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The Juvenile Development of Lichen Thalli from Vegetative Diaspores

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Abstract

Three lichen species were cultivated from soredia to the mature thallus in their natural habitat. The courses of development were similar; however, the individual stages of development showed enough species-specific features to distinguish between the species at any time. The use of this culture method allowed statements to be made about ecological adaptations of the various developmental stages.

Keywords: Lichens, culture method, soredia, ontogeny, ecological adaptations

1. Introduction

Many lichens reproduce primarily by different kinds of vegetative diaspores. The most effective organs of distribution and reproduction appear to be soredia (Jahns, 1984). However, the developmental steps which lead from soredia to the mature thallus are almost completely unknown. These ontogenetic stages are of an utmost significance to the investigations of many problems, such as the colonization of different substrates, the influence of pollution, and the effects of the microclimate (Schuster, 1985). Naturally, the ontogeny can only be useful if the juvenile stages and their development are well known. Therefore, it seems important to determine whether soredia and developmental stages of the thalli of various species differ enough to be recognized in field observations.

In order to answer these questions, I have carried out culture experiments in the natural habitat. Successful investigations of this kind have already taken place in our workgroup (Schuster, 1985; Schuster et al., 1985). In this paper the ontogeny of three soredious lichens will be described. The typical development of soredia to thalli was observed, and the rate of development and its dependance on the respective location were also investigated (Ott, in prep.). The development of a lichen thallus by relichenisation has been described elsewhere (Ott, 1986).

2. Materials and Methods

Lichen thallus development from soredia was examined in cultures in the natural habitat. Thalli of *Hypogymnia physodes*, *Physcia tenella*, and *Parmelia sulcata* were collected close to the sites of the culture experiments. The soredia were brushed off from the soralia with a paint brush onto small pieces of *Sambucus nigra* bark which served as substrate. These pieces were brushed down, but not sterilized, and stuck onto SEM slides. Brushing removed all lichen soredia and most of the thick algal layers present on the bark, while some single algal cells remained and were available for the culture experiments. The slides were screwed onto palettes and exposed on trees in a dune area of the Dutch island of Schiermonnikoog (Ott, 1987). At intervals of several months slides were removed, subsequently dried, and examined with the SEM.

3. Results

Development of Hypogymnia physodes, from the soredium to the clump of tissue

The development of *Hypogymnia physodes* has already been described for a submontane area by Schuster (1985). By comparing his results, my investigations can show whether deviations in the developmental process occur under the influence of an oceanic climate. This will help to differentiate between reactions that are species specific (i.e. genotypic) and others which are influenced by the environment.

The soredia of *H. physodes* have a typical globular form, which is also characteristic for the soredia of most other lichens, and consist of few algae surrounded by hyphae. The surface structure of the soredia is irregular (Fig. 1). Differences exist between the surface structure of *H. physodes* and those of other species.

For colonization, the dispersed soredia prefer small depressions, holes and fissures in the substrate, although soredia could also anchor themselves to the relatively smooth surface of the tree-bark. The soredia attach themselves to the substrate by outgrowing hyphae and the excretion of jelly. During further development, I could not observe any difference between soredia which lay in fissures and those on the surface of the bark. In contrast to this, Schuster (1985) reported clear advantages for lichen primordia which developed in fissures. Thus it would appear that for *H. physodes* the microclimatic advantages of the fissures are only significant under continental climatic conditions, whereas there is sufficient moisture present in the oceanic climate for development on exposed surfaces.

After attachment to the substrate, the number of hyphae growing out from the soredia and the secretion of gelatinous substances increases. The originally spherical soredium becomes more irregularly shaped. This developmental stage is called here the soredia-like primordium (Fig. 2).

The hyphae quickly spread over the substrate and in this way interconnect the distinct soredia-like primordia. At this stage, the development is very rapid (less than one month) and the arachnoidal stage described by Schuster (1985), in which the soredium or the soredia-like primordium are surrounded by a circle of outgrowing hyphae, could scarcely be observed.

The spreading hyphae initiate the formation of a flat basal tissue, into which foreign algae lying on the substrate can also be incorporated (Fig. 3). Not every part of the basal tissue is capable of further development. Usually algae, hyphae and jelly increase in several parts of the basal tissue, until a clump of tissue develops, which represents the next ontogenetic stage. A distinction is possible between clumps of tissue developed from single soredia and others, which originate from parts of the basal tissue.

The differentiation of the thallus

Increased secretion of gelatinous substances at the surface of the clump of tissue gives this stage a flattened shape. The gelatinous layer is evenly distributed over the surface, or has gaps, which expose the underlying network of algae and hyphae (Fig. 4). For the further development of the clumps of tissue it is of no consequence whether it was formed from basal tissue or from single soredia. Phases of intensive growth can be clearly recognized, resulting either in a lateral growth of the clumps of tissue or in the addition of new layers onto its surface (Fig. 5). The hyphae grow out from the surface, form more jelly and incorporate all suitable algae. The clump of tissue gradually becomes club-shaped, and at the same time its surface becomes increasingly smooth. At this point of development external and internal, differentiation sets in and the thallus primordium begins to resemble the future thallus.

In *H. physodes*, the clump of tissue is largely included into the development of the thallus structure (Fig. 6). The club shaped thallus primordium broadens by continued lateral growth. During this phase, a surface structure of gelatinous scales, between which there are still gaps and fissures, is formed (Fig. 6). This structure is also typical of the mature lobes of *H. physodes.* After reaching a certain size ($\sim 750\mu$) and degree of of differentiation, the primordium begins to develop lateral branches by intensified growth of any given part at its margin.

Young thallus lobes which have grown at a shallow angle form a clump of tissue can soon bridge over gaps in the substrate. In some cases they are then attached by gelatinous outgrowths (Fig. 7) which do not fit the typical picture of rhizines. Rhizines do not occur in *H. physodes.*

Several thallus primordia usually emerge from a single clump of tissue, develop into branched lobes, and very rapidly show the typical rosette-shaped habit of the small, young thalli of *H. physodes* (Fig. 8). The figure also shows that several neighbouring thallus primordia may overlap like tiles of a roof. This arrangement is not only characteristic for *Hypogymnia physodes*, but, also occurs in *Physcia tenella* and *Parmelia sulcata* at the same stage of development.

Development of Physcia tenella, from the soredium to the clump of tissue

The soredia of *Physcia tenella* are small spherical structures, consisting of a loose tangle of algae and hyphae, and relatively little surrounding jelly. When the soredia are scattered over the bark, single hyphae very quickly grow out and anchor it to the substrate. This process takes between a few days and four weeks. The few germinating hyphae separate and spread either in different directions (Fig. 9) or grow close together in only one direction. These hyphae may be very short and attach the soredium to the substrate at many points. Often, the soredium is additionally attached by gelatinous substances and can be raised by a gelatinous base (Fig. 10).

It is common for the development to proceed not from one single soredium, but from a group of about 4–6 soredia, which amalgamate during further development (Fig. 10). The soredia probably already stick to one another in the soralia and are distributed together.

After the attachment of the soredium to the substrate, increased secretion of jelly on the underside of the soredium leads to further adhesion to the substrate. Once the soredium is finally attached to the substrate, the soredium develops by several intermediate stages into the clump of tissue. The soredium loses its spherical shape, but the general habit of a soredium still persists. This stage is called here a soredia-like primordium.

This step of development usually exists for only a short time and then progresses to the stage of the basal tissue. In this phase, an undifferentiated clump of tissue of variable shape is formed. Obviously, its appearance depends on the original type of attachment of the soredium to the substrate. For example, a clump of tissue can spread horizontally (Fig. 11) or assume a more lumpy habit. The clumps of tissue consist of an undifferentiated tangle of algae, hyphae and jelly. Increased secretion of jelly at one side of the clump is common (Fig. 12). Large areas of the undifferentiated tissue can be covered by the jelly, which is unique to the development of *Physcia tenella.*

Differentiation of the rhizines

The first step in differentiation of organs or tissues appears in the next stage of development in which the lumpy tissue has changed into an oval structure. From these oval stages, still internally undifferentiated, rhizines often grow outward (Fig. 13). The first developmental stage of a rhizine is a sharply pointed bundle of a few parallel-aligned hyphae, bound together by jelly (Fig. 14). Even at this juvenile stage the rhizine is already attached to the substrate by a small gelatinous base. The actual differentiation of the rhizine follows attachment. Whether the contact with the substrate has a stimulating effect on further development of the rhizine is not known.

The rhizine thickens by the external addition of hyphae, which grow from the undifferentiated clump of tissue. Figure 15 clearly shows that the added hyphae are shorter than the old hyphae of the rhizine. Simultaneously the rhizine becomes longer. Since the distance between the base of the rhizine and the substrate remains the same, the lengthening rhizine becomes bent. By this growth process, tension gradually build up in the rhizines, and eventually the clump of tissue is detached from the substrate and raised upwards. In the course of lifting the primordia, old rhizines become straightened out. Normally two or three rhizines grow out to form a small, flat gelatinous base and an adhesive holdfast of outgrowing hyphae on the substrate (Fig. 16). During further growth the rhizines lengthen and bend (Fig. 17), lifting up the still undifferentiated clumps of tissue, so that a hollow space is created between the substrate and the underside of the clump. This space between primordium and substrate remains in mature thalli of *P. tenella*, since differentiated thalli are only attached to the substrate by rhizines and in general show no contact between the underside and the substrate. The interstices between the thallus and the substrate are probably of great significance to the water economy of the lichen.

Differentiation of the thallus

Differentiation of a true thallus primordium (Fig. 13) begins with the appearance of the first rhizines. In general, the oval structure, shown very clearly in Fig. 13, is retained during further development, until the first signs of lateral branching are observed. In rare instances branching begins even before the surface of the young thallus structure is closed by jelly secretion.

Differentiation continues in parallel with the degree of the jelly deposition on the surface of the thallus. The more the surface becomes covered, the more commonly branching in several directions may be observed, as it is typical for mature lobes of *P. tenella*.

The surface structure of this stage, which is easily recognized by its rhizines (Fig. 18), is characteristic of *P. tenella*. It consists of small gelatinous scales, a form which does not occur in the other investigated species.

Figure 19 shows how vigorous growth is at this developmental phase. New jelly can apparently not be produced quickly enough during the branching process and the hyphae become stretched to parallel cords.

Parallel to the formation of a closed surface, more rhizines appear. At this stage, the thallus primordium is also internally differentiated into cortex, algal layer and medulla. If several thallus primordia lie close to one another, this developmental step results in a tile-like growth of young thalli as typical for adult specimens of *P. tenella* (Fig. 20). The rhizines, already present in abundance, grow into the surfaces of underlying thallus primordia, a process also common in the mature lobes (Fig. 21). At this point, the development of the upper cortex is complete and one can now refer to it as a normally developed thallus lobe of *P. tenella*.

Development of Parmelia sulcata, from the soredium to the clump of tissue

Development begins with the dispersed soredium, which usually shows a spherical form and consists of a small loose bundle of algae and hyphae. The algae and hyphae are surrounded by a relatively large quantity of jelly, which is an important distinguishing feature from the soredia of the other lichen species described here.

As in *H. physodes*, the soredia of *Parmelia sulcata* settle in depressions, holes and fissures of the tree bark. This appears to be characteristic to both species. The soredia develop single as well as in groups usually consisting of 3 to 6 soredia.

The development starts with an abundant secretion of jelly at the edge of the soredia, by which they are attached to the substrate. Subsequently, single hyphae grow out in various directions and secrete a relatively large volume of jelly, in order to further anchor the soredium to the substrate (Fig. 22). Once the soredium is firmly anchored, it develops a more oval shape, but retains a soredium-like primordial appearance.

In the course of further development, the structure enlarges and covers the substrate with an undifferentiated layer of hyphae and algae, among which foreign algae can also be found. The entire basal tissue (Fig. 23), is held together by the secretion of gelatinous substances from its surfaces. As can be clearly seen in Fig. 23, the points of further differentiation of the basal tissue are distinguished from the surrounding undifferentiated and loose tangle of hyphae by increased jelly secretion. From the more gelatinous areas, the following stage, known as the clump of tissue, is formed.

A clump of tissue can form from a horizontal basal tissue, from one single soredium, or from a group of soredia lying close to one another. In the earliest stages the clump of tissue is shapeless and distinctly larger than a soredium. Its jelly forms quite a thick layer in some parts (Fig. 24). In the process of further development, the clumps of tissue continue to grow in all directions, although horizontal growth is more common. During this growth phase a great amount of jelly is produced, which already has a smooth surface in certain areas (Fig. 25). From the margin of relatively large clumps hyphae often grow at an angle towards the substrate and give the clumps of tissue the appearance of standing on stilts (Fig. 26). Although this picture is typical for *P. sulcata* it is not so readily distinguished in all observed clumps of tissue. During continued growth, the clumps expand to relatively wide and large tissues; smaller clumps are seldom seen. Figure 27 clearly shows an advanced stage of a clump of tissue. This clump obviously arose from a group of soredia, which initially developed separately and then amalgamated.

Differentiation of the thallus

The clump of tissue represents the last stage of development still consisting of an undifferentiated tangle of hyphae and algae. Even at this early stage, thallus primordia show the typical form of *P. sulcata* (Fig. 28). One can clearly see that the clump of tissue is anchored in a depression of the tree bark and that a young thallus primordium emerges from the edge of the undifferentiated clump.

The thallus primordium is half-moon shaped and covered with fairly smooth jelly along the edge. Sporadically, small holes are visible in the gelatinous surface, which are much more common in the older thalli. These holes at the thallus edge are an important distinguishing feature from the other lichen species investigated. At similar developmental stages of *P. tenella*, proper rhizines are already produced, while *P. sulcata* is still only anchored by hyphae.

With the differentiation of the first thallus primordia the clumps of tissue cease growth. Young thallus primordia commonly grow in groups next to one another at the edge of a flat clump of tissue (Fig. 29). They have the typical half-moon shaped habit mentioned above (Fig. 28) and become increasingly flattened during continuing growth.

In the course of further development the thallus primordia form a thicker and more closed gelatinous layer over their entire surface and assume a flat shape. The pores in the gelatinous layer, which were present in the earliest stage of the primordia, remain clearly recognizable. They will not disappear until the thallus lobe is mature and no longer growing. Figure 30 shows such a flat, perforated thallus primordium.

Formation of adhesive organs and lateral branches

The lobe-shaped primordia continue to make contact with the substrate. Figure 31 shows part of a primordium which has produced hyphae at certain intervals along the edge, which with the aid of abundant jelly have anchored themselves to the surface of another thallus primordium. Such pictures are characteristic of this stage of development. At the corresponding stages of development in *P. tenella* rhizines are differentiated; in *P. sulcata* attachment has occurred only by hyphae. In *P. sulcata*, rhizines, which represent a further step in differentiation, are first formed at the margin of mature lobes. This does not mean that the differentiation of medulla, algal layer and cortex also begins this late. While in *P. tenella* the rhizines are formed before the thallus layers, in *P. sulcata*, the succession of these steps in differentiation is reversed.

Rhizines appear at the edge of the lobes, which show a typical surface structure (Fig. 32). The young rhizine consists of a bundle of parallel aligned hyphae without an outer covering sheath. Since a space exists between the rhizines and the substrate, their development cannot be initiated by contact with the substrate (Hannemann, 1973). It is only later that the mature rhizine develops the smooth surface characteristic of appendages of *Parmelia*. With formation of the rhizines, the differentiation of the thallus lobes is essentially complete. Fig. 33 shows mature thallus lobes with several rhizines and the beginning of branching. The surface of the lobes is mostly closed with jelly and shows the characteristic pores towards the edge (Fig. 34). The rhizines differ from those of *Physcia tenella* in their growth form. In *P. tenella*, they are usually curved whereas in *P. sulcata* they grow directly down to the substrate and attach there by a broad gelatinous holdfast (Fig. 34). At the basal part of the thallus lobe (Fig. 33) one can often observe a plentiful secretion of jelly, which connects the lobe to the undifferentiated tissue primordium.

As mentioned above, the juvenile stages of *P. sulcata* usually grow in depressions or fissures of the substrate. However, young lobes grow up to the open surface. Figure 35 shows an example of a thallus lobe which has grown out from a fissure. The lobe is relatively young, as still no rhizines are to be seen.

The branching of a lobe represents a further degree of differentiation. If several thallus lobes develop close to one another, they soon begin to grow in a tile-like arrangement (Fig. 36). One of the thallus lobes shown in this figure has clearly reached an advanced stage of development. Lateral branches are formed and the rosette-shaped habit of the mature thallus lobe can be seen. At this stage, the development is complete. The thallus lobe continues to increase in size, forms more rhizines on the lower surface, and completes the life cycle typical of *P. sulcata*.

4. Discussion

Culture experiments have shown that the growth of lichens in their natural location can be successfully observed by the methods employed. All the specimens developed normal adult thalli during the period of observation. Cultivation in the field therefore represents a good supplement to laboratory cultures, as they have been developed by Ahmadjian and his coworkers (Ahmadjian, 1973; Ahmadjian and Jacobs, 1982; Ahmadjian et al. 1980).

The rate of development in the different species and at several sites varies. The problem is very complex and shall therefore be discussed in a separate paper (Ott, in prep.). Thallus development at the oceanic sites was faster than at the submontane location examined by Schuster (1985). The better water supply in the oceanic climate is probably responsible for this difference and also for the fact that soredial development was less limited to fissures in the substrate than was the case in Schuster's observations (1985). However, the varying rate of development does not alter the stages of development and their morphology.

Similarities in the development of the different species

If one looks at the entire course of development from the soredium to the young thallus lobe the ontogeny is basically the same in all species examined. The three species begin their development by anchoring the soredium to the substrate by means of a number of hyphae. The soredia change and become a soredia-shaped primordium, in which copious quantities of jelly are secreted for attachment. These soredium-shaped primordia enlarge and develop into a clump of tissue. The differentiation of a thallus primordium follows, which will then change into a thallus lobe by several steps of differentiation. All three lichens also have in common that branching already begins at the stage of thallus primordia, which results in a rosette-shaped arrangement of the thallus lobes. Furthermore, in all three species the differentiated thallus lobes grew over one another and overlapped like the tiles of a roof. All lichens finally develop rosette-like thalli. Varying numbers of clumps of tissue can take part as starting points in the process. For *P. sulcata*, it is typical for several thallus primordia to grow simultaneously in various directions. It should be emphasized that jelly is of greatest importance for juvenile development in all three species. It is necessary at the beginning for attachment to the substrate and later serves in the differentiation of the surface, uniting hyphae in a compact layer. The gelatinous sheath may also be a protection against evaporation and therefore could be important for the water relations of young developmental states.

A few features appear common between only two of the species. The soredia of *H. physodes* and *P. sulcata* develop preferingly in depressions, holes and fissures of the substrate; this was seldom observed in *P. tenella*. In *P. sulcata* and *P. tenella* the clump of tissue is not included into the development of the thallus primordium which emerges from the edge of the clump. In contrast to *H. physodes*, both species form rhizines in the course of juvenile development.

Differences in the development of the three species

The basic similarities in the courses of development should not obscure the fact that there are small differences between the species. Even the shape of the soredia is species-specific. The morphology of the clumps of tissue also differs. The clumps of tissue in *H. physodes* have a flattened upper surface. In *P. sulcata*, they grow in a relatively flat and thin layer on the substrate and their surface is usually very smooth due to copious jelly production. The clumps of tissue in *P. tenella* can be flat or misshaped. However, even in the case of the flat clumps of tissue they differ from the flat primordia of *P. sulcata*, due to the very different surface structures.

The next important difference appears during differentiation into a thallus primordium. In *H. physodes* the clump of tissue is included into the differentiation, and the entire clump transforms itself into the thallus primordium. In *P. sulcata* and *P. tenella*, the thallus primordium grows from a distinct part of the clump of tissue, which simultaneously ceases its own growth.

In contrast to *H. physodes*, *P. sulcata* and *P. tenella* possess rhizines on their underside, which are formed in the course of juvenile development. The differentiation of the rhizines starts during different developmental stages in the two species. In *P. tenella* rhizines are already growing out from the margin and the lower surface of the clump of tissue and the thallus primordium, and attaching themselves to the substrate with a broad gelatinous base. The rhizines are responsible for the formation of a space between primordium and substrate, which obviously has an important function in the water supply. Only afterwards the primordium differentiates into a mature thallus lobe. By contrast, the rhizines in *P. sulcata* only develop after the thallus lobes are already differentiated, i.e. the differentiation of the thallus lobes is finally completed with the formation of the rhizines. The rhizines of *P. sulcata*, unlike those of *P. tenella*, do not lift the lobes upward from the substrate. The thallus primordia of all three lichens show distinct differences in their surface structure. While the differences between *H. physodes* and *P. tenella* are small, *P. sulcata*, even in the initial stage, forms pores of various sizes around the edge of the primordium which may still be observed in the mature thallus lobe. The three lichens discussed here have the same reproductive strategy, and their vegetative diaspores belong to the same soredia type. The similarity in the course of development is therefore not surprising.

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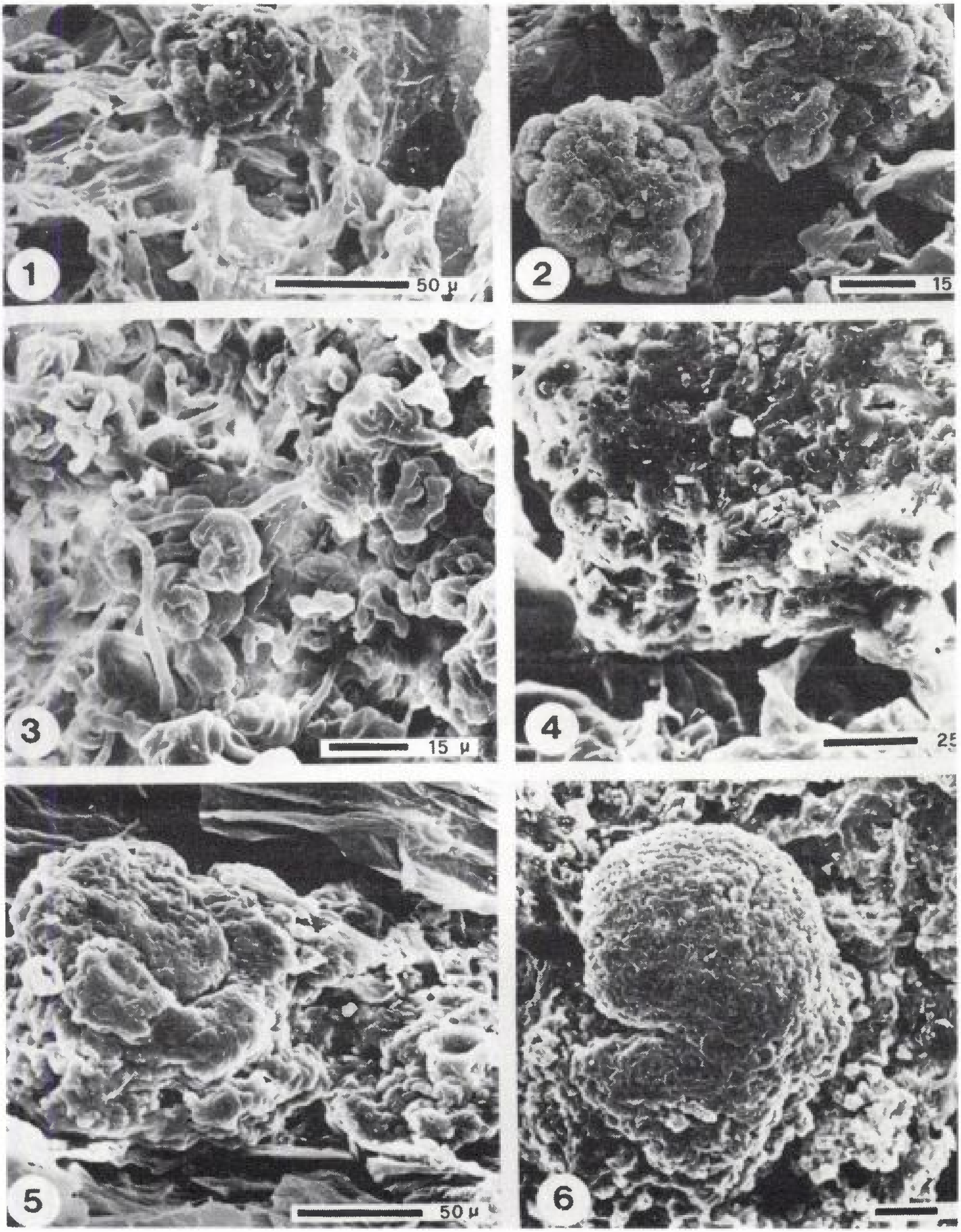

Figure 1–6. 1) An unaltered soredium of *Hypogymnia physodes* on the tree-bark. 2) A soredium-like primordium, typical for *H. physodes.* 3) *H. physodes*, the hyphae grow out and incorporate foreign algae. 4) *H. physodes*, a clump of tissue with jelly and the characteristic structure of the surface. 5) *H. physodes*, a more developed clump of tissue than in Fig. 4, with a thicker gelatinous layer on the surface. 6) *H. physodes*, a club-shaped primordium with a typical surface structure of gelatinous scales.

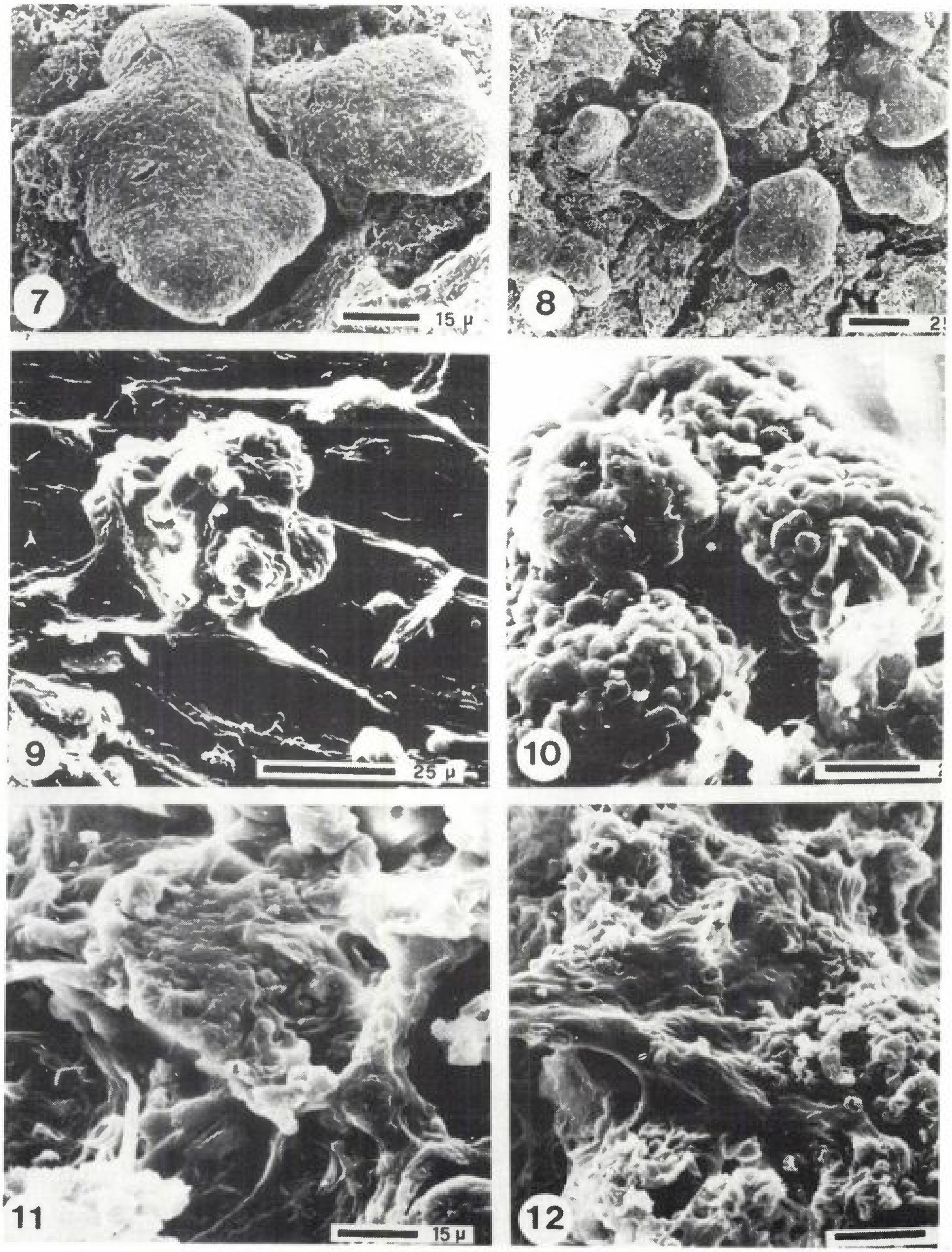

Figure 7–12. 7) Young thallus lobes of *H. physodes*. 8) A group of young thalli with the typical rosette-shaped habit of *H. physodes*. 9) A soredium of *Physcia tenella* with few germinating hyphae. 10) Soredia of *P. tenella* attached by gelatinous substances. 11) *P. tenella*, a clump of tissue spreading horizontally over the substrate. 12) *P. tenella*, typical secretion of jelly on the clump of tissue.

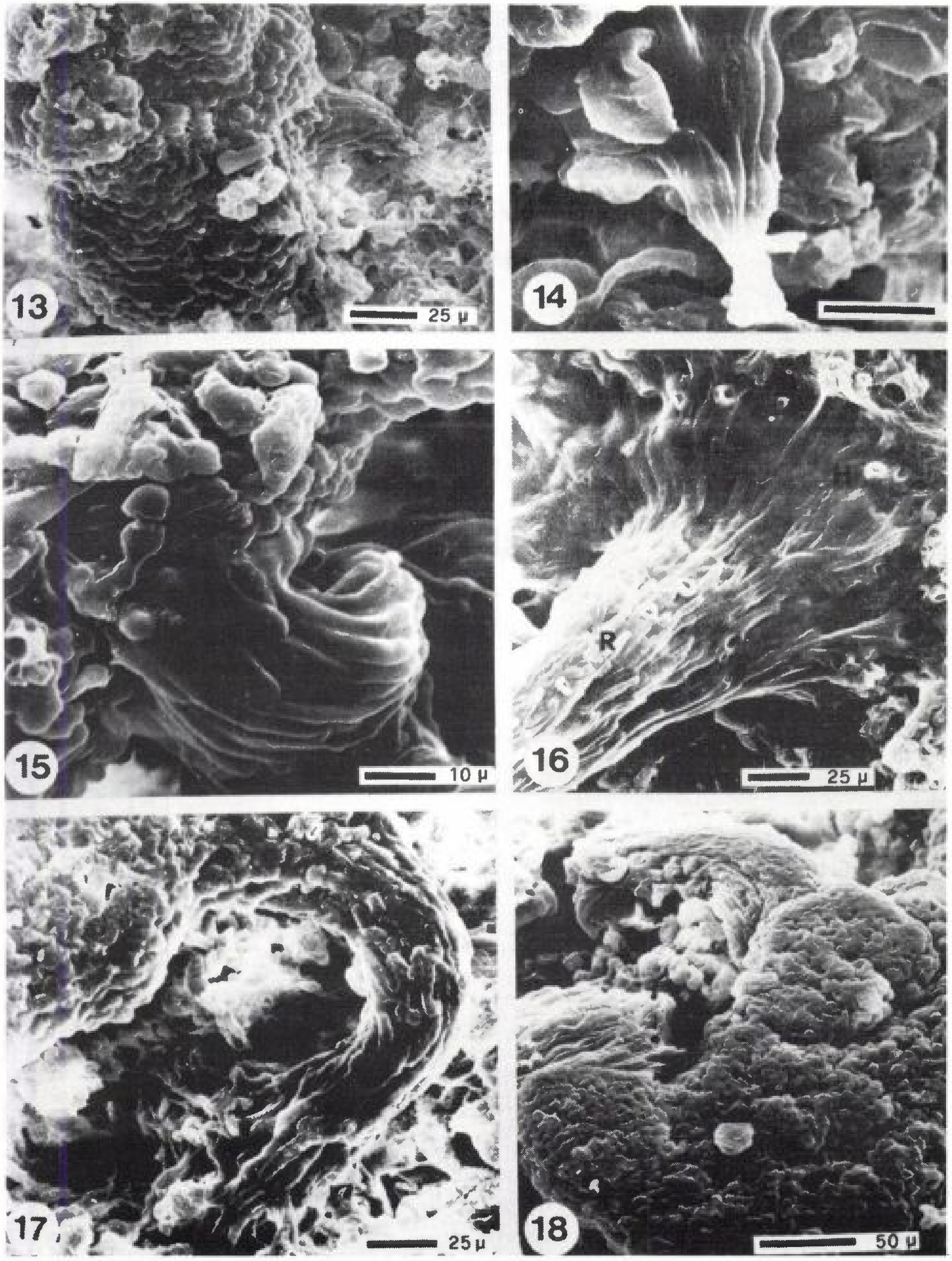

Figure 13–18. 13) *P. tenella*, a clump of tissue with an emerging rhizine. 14) *P. tenella*, the first developmental stage of a rhizine. 15) *P. tenella*, a part of an older rhizine with short newly added hyphae. 16) *P. tenella*, an adhesive holdfast (H) of a rhizine (R) on the substrate. 17) *P. tenella*, a well-developed rhizine. 18) The characteristic surface structure of a primordium of *P. tenella*.

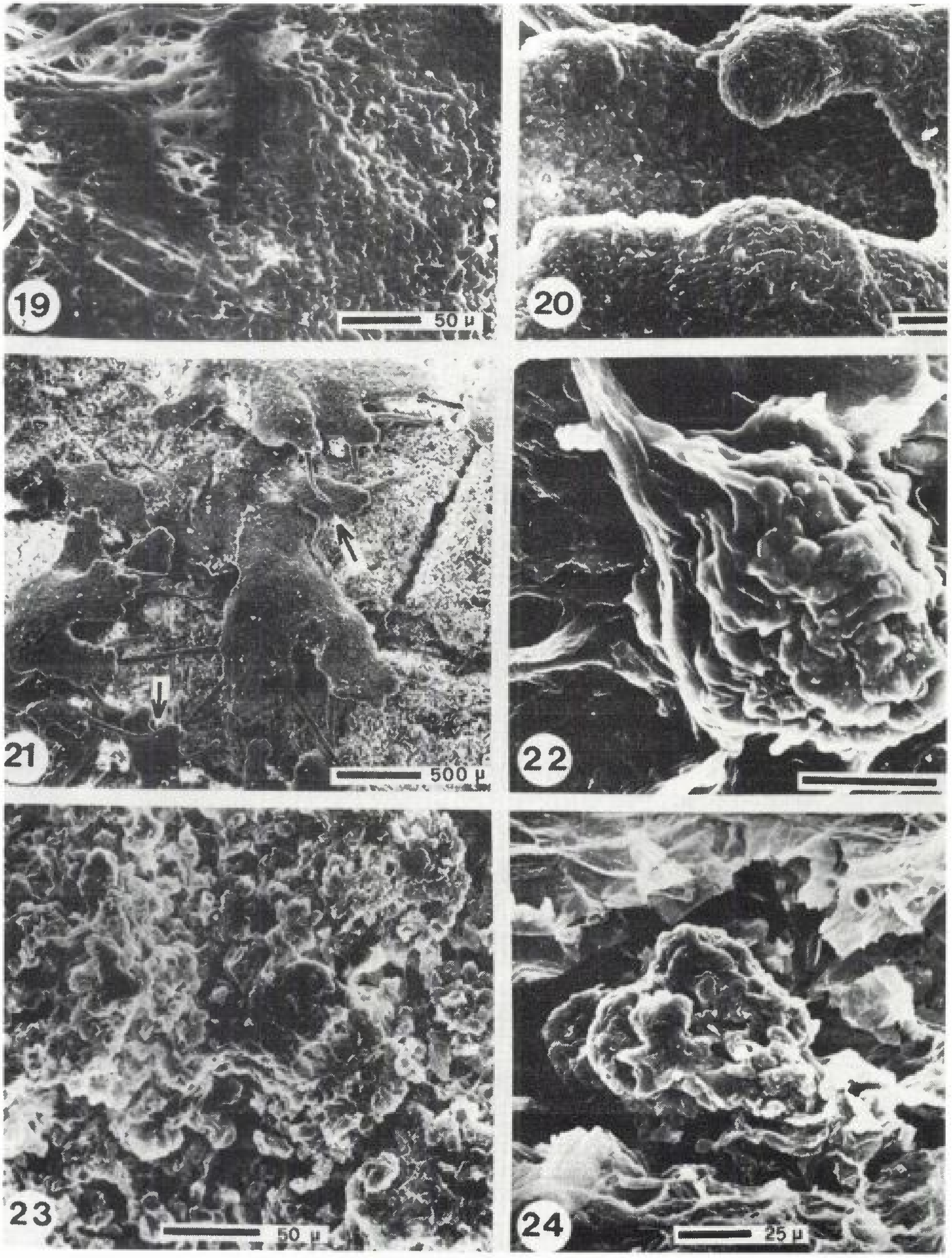

Figure 19–24. 19) *P. tenella*, rapid growth leads to gaps in the gelatination of the tissue. 20) The tile-like growth of young thalli of *P. tenella*. 21) *P. tenella*, rhizines growing into the surface of underlying thalli (arrow). 22) A typical soredium of *Parmelia sulcata*. 23) *P. sulcata*, the basal tissue with secretion of jelly. 24) A small clump of tissue of *P. sulcata* lying in a depression of the substrate.

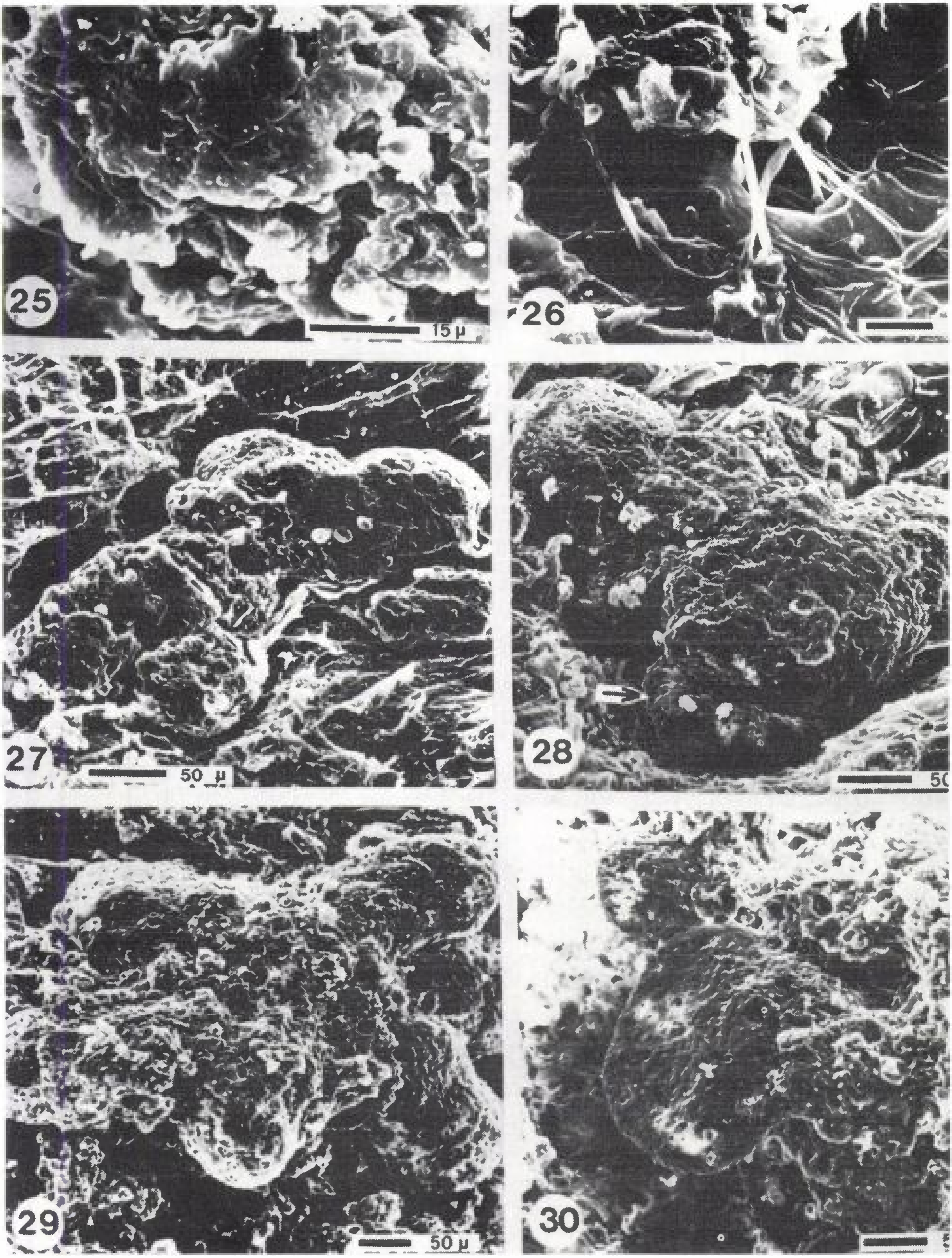

Figure 25–30. 25) *P. sulcata*, abundant jelly production. 26) *P. sulcata*, hyphae growing out of a clump of tissue. 27) Fairly wide and large clumps of tissue, typical for *P. sulcata*. 28) *P. sulcata*, a further developed clump of tissue with an emerging young thallus primordium (arrow). 29) *P. sulcata*, numerous thallus primordia growing from a single clump of tissue. 30) The flat perforated thallus primordium of *P. sulcata*.

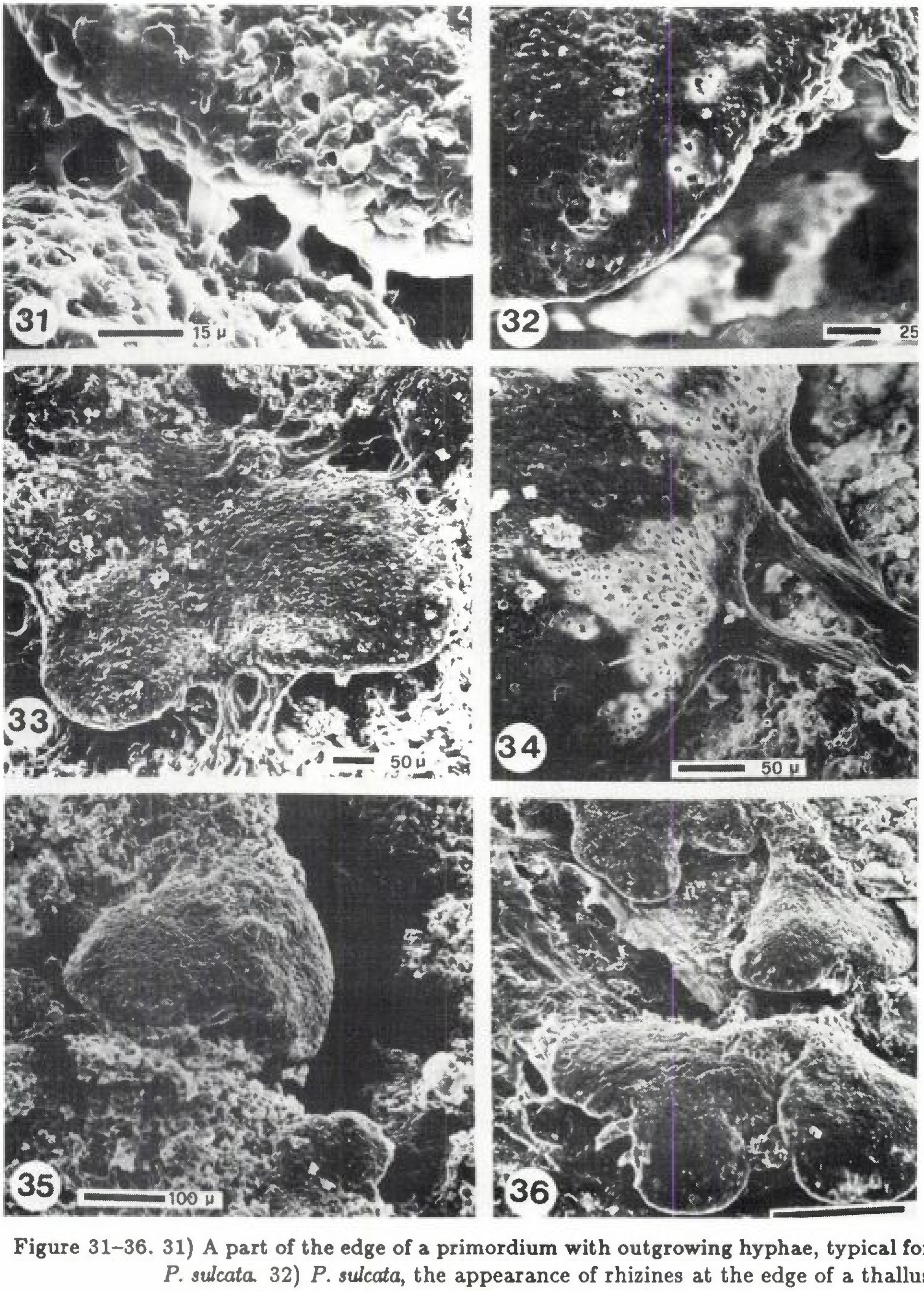

Figure 31–36. 31) A part of the edge of a primordium with outgrowing hyphae, typical for *P. sulcata*. 32) *P. sulcata*, the appearance of rhizines at the edge of a thallus lobe. 33) *P. sulcata*, mature thallus lobes with several rhizines and the beginning of branching. 34) The characteristic pores of lobes of *P. sulcata*. 35) *P. sulcata*, a thallus lobe, growing out from a fissure. 36) The typical tile-like arrangement of young thallus lobes of *P. sulcata*.