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KUNGLIGA SVENSKA

VETENSKAPSAKADEMIENS

HANDLINGAR.

NY FÖLJD.

FEMTIOFÖRSTA BANDET.

STOCKHOLM
ALMQVIST & WIKSELLS BOKTRYCKERI-A.-B.
1913—15

KUNGL. SVENSKA VETENSKAPSAKADEMIENS HANDLINGAR. Band 51. N:o 7.

LEPIDOPTERIS OTTONIS (GÖPP.) SCHIMP.

AND

ANTHOLITHUS ZEILLERI NATH.

BY

ERNST ANTEVS

WITH 3 PLATES

COMMUNICATED APRIL 8TH 1914 BY A. G. NATHORST AND G. LAGERHEIM

UPPSALA & STOCKHOLM
ALMQVIST & WIKSELLS BOKTRYCKERI-A.-B.
1914

As the combination *Lepidopteris Ottonis—Antholithus Zeilleri* may seem somewhat remarkable, I will begin by pointing out that there are several facts which speak for their belonging to the same plant. This cannot, however, be fully proved.

The investigation was commenced some years ago by Prof. A. G. NATHORST who, however, was prevented by other work from completing it. In the course of his researches he already noticed the great conformity between the frond and the male reproductive organ here treated, and I have only had to continue on the way staked out by him.

I am very much indebted to Professor NATHORST for his kindness in placing this interesting material at my disposal, and I have also to express my deep gratitude to him and to Dr. T. G. HALLE for a great deal of good advice and directions.

Lepidopteris Ottonis (GÖPPERT) SCHIMPER.

Pls. 1, 2.

? "Teile von einem Farnkraut", BERGER 1832, p. 10; pl. 2, fig. 4.
Alethopteris Ottonis, GÖPPERT 1836, p. 303; pl. 37, figs. 3, 4.
Pecopteris? Ottonis, PRESL in STERNBERG 1838, p. 161.
Lycopodites Meyerianus, GÖPPERT 1845, p. 201.
Pecopteris Ottonis, GÖPPERT 1845 a, p. 144; pl. 1, figs. 4—10.
"Farn-Wedel", SCHLÖNBACH 1860, p. 525; pl. 4, fig. A.
Pecopteris Grumbrechti, BRAUNS 1866, p. 244; pl. 36, figs. 1, 2.
Asplenites Ottonis, SCHENK 1867, p. 53; pl. 11, figs. 1—3; pl. 14, figs. 3—5.
Pecopteris Grumbrechti, SCHIMPER 1869, p. 535.
Lepidopteris Ottonis, SCHIMPER 1869, p. 574.
Asplenites Ottonis, RÖMER 1870, p. 178; pl. 13, fig. 1.
"Fossila ormbunkar", ERDMANN 1873, p. 203; pl. 18, figs. 1, 1 a, 1 b.
Asplenites Ottonis, NATHORST 1866 a, pp. 30, 39, 40.
Lepidopteris Ottonis, NATHORST 1878, pp. 10, 29; pl. 1, fig. 4 a; pl. 2, fig. 1.
Pecopteris simplex, NATHORST 1878, pp. 10, 29; pl. 5, fig. 2.
Aroides? Erdmanni, NATHORST 1878, pp. 12, 21.
Lepidopteris Ottonis, NATHORST 1878 a, pp. 7, 12; pl. 1, fig. 5.
Lepidopteris Ottonis, SCHIMPER 1879 in SCHENK & SCHIMPER 1890, p. 128.
Lepidopteris Ottonis, NATHORST 1886, p. 117; pl. 26, figs. 8—10.
Lepidopteris Ottonis, ZITTEL 1890, p. 128.
Lepidopteris Ottonis, GOTHAN 1909, No. 110; figs. 1, 2.
Lepidopteris Ottonis, ERDMANN 1910, p. 21.
Lepidopteris Ottonis, NATHORST 1910, pp. 12, 35.

Frond (bi- to) tripinnate, narrowing sharply towards both ends. Main rachis broad, with close, rounded tubercles. Pinnae of first order close, sub-opposite to alternate, long and not very broad, lanceolate or all but linear; rachis with tubercles. "Zwischenfiedern". Pinnae of second order close, linear to lanceolate, narrowing towards the apex. Pinnules small, very close, linear, with rounded apex, confluent at the base. This segmentation rather seldom fully developed; representing usually an intermediate stage between bi- and tripinnate division with oblongly triangular, more or less lobed segments. Pinnules sometimes a little rough. Venation not distinguishable in unmacerated fronds; alethopteridic. Consistence thick and firm. Epidermis with isodiametrically polygonal, at times somewhat oblong cells, with thick, straight walls. Stomata on both sides, though rather few in number on the upper one; surrounded by 4 to 6 regular subsidiary cells with cuticular lobes all but closing the entrance; guardian cells sunk below the epidermis.

The genus *Lepidopteris*, the principal representative of which is this very species, was instituted in 1869 by Schimper (1869, p. 572) for some fossil plants from the Keuper, characterized, as he thought, and as the name indicates, by their scaly rachises. Already long before different writers had pointed out that the plants in question were very characteristic on account of that supposed scaliness, and that nothing similar was ever found in other fossils. They seem, however, to have attached no systematic value to this fact, but the fossils were classified with those genera with which they showed the greatest habitual conformity: *Aspidoides* Jaeg., *Pecopteris* Brngn., *Aspidites* Göpp., and *Alethopteris* Sternb. It is Nathorst (1886, pl. 26, figs. 8—10) who first speaks of tubercles in the epidermis in these plants instead of scales, and thus gives the right explanation of the characteristic structures. Recently Gothan (1909, No. 109) also remarked that he had not been able to find the smallest vestige of scales in either one or the other species. The explanation of the tubercles which he gave, he has, however, according to a kind communication by Professor Nathorst, later on given up (in a letter to Professor Nathorst). Finally, Zeiller (1911, p. 3) has adopted Nathorst's explanation after examining *Lepidopteris stuttgardiensis* (Jaeg.) Schimp.

As will appear from the drawings and the photographs (pl. 1; pl. 2, figs. 5—8), tubercles occur on the rachises of the first order as well as on those of the second order. As their formation evidently requires that the rachis has reached a certain breadth, they are always, or almost always, missing from a rachis of higher order. At times the lamina has a touch of roughness, too. A narrow rachis has only one row of tubercles. It has a strange, articulated appearance, caused by the circumstance that sharp folds were formed, when the tubercles were pressed down. On a rachis of greater width there are several rows of similar tubercles parallel with each other.

Both with regard to the size and the form of the tubercles, there prevails a certain difference between the two sides. On one side (pl. 2, fig. 8), probably the upper one, they are rather large, rounded, or more or less oblong, with the greatest diameter in the transverse direction, while those on the other side (pl. 2, fig. 7) are circular, smaller and therefore more numerous. Between the large tubercles small ones occur on the one as well as on the other side. The tubercles would develope earliest on the upper side, as they can be seen distinctly here, while those on the lower side are hardly discernible yet.

As for the degree of distinctness with which the tubercles appear, there is a great variation in different specimens. They are often sharply conspicuous, but at times they are only distinguished by slight folds on the macerated rachis. This variation seems to stand in intimate connection with the thickness of the cuticle, while, in a much lesser degree, it depends on the size of the specimens, for very broad stalks with a thin cuticle can have often only very inconsiderable tubercles.

The epidermal structure of the tubercles does not differ in any respect from that of other parts of the plant. The very biggest tubercles, however, possess calottes of a more strongly cutinized tissue.

It is quite a common thing for the calottes of the tubercles to be missing (pl. 2, fig. 8), so that the cuticle has more or fewer round or ovate holes. The formation of these holes may be due to different factors. As a thick fossil cuticle is often rather brittle, some of them probably arose during maceration, while others were obviously formed while the plant still lived. I will come back to this subject later on.

Recent Succulents sometimes possess similar tubercles on their laminae. But what mission they have to fulfil, I have not succeeded in ascertaining, and I am, of course, still less in the position to make a statement concerning those in *Lepidopteris Ottonis*.

As to its structure the epidermis of the rachis (pl. 2, figs. 6—8) agrees perfectly with that of the lamina, and is composed of rather thick-walled, isodiametrically polygonal, at times somewhat oblong cells, which sometimes possess, and sometimes lack, distinct papillae. Stomata occur on both sides but are rather few in number. They (pl. 1, fig. 6) are surrounded by 4 to 6 regular subsidiary cells. The guardian cells are immersed. The subsidiary cells seem, probably on account of an oblique position of the walls, somewhat thicker than the rest of the cells, and each of them puts forth a rounded cuticular lobe from the wall directed towards the entrance. These lobes meet in the centre of the entrance, which becomes reduced to a star-shaped passage. Hereby the efficacy of the stoma, no doubt, was greatly enhanced.

Schenk (1867, p. 54), who besides others examined the cuticle of this plant, mentions the regular arrangement of the subsidiary cells. But on the other hand he seems to have overlooked the occurrence of the lobes. Though he has supplied drawings of the epidermis, these do not include any stomata.

Stomata of quite the same construction have already been described by Zeiller (1882, p. 234; pl. 11 and 1900, p. 274; fig. 196) in *Frenelopsis Hoheneggeri* (Ett.) Schenk, and by other authors in other species of the same genus. What I have spoken of as lobes here, Zeiller, and others after him, have, however, interpreted as guard-cells in a stoma with 4 to 6 such cells, an opinion whose incorrectness Thompson (1912, p. 63) recently pointed out.

As has been mentioned, the epidermal structure of the lamina (pl. 2, figs. 1—4, 10) agrees with that of the rachis. The whole surface is unvaried with the exception that the stronger veins — midrib and lateral veins in a pinnule which will soon undergo further segmentation; midrib in a small pinnule — generally are characterized by some rows of somewhat oblong cells on the lower side and by the localisation of most of the stomata (pl. 2, fig. 1), which are not very numerous, to a comparatively narrow strip above them on the upper one. On the lower epidermis the stomata are far more numerous than on the upper; and here they are equally distributed over the whole surface of the pinnule. According to SCHENK (1867, p. 54), they should be quite missing on the upper side. The cutinisation is strong and similar on both sides, and the plant may have been succulent. The cells usually have papillae (pl. 2, fig. 4), but this is not always the case.

When examining the macerated fronds, the attention is necessarily drawn to the strange fact that practically every segment has one or more holes (pl. 2, figs. 2, 3, 10). These holes vary in a high degree as to their size, being in some cases quite small and in others rather large, and are usually rounded or a little oblong, but are sometimes of irregular form. They are either sharply marked against the uninjured part of the lamina or bordered by a very thin cuticle. In the latter case, one has obviously to do with a hole above which the epidermis has partly been regenerated, for it is by no means seldom that one sees spots where this regeneration has had time to become complete (pl. 2, fig. 3), and where nothing but the thinness of the cuticle indicates that holes once existed. The parts nearest the holes are generally somewhat more strongly cutinized than the rest of the epidermis, which is probably result of the reaction of the plant at the bursting of the cuticle.

In explaining the formation of the holes, it is, of course, of importance to know whether they are limited to a certain side of the frond, or whether to fixed parts of it. I have already mentioned that they occur on the rachis, and an examination of a great number of leaf-fragments has shown that they can be found on any part of the plant, and on either side. The majority, however, occur near the veins on the lower side of the segments. They are not infrequently found at the margins of the pinnules (pl. 2, fig. 10).

The holes in question often remind one to no small extent of the water-pores in *Polypodium vulgare* L. But their mode of occurrence, as do other circumstances, argue decidedly against their having a similar function to fill or, on the whole, having anything direct to do with the plant as such at all. On the contrary, everything suggests that they are indebted to some external influence for their formation. It is possible that they are caused by insects or a parasitic fungus, perhaps more probably the latter, as that would best explain their constant occurrence. This fungus would have developed under the epidermis, and finally have burst it. If it became ripe long before the embedding of the plant, the resulting wound would have had time to heal, and new cuticle to be formed.

The segmentation of the frond has been the subject of different interpretations on the part of different authors. The differences of opinion have been in reference to this very species, as the other representatives of the genus have always been regarded as being only bipinnate, which they apparently are. As for the species in question, there are two opinions, one being that the frond is tripinnate, and the other that it is only bipinnate. The former opinion was first pronounced by GÖPPERT (1845 a, p. 144), and was later on taken up and cleared up by NATHORST (1878, p. 30), while the latter, which some years ago was adopted by GOTHAN (1909, No. 109), derives its origin from SCHENK (1867, p. 53). What GÖPPERT and NATHORST regarded as pinnules are, according to those authors, only fortuitous lobes formed by a "nachträgliches Einreisen der Spreite", which was supported by the dentation of the margin. GOTHAN considers further that those scores followed the course of the lateral veins.

Now we can take it for a fact that the pinnules stand very close and are never entirely free, and that only the very biggest specimens are characterized by a tripinnate segmentation (pl. 1, figs. 2, 5; pl. 2, fig. 9), while the great majority takes up an intermediate position between bi- and tripinnate. It is accordingly evident, and it appears also from their drawings, that SCHENK and GOTHAN have only had to do with fronds not yet fully developed. GOTHAN's opinion, however, is for two reasons somewhat strange, the first being that the veins would not run out into the teeth but exactly between them, and the second that the cuticle in this so xerophilous plant would be extremely thin above the veins.

As for the venation, neither GÖPPERT nor NATHORST could come to a definite conclusion, though each thought he had discerned a midrib in each pinnule. According to SCHENK and GOTHAN, however, it is alethopteridic with a more or less distinct midrib and with generally indistinct secondary veins, which according to the former are dichotomical, and according to the latter always simple. That which GOTHAN says of the "Einreisen der Spreite" along the veins, however, proves that what he has understood to be veins are not such.

Nor have I myself been able to discern any trace of venation in unmacerated fronds, but an examination of macerated ones may show that it is alethopteridic. In most specimens it is possible to distinguish a certain differentiation in the shape of the epidermal cells on the lower side, these being somewhat oblong in narrow strips in the middle of the pinnules indicating the course of midribs.

The distribution of the stomata, however, will show the nature of the venation more exactly. As already mentioned, there is no difference between the upper and the lower epidermis save the stomata on one side, probably the upper one, not being equally distributed over the whole surface but more numerous in comparatively narrow strips. In a large pinnule, i. e. a pinnule which will soon undergo a further segmentation, those strips occur partly above the future rachis, partly above the middle of each future pinnule (pl. 2, fig. 1). That the bands in question lie above and mark the veins, is fully evident from their occurrence. Whether the secondary veins in their turn already send out lateral veins, cannot be decided, but, of course, they will do so sooner or later.

There is another species, *Lepidopteris stuttgardiensis* (JAEG.) SCHIMP., in which the venation, according to GOTHAN (1909, No. 11; fig. 1 B), is likely to be alethopteridic.

The basal portion (pl. 1, figs. 3, 4) of the stalk is oblique, widened, and shows clearly that the specimen represents the base of the whole frond.

The first description of *Lepidopteris Ottonis* was given by GÖPPERT in 1836, though BERGER already some years earlier had mentioned and figured a couple of leaf-fragments, probably belonging to this species. Some years afterwards GÖPPERT (1845, p. 201) described the plant for the second time, now under a new name, a mistake which he himself, however, immediately corrected (1845 a, p. 144). About two decades later, BRAUNS, who had obviously overlooked the earlier authors, again described the plant as a new species, and SCHENK gave a detailed description and discussion of it.

While these authors in their classifications, as mentioned, allowed the segmentation and the habit to decide the matter, SCHIMPER (1869, p. 572) raised another attribute, the supposed presence of scales, to the rank of specific generic character, and instituted for this as well as for some other forms a new genus *Lepidopteris*. But he overlooked the fact that BRAUNS's *Pecopteris Grumbrechti* was identical with *Lepidopteris Ottonis*.

SCHIMPER's idea of forming a separate genus for these plants, was no doubt very good, for, on account of the roughness of the epidermis, they are very characteristic and well separated from other forms agreeing in habit.

Finally, NATHORST (1878, pp. 11, 21, 29) described the species from Scania under different names; later on, however, he (1886, p. 117) undertook the necessary unions. The fragment figured as *Asplenites Ottonis* in the Flora at Pålsjö (1876, pl. 2, fig. 8) has no connection with this species.

In the roughness of the rachis, in the thick consistence as well as in the general shape, the species here treated presents a great resemblance to *Lepidopteris stuttgardiensis*. But in most cases they are well separated, as the latter always seems to be bipinnate, and possesses more linear, at the apex rounded pinnules, which are often closely occupied by tubercles similar to those on the rachis.

On account of the fern-like habit, writers on the the subject have from the very beginning regarded the systematic position of the plants in question as settled, and disagreement has only been in reference to the nature of the sori. On this point, however, opinions have divided, one author having described sori of one type, another author of quite a different one. Thus, GÖPPERT (1845 a, p. 144) thought he had found rounded sori in one row on each side of the midrib, SCHENK (1867, p. 53) oblong ones along the lateral veins, and finally NATHORST (1886, p. 117) rounded sori near the margins of the segments. SEWARD (1900, p. 140 and 1910, p. 346) has on two occasions made the suggestion that *Asplenites Ottonis* (= *Lepidopteris Ottonis*) is the fertile form of the frond ascribed by SCHENK to *Asplenites Rösserti* (PRESL.) SCHENK. Quite recently GOTHAN (1909, No. 110) adopted SCHENK's opinion. Finally, there are authors who believe they have also found sori in other species of the same genus, *viz.* in *Lepidopteris stuttgardiensis* (SCHIMPER 1869, p. 574; pl. 34, fig. 1 and GOTHAN 1909, No. 111) and in *Lepidopteris rigida* (KURR.) SCHIMP. (SCHIMPER 1869, p. 573; pl. 34, figs. 2, 3).

A critical examination of the drawings of these authors, however, shows that no importance should be attached to these statements, as they are all in the highest degree unreliable. Thus, GÖPPERT regarded tubercles and SCHENK and GOTHAN the existing convexity of the lamina between two not yet developed segments of the third order as sori, whilst other authors gave a wrong interpretation of something else. The incorrectness of SCHENK's opinion was already long ago pointed out by NATHORST (1878, p. 30), who with good reason considered GÖPPERT's statement as not quite reliable either. NATHORST's statement was founded on the specimen pl. 2, fig. 5. On microscopical examination after maceration, however, the rounded structures interpreted as sori proved, as he has kindly told me, to be protuberances in the matrix.

Accordingly, we may assume that sori have never been seen, and it is noteworthy that in the great number of macerated as well as unmacerated fronds of *L. Ottonis* which Professor NATHORST and the writer have examined, there was never found the very least vestige of anything which could be interpreted as reproductive organs.

There is, accordingly, no direct ground for the theory that *Lepidopteris* belongs to the Ferns. Not even the habit speaks directly in favour of this supposition, for, since the discovery of the Pteridosperms, an agreement on this point no longer constitutes a criterion as to a plant belonging to the group in question; whereas, facts speaking in favour of an opposite opinion are not quite missing. Among these the construction of the stomata and the thick consistence of the epidermis should be noticed. The cuticle, it is true, has only been examined in *Lepidopteris Ottonis;* but it is, I suppose, probable that the stomata and the epidermis in the other species, which fully agree regarding consistence, are on the whole of essentially the same construction.

As already mentioned, the stomata of *L. Ottonis* have in the Gymnosperms their nearest analogy among those in recent plants. Moreover, as similar stomata and such a pronounced xerophytism have not been found in indubitable fossil Ferns, and have no analogy in recent ones, these facts, as I (1914, p. 19) have more particularly tried to show somewhere else, give positive support to the opinion that the genus is not a filicinean one.

Further on I shall put forward circumstances speaking for *L. Ottonis* belonging to the same plant as the male organ described by Professor NATHORST (1908, p. 20) as *Antholithus Zeilleri.* If we assume this affinity — which, however, cannot be fully proved — *L. Ottonis* would belong, perhaps not to the Pteridosperms, but rather to some Mesozoic successor of this plant-group, a successor in which the sporophylls had become more differentiated from the vegetative foliage.

As for its geological appearance, *L. Ottonis* is restricted to the Rhaetic, for which formation it constitutes an important 'Leitfossil'. The geographical distribution also seems to have been limited, the plant having been found up to the present only in Germany, Sweden, and Poland. In Germany it has been described from Wilmsdorf, Matzdorf, and Ludwigsdorf in Upper Silesia, Coburg in Thuringia, and Seinstedt in Brunswick. In Poland it has been found near Wielun. In Sweden

L. Ottonis is known from several localities in Scania, and occurs in great numbers in some strata. At Bosarp it even almost entirely alone forms a layer, which is comparable with the 'Blätterkohle' of *Bothodendron* in Tula, Russia. Besides at Bosarp it occurs very frequently in the plant-bearing strata α and 4 at Bjuf and the layer 4 at Billesholm. Other occurrences are Bjuf 1 and 3, Skromberga the lower seam, Stabbarp 1 to 3, Höganäs 'the lower', and Hyllinge. The zones in which it is represented are thus those with *Dictyophyllum exile, Camptopteris spiralis,* and *Lepidopteris Ottonis;* and in the last-mentioned zone — plant-bearing layer 4 — it is met with most frequently.

Genus **Antholithus** Linné.

Antholithus, Linné 1768, p. 172.

The name of *Antholithus* was formed by Linné in order to indicate 'Phytolithus floris', and was readopted by Nathorst (1908, p. 23) in its original sense, as a collective name of fossil flowers in general.

Antholithus Zeilleri Nathorst.

Pl. 3, figs. 1—16.

Antholithus Zeilleri, Nathorst 1908, p. 20; pl. 2, figs. 59, 60; pl. 4.
Antholithus Zeilleri, Coulter & Chamberlain 1910, p. 193.
Antholithus Zeilleri, Nathorst 1910, p. 13.

Since Professor Nathorst some years ago described the male reproductive organ *Antholithus Zeilleri,* it has for several reasons proved desirable to undertake a renewed examination of the same, especially with regard to the cuticle, and also to go through the existing material of 'Blätterkohle' from Bosarp, where it was expected to be found. This 'Blätterkohle' has entirely the same appearance as that which *Bothodendron* forms in Tula in Russia, and consists for the most part of cuticles of *Lepidopteris Ottonis.* In order to soften the rather firm and hard cakes, I boiled them with soda, a procedure which proved to be a very good one, as after this the washing was easily done.

What immediately struck me on doing the washing, was the extraordinary uniformity of the layer. In thera ther large amount of material I went through I found, besides fragments of *Lepidopteris Ottonis* — which, as just mentioned, constituted the great bulk — several stalks (fronds?) of an undeterminable plant, some specimens of *Antholithus Zeilleri* and a great many free pollen-sacks of this latter, about ten seeds, one or two segments of a cycadean frond, and some animal remains. Éverything was small and broken, and there were seldom even entire pinnae.

No complete specimens of *Antholithus Zeilleri* were found which could throw any light upon its construction, but, on the other hand, I found some of a somewhat different aspect from those described by Professor NATHORST.

As Professor NATHORST thought he had to do with the male flower of a Ginkgophyte, he called the structures in question 'Staubblätter'. Later on I will point out some facts speaking for *Antholithus Zeilleri* being the male organ corresponding to *Lepidopteris Ottonis*. Presuming this affinity, it would either be lobes of a fertile frond, such as in the Pteridosperms, or itself constitute differentiated sporophylls.

Microsporophylls or lobes of fertile frond reaching a length of 15 mm., attached several together; position in other respects unknown. Each lobe or sporophyll consisting of a 5 to 7 mm. long, narrow, stalk-like portion, divided into from 3 to 5, generally 4, segments. Segments up to the length of 6 mm., linear with rounded apex, or very short and broad, ovate. Each segment bearing in the middle line of the lower side ovate pollen-sacks; these directed obliquely outwards, opening with a longitudinal fissure. Pollen-grains ovate. Cuticle of sporophylls or lobes rather thick, composed of isodiametrically polygonal or somewhat oblong cells, sometimes having, sometimes lacking papillae. Stomata bordered by a ring of 4 to 6 regular subsidiary cells, sending out rounded cuticular lobes towards the centre of the entrance. Guard--cells submerged below the epidermis. Cuticle of pollen-sacks with rather thin-walled oblong cells.

The figures (pl. 3, figs. 1—9) should give a good idea of the size and the appearance of the structures in question. The stalk-like portion below the segments has the length of 5 to 7 mm.; it is narrow, somewhat increasing in breadth in the upper part. The number of the segments varies from three to five, though they are generally four. They sometimes reach a length of 6 mm., but more often they are shorter and at the same time broader; some, as can be seen, are ovate. The margin of the segment is not quite straight but has a couple of incisions on each side, which are hardly discernible with the naked eye (pl. 3, fig. 10).

In spite of the variation in the number and the shape of the segments, there can be no doubt that all the specimens belong to one and the same species.

No specimen gives any light as to how the lobes or sporophylls were placed; but it is evident from pl. 3, figs. 2 and 8 that they occurred several together, though their position cannot be more exactly stated.

The pollen-sacks (pl. 3, figs. 1, 9) are ovate, and occur to the number of eight on each segment. They are attached to one side, probable the lower one, and are directed obliquely outwards. According to the length of the segments their position is somewhat different. In a short segment (pl. 3, fig. 1) they issue from a common point near the apex, and radiate, while in a longer one (pl. 3, fig. 9) they are in two parallel rows in the middle line of the segment. The opening took place by a longitudinal fissure, which extended all along one side and a short way down on the opposite one (pl. 3, fig. 9).

Several pollen-sacks are quite filled with ovate pollen-grains (pl. 3, fig. 14), which according to NATHORST's (1908, p. 21) measurements are 36 to 48 μ, generally 40 to 43 μ, long. As for the shape the pollen-grains (pl. 3, figs. 15, 16) agree with those of *Ginkgo* and Cycadophytes and also with the spores of several Ferns.

The cuticle (pl. 3, figs. 10, 11) of *Antholithus Zeilleri* is rather thick und firm and quite similar on both sides. It has, especially on the segments, a number of folds, and probably had rather a rough surface. On the stalk-like lower part the folds are generally longitudinal, though cross-folds are not wanting. Here and there are holes (pl. 3, fig. 11), which quite agree with those I have described above in *Lepidopteris Ottonis*. They are generally rounded or a little oblong, being either sharply delimited against the intact cuticle or bordered by a regenerated, thin cuticular zone. At times the regeneration of new cuticle has been complete.

Judging from the perfect agreement, the holes here are quite comparable with those of *Lepidopteris Ottonis*. As pointed out in speaking of that plant, it is practically certain that they have nothing to do with the plant itself but most likely were caused by a parasitic fungus (p. 6).

The epidermal cells (pl. 3, fig. 11) are isodiametrical or a little oblong, and in some cases have, and in other cases lack papillae. The walls are straight, and fairly thick. Stomata occur rather sparsely. They are equally distributed, and neither by their occurrence nor by any other attributes of the cuticle is it possible to distinguish an upper or a lower side. The guard-cells are immersed below the epidermis, and the entrance is surrounded by a number of regular subsidiary cells, whose walls parallel with the entrance form two concentric rings (pl. 3, fig. 12). From the inner of these walls issues one rounded cuticular lobe corresponding to each cell. These lobes almost close the entrance, only leaving a star-like opening.

NATHORST (1908, p. 21) remarks that the stomata are 'recht ähnlich' those of *Baiera* but does not give any detailed description of them. This remark is undoubtedly quite right, but a closer examination shows that there is a certain difference and that the stomata of the genera can be comparatively easily distinguished.

As Professor NATHORST's (1906, p. 8) researches show, and as I myself have, ascertained, the stomata of *Baiera* are also bordered by a number of subsidiary cells with lobes. These latter consist of papilla-shaped prolongations of the cells in an oblique upward direction. They are sometimes long, sometimes short but do not close the entrance in the same degree or in the same manner as the horizontal cuticular lobes in *Antholithus Zeilleri*.

I have copied from NATHORST a couple of drawings of stomata in *Baiera* (pl. 3, figs. 17, 18), and the difference may be made most clear by a comparison between these and those of *A. Zeilleri*.

The cuticle of the pollen-sacks (pl. 3, figs. 13, 14) is considerably thinner than that of the lobes or sporophylls otherwise, and totally lacks stomata. The cells are polygonal, oblong in the longitudinal direction of the pollen-sacks, and have rather thin walls. Papillae do not occur.

Among known reproductive organs that described by LEUTHARDT (1903, p. 7; pl. 7) as the male flower of *Baiera furcata* HR. will present the closest analogy. With reference to these, the writer just mentioned says that "Gruppen von Pollensäcken alternierend zu 10 bis 15 um eine gemeinsame Achse sich lagern. — — — An der Hauptspindel entspringen ein 3 mm. langes Filament, das sich flächenartig erweitert. Von dieser Staubblattfläche aus strahlen in regelmässigen Abständen vier Antherengruppen zu je drei Pollensäcken aus. Jede Gruppe steht auf einem besonderen Stiele." To this description should be added that the organs regarded as pollen-sacks stand right out, and constitute a direct continuation of the sporophyll without being set off against it in any manner.

Accordingly, the difference between the two male organs in question is, as far as is known, principally to be found in the position and the number of the pollen-sacks as well as in their shape. The existing resemblance between them is in all probability due rather to an agreement in function than to any close relationship.

LEUTHARDT does not hesitate to take for granted the identity of his flower and of the fronds described as *Baiera furcata*. But substantial evidence is, I think, necessary to prove this, for the agreement with the male flower of *Ginkgo biloba* may be far from being so great, as he is inclined to suppose.

As for the systematical position and the relationship of *Antholites Zeilleri* NATHORST expresses himself with the greatest caution. He points out the possibility of its belonging to a Ginkgophyte; but on the other hand he does not consider it impossible that it is a case of a Cycadophyte. Later on he observed some correspondences to *Lepidopteris Ottonis*, and now considers it, as he has kindly told me, rather possible that it constitutes the male organ corresponding to this frond. This supposed relationship cannot be fully proved with the material at disposal; but the fact that there is much which speaks for it, should be clear from the discussion of the matter which I will now give.

In trying to find out to which frond *Antholithus Zeilleri* corresponded, the first questions must be: do we know this frond, or do we not? which is more likely?

It is, of course, not possible to be perfectly certain that it is known, but the scale weighs heavily in the balance, when one considers how infinitely much more readily these small organs are lost and escape the attention than fronds, which must be far more numerous, and further in this case must be of a very firm consistence — the scale weighs, however, so decidedly in favour of this, that it seems to be rather a reasonable supposition. In this connection it is worthy of remark that *A. Zeilleri* is known from four localities, and in one of them it is not a very great rarity.

As NATHORST brought forward the supposition of *A. Zeilleri* possibly being the flower of a Ginkgophyte, I will first discuss this possibility.

There are a number of Ginkgophytes known from Scania, but several are rare, and others are out of the question, because they do not occur in the same layers as *A. Zeilleri*. Thus, there are only two *Baiera*-species, which — at Billesholm — occur in association with this. And *Baiera* is in all probability the only genus which can come in question.

On comparing *A. Zeilleri* and the male flower of *Ginkgo biloba* the matter already becomes rather suspicious, for the difference is enormous, and one may reasonably ask with COULTER & CHAMBERLAIN (1910, p. 193) whether, as it seems, such closely allied genera as *Ginkgo* and *Baiera* can differ so immensely with regard to their reproductive organs.

A noteworthy fact is the circumstance just mentioned that the resistant fronds of *Baiera* only occur at Billesholm in connection with *A. Zeilleri* but not in the other localities, above all, not at Bosarp. For it would only be what might be expected if at least some frond-fragment had gone astray to this layer, in which the corresponding flower occurs as frequently as it does here.

But even if one does not wish to ascribe any importance to this circumstance, the construction of the cuticle, and, above all, that of the stomata, speaks against the affinity of the fossils in question. For on comparing them, it is clear that the *Baiera*-species in question differs from *A. Zeilleri* by a cuticle which is thinner throughout, as well as by somewhat different stomata (see p. 12).

It is therefore probably necessary to search elsewhere for the plant of which *A. Zeilleri* constituted the male organ.

In the paper mentioned NATHORST also points out the possibility of the mother--plant being a Cycadophyte. There is, however, no reason to suspect any particular species; and of those whose cuticle has been microscopically examined — and this purpose is the case with almost all in which it has been sufficiently well preserved for that — none can come in question.

Under such circumstances Professor NATHORST's suspicion fell upon *Lepidopteris Ottonis,* and after proving that the existing statements as to sori have no justification in reality, there no longer exists any reason against presuming this to be the mother-plant.

The fact which first turned NATHORST's thoughts to the relationship of the fossils mentioned, was their occurrence together. By itself this circumstance, of course, is of no importance, but it was the very repetition which attracted his attention, and, when taken in connection with other circumstances, it obtains a by no means little value. For it is noteworthy that, although *Antholithus Zeilleri* is certainly not known from anything like all the localities of *Lepidopteris Ottonis,* yet on the other hand, it has never been found in any strata except with this plant, and at Bosarp itself, in a layer consisting almost entirely of *L. Ottonis,* it is met with more frequently than anywhere else.

Having carefully examined the cuticle of the respective plants, I have found that they agree so perfectly that it is impossible to point out any difference whatever. The thickness of the cuticle and the cell-walls, and the shape and the size of the cells are the same. Both are characterized by the absence or the occurrence of papillae. Finally, the construction of the stomata is perfectly similar, a fact to which I ascribe great significance, as fully agreeing ones have not been found in other fossils from Scania.

Though *A. Zeilleri* does not present such tubercles as *L. Ottonis,* it seems to have had rather a rough surface. It accordingly appears to show a certain resemblance with *L. Ottonis* on this point, but, at any rate, the absence of such tubercles is of no importance. Finally, both of them have holes, but such are also found in other fossil plants from Scania.

To sum up, it can be said that there are many circumstances which speak for, and none which speak against, there being a connection between *A. Zeilleri* and *L. Ottonis*. As I have already pointed out, the arguments are not perhaps fully sufficient, and consequently the matter cannot be regarded as quite settled. But on the presumption that the fossils in question belong to the same plant, it will not be out of place to say a word or two on its systematical position.

No seeds concerning which there exists any sort of evidence of their connection with *Antholithus Zeilleri* have been found; but it must, I think, be presumed that it constituted the male reproductive organ of a seed-plant.

Although our knowledge of the male organs of the Pteridosperms is too limited for us to be able to make any statement as to their possible variation of shape and anatomy, they do not seem to differ essentially from the isosporangia of Marattiaceous Ferns. As, however, it is not known whether the structures here described corresponded to segments of fertile fronds, such as in the Pteridosperms, or whether they themselves constituted differentiated microsporophylls grouped together in a kind of flower, and as the female organs are not known either, it is perhaps better not to count the hypothetical plant in question to this group. It is conceivable that in Mesozoic times the Pteridosperms were succeeded by a plant-group in which the male and the female sporophylls had reached a higher stage of evolution, and were more differentiated from the vegetative foliage still having filicinean habit.

Antholithus Zeilleri is only known from the Rhaetic deposits of Scania — to be more exact from the plant-bearing layer 4 (zone with *Lepidopteris Ottonis*). It occurs most frequently in the 'Blätterkohle' at Bosarp but also in solitary specimens at Billesholm and Bjuf.

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Explanation of Plates.

(All figures are in natural size, if not otherwise stated.)

Plate 1.

Lepidopteris Ottonis (GÖPP.) SCHIMP.

Figs. 1—3, 5. Bi- to tripinnate fronds.
Fig. 4. Lower portion of fig. 3 magnified. $^{1,5}/_1$.
» 6. Portion of epidermis with a stoma. $^{610}/_1$.

Plate 2.

Lepidopteris Ottonis.

Fig. 1. Portion of a pinna of second order shortly before a further segmentation. Observe the occurrence of the stomata in the middle of the pinnule and the future ones. $^{22}/_1$.
» 2. Hole in the cuticle. $^{80}/_1$.
» 3. Hole above which the cuticle has been regenerated. $^{80}/_1$.
» 4. Portion of cuticle seen from the side. $^{300}/_1$.
» 5. Portion of a frond the segments of which have rounded structures near the margin. They are not sori.
» 6. Portion of a rachis of second order with one row of tubercles. Upper side. $^{22}/_1$.
» 7. Portion of a rachis of first order with several rows of tubercles. Lower side. $^{22}/_1$.
» 8. Corresponding (fig. 7) upper cuticle. The greatest diameter of the tubercles goes right across the stalk. $^{22}/_1$.
» 9. Portion of a pinna of first order. Photograph of the cuticle.
» 10. Portion of a segment with holes at the margin. $^{80}/_1$.

Plate 3.

Antholithus Zeilleri NATH.

Fig. 1. Specimen with 8 pollen-sacks seen from the upper side. After NATHORST 1908, pl. 4, fig. 81. $^{11}/_1$.
» 2. Four sporophylls or lobes. After NATHORST 1908, pl. 4, fig. 82.
» 3. Specimen with 3 lobes. $^{3,5}/_1$.
Figs. 4, 5, 7. Specimens with 4 lobes. Figs. 4, 5: $^{3,5}/_1$; fig. 7: $^{2,5}/_1$.
Fig. 6. Specimen with 5 lobes.
» 8. Some sporophylls or lobes occurring together. After NATHORST 1908, pl. 4, fig. 90.
» 9. After NATHORST 1912, pl. 1, fig. 5. $^{4}/_1$.
» 10. Lobe of fig. 5. Two incisions on each side. $^{25}/_1$.
» 11. Portion of cuticle with a hole. $^{80}/_1$.
» 12. Portion of cuticle with a stoma. $^{610}/_1$.
» 13. Portion of cuticle of a pollen-sack. After NATHORST 1908, pl. 4, fig. 87. $^{90}/_1$.
» 14. Pollen-grains. $^{100}/_1$.
Figs. 15, 16. Pollen-grains. After NATHORST 1908, pl. 2, figs, 59, 60. $^{500}/_1$.

Baiera spectabilis NATH.

Fig. 17. Stoma seen obliquely from the side. After NATHORST 1906, fig. 8, p. 8. $^{150}/_1$.
» 18. Stoma seen from above. After NATHORST 1906, fig. 5, p. 8 (upper portion). $^{150}/_1$.

Tryckt den 16 juni 1914.

Uppsala 1914. Almqvist & Wiksells Boktryckeri-A.-B.

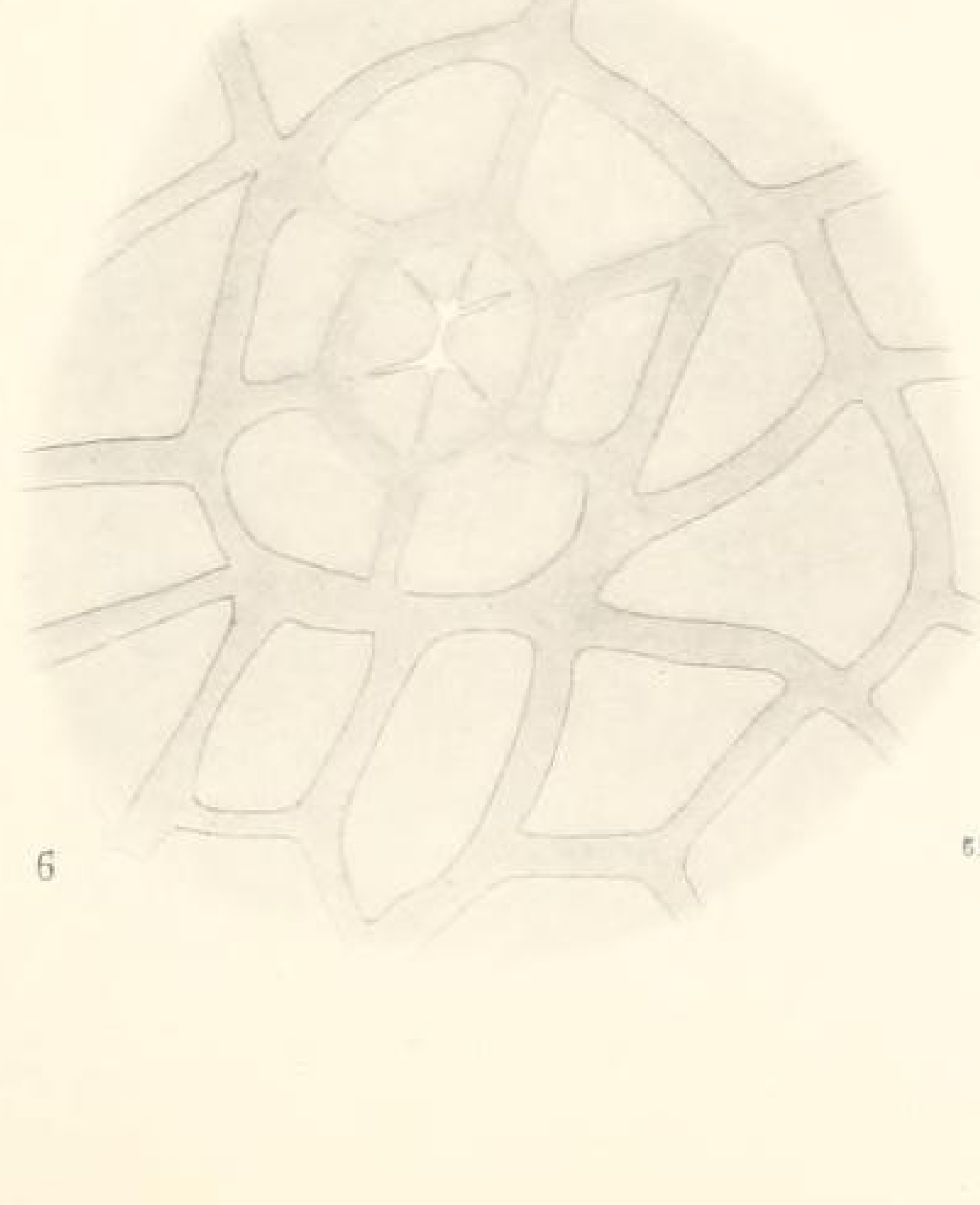
1

4

1,5/1

2

5



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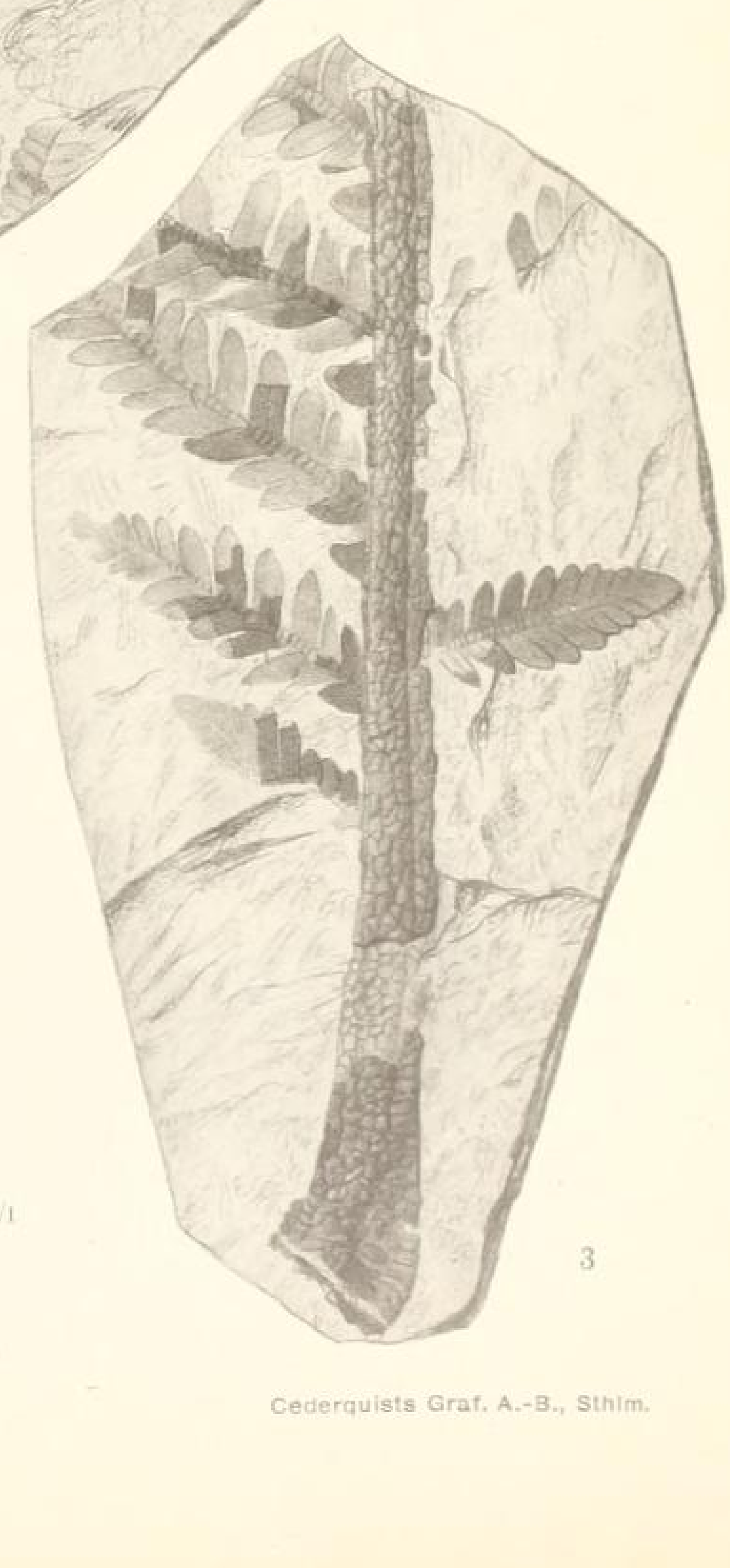
610/1



3

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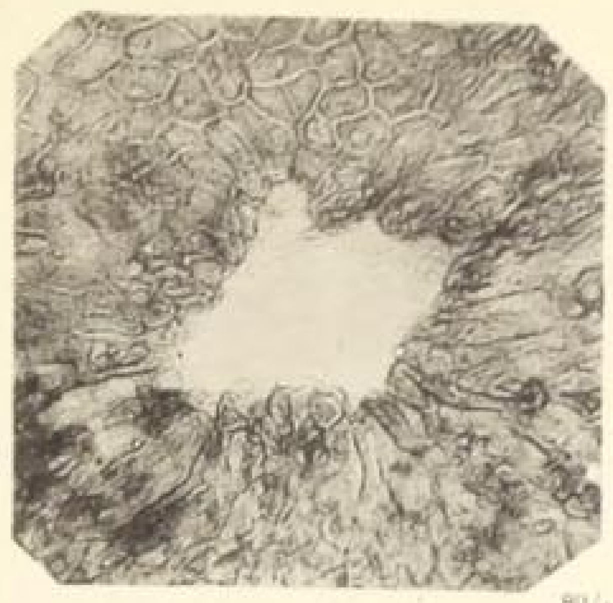
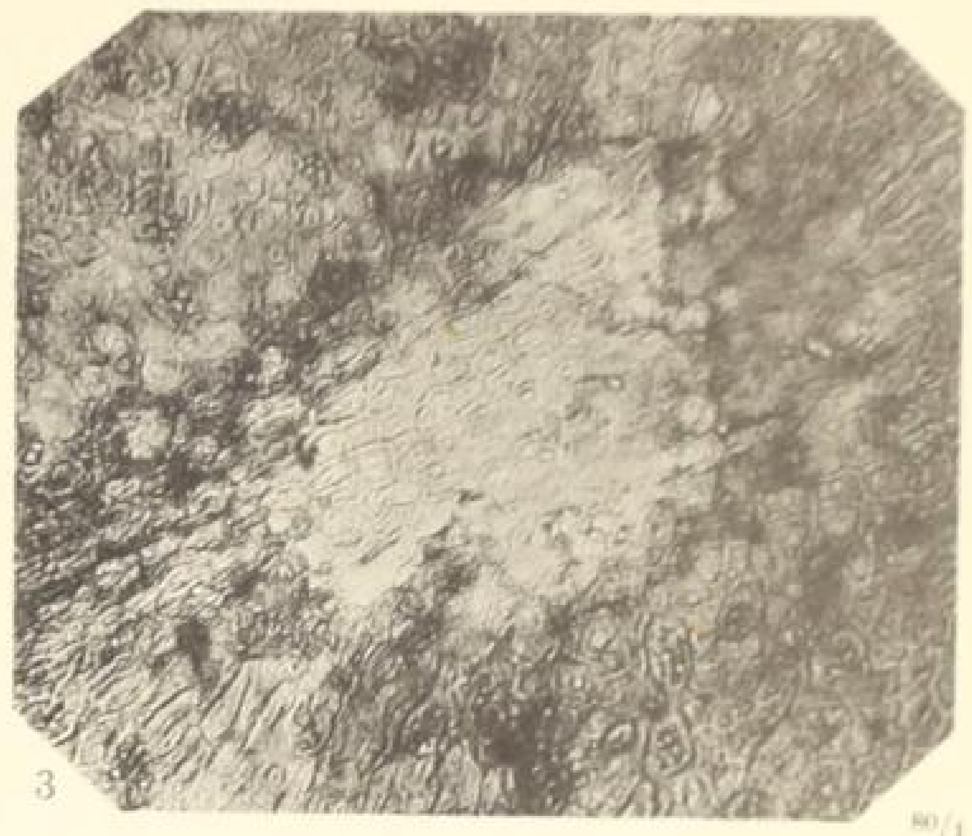
Cederquists Graf. A.-B., Sthlm.

1 $^{22}/_{1}$



2 $^{80}/_{1}$



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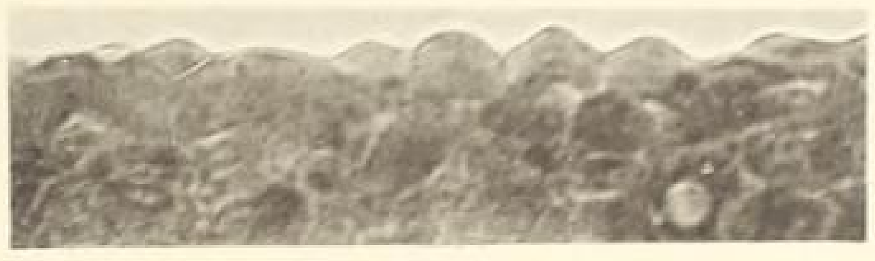
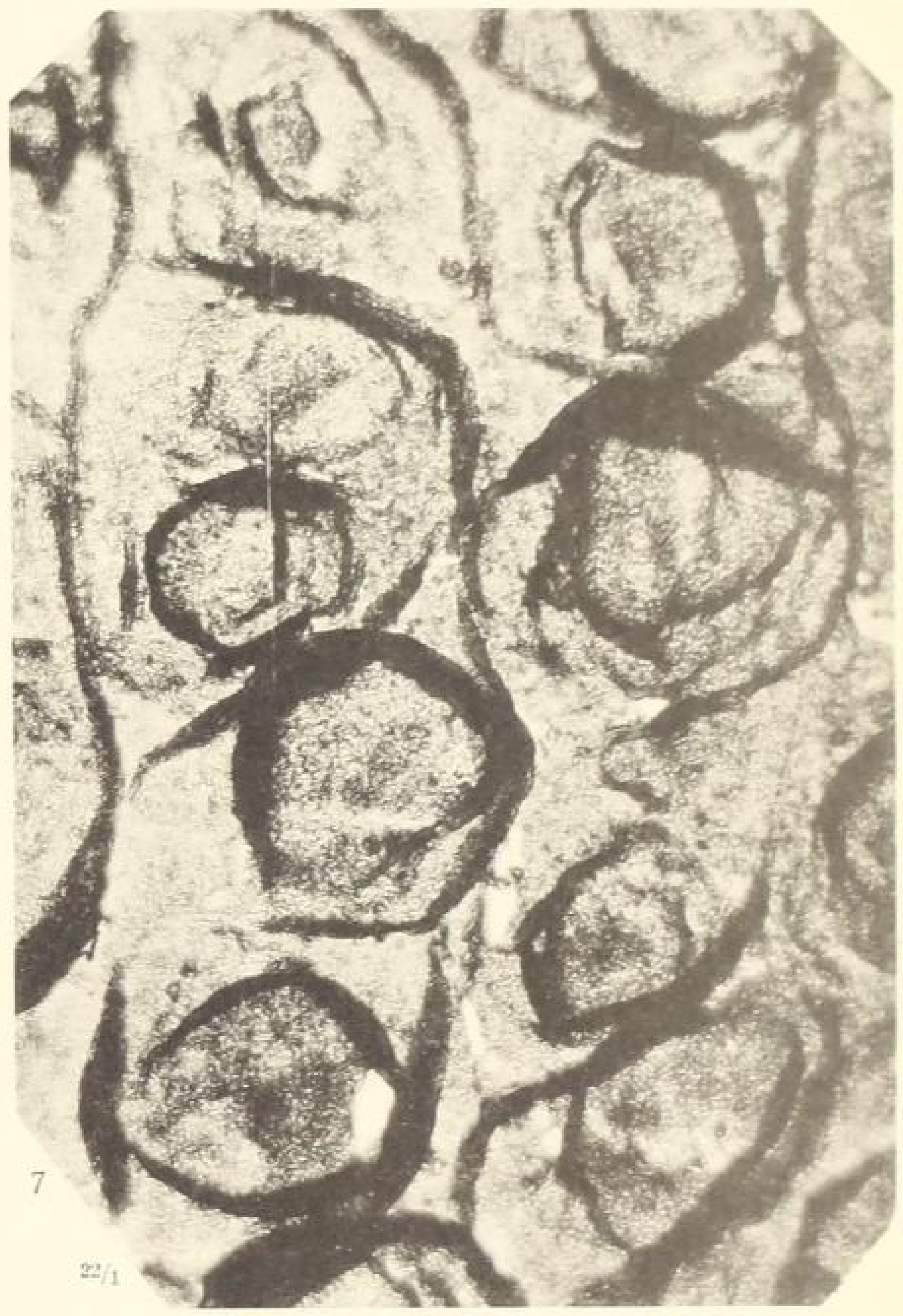


4 $^{300}/_{1}$

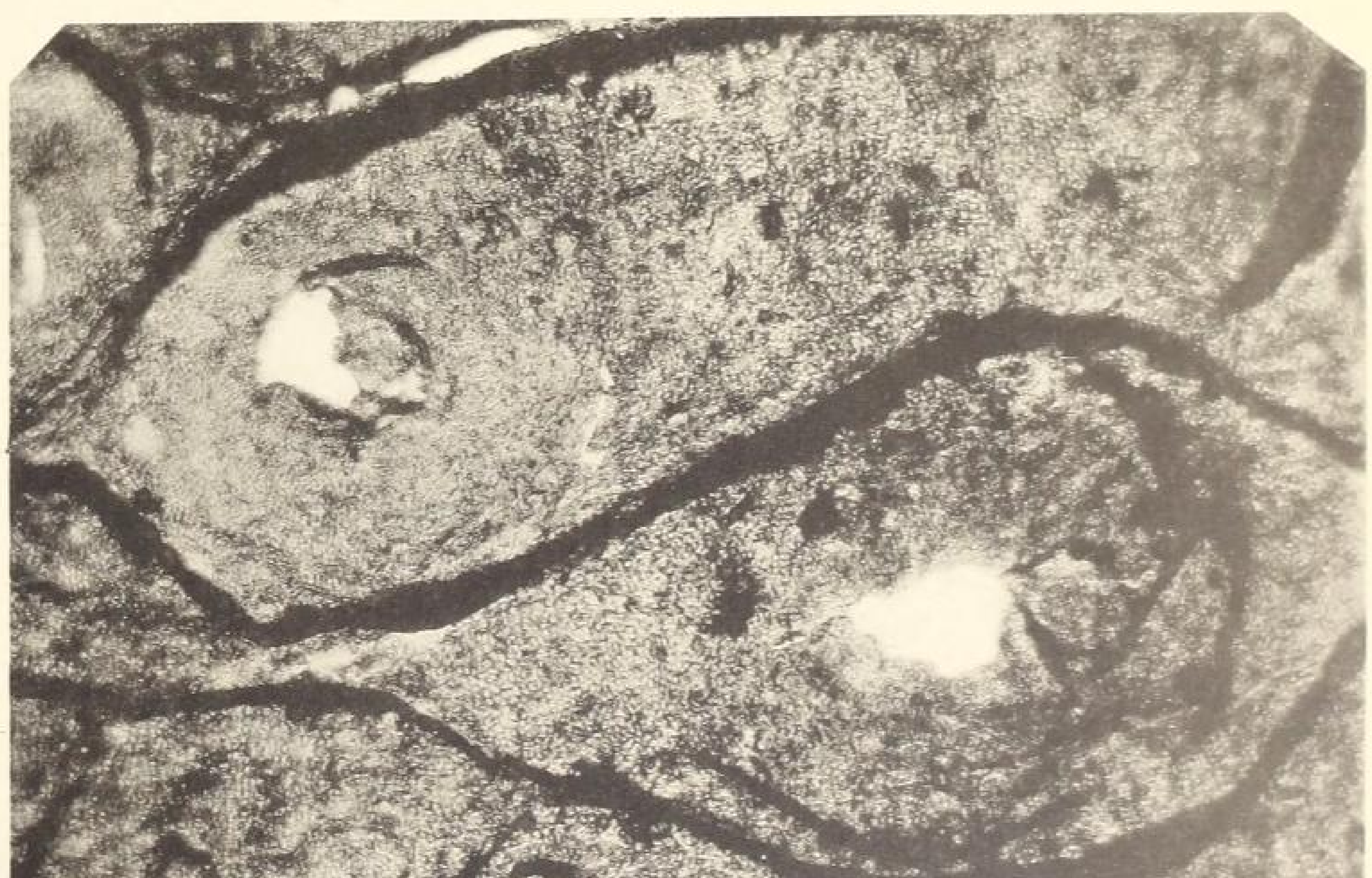
5

6 $^{22}/_{1}$



7 $^{22}/_{1}$

9



8 $^{22}/_{1}$

$^{80}/_{1}$ 10

Th. Ekblom et E. Antevs phot.

Cederquists Graf. A.-B., Sthlm.