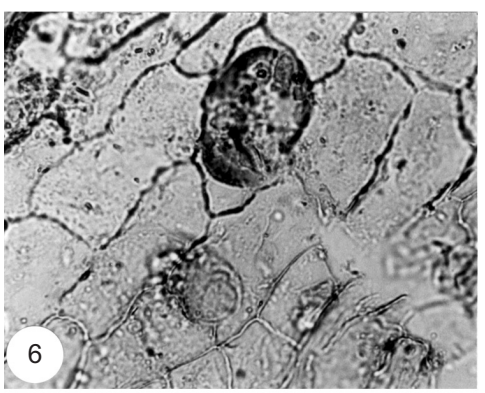
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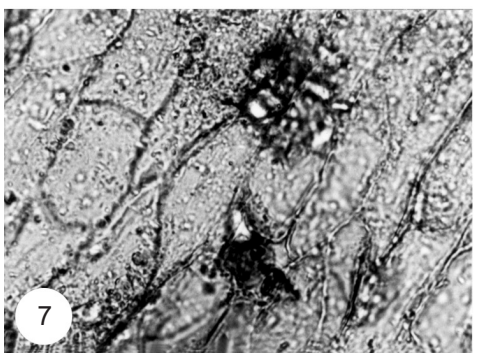
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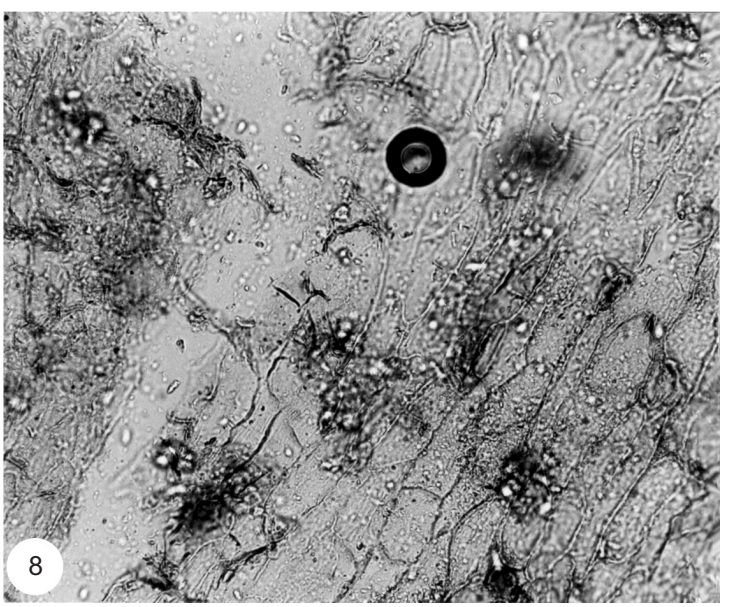
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