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Objekttyp: **Article**

Zeitschrift: **Botanica Helvetica**

Band (Jahr): **97 (1987)**

Heft 1

PDF erstellt am: **26.09.2024**

Persistenter Link: https://doi.org/10.5169/seals-67861

Botanica Helvetica, vol. 97, 1 (1987)

0253-1453/87/010147-06 $ 1.50+0.20/0

Isidium formation and the development of juvenile thalli in *Parmelia pastillifera* (Lecanorales, lichenized Ascomycetes)*

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Manuscript accepted April 1, 1987

Abstract

Honegger, R. 1987. Isidium formation and the development of juvenile thalli in *Parmelia pastillifera* (Lecanorales, lichenized ascomycetes). Bot. Helv. 97: 147–152.

Isidium formation in *Parmelia pastillifera* was investigated using light microscopy of semithin methacrylate sections and scanning electron microscopy. Of all isidia-bearing taxa so far investigated the idisia of *P. pastillifera* are the only ones which reach a high degree of external and internal differentiation on the mother thallus in an inversed position. Mature isidia represent dorsiventrally organized, juvenile thalli which adhere to the substrate with their morphological upper side after detachment from the mother thallus.

Introduction

About 25–30% of foliose and fruticose lichen species form isidia (Hale 1983). These corticate protuberances of the upper thallus surface contain mycobiont and photobiont cells. Isidia may be globose, cylindrical, claviform or coralloid (du Rietz 1924). Very peculiar scutelliform isidia occur in some taxa of tropical foliicolous lichens (Santesson 1952, Vezda 1975). Both shape and size of isidia are species-specific and genetically fixed. In contrast to the dorsiventrally organized, internally stratified blastidia and phyllidia, two other types of corticate, photobiont cells containing protuberances formed by some groups of lichen-forming fungi, isida are, with few exceptions, internally not stratified or otherwise differentiated (Rosendahl 1907, du Rietz 1924, Hale 1983, Hawksworth & Hill, 1984). As most types of isidia are basally constricted and break off quite easily they serve as vegetative propagules of the symbiotic state of both mycobiont and photobiont.

A very peculiar type of isidia is formed in *Parmelia pastillifera* (Harm.) R. Schubert & Klem. The central, subsenescent part of this greyish, foliose species is covered by relatively large, brown to black, button-shaped protuberances with flat or even slightly concave, warty upper surface. These isidia break off very easily, leaving a crater-shaped

* This study is dedicated to Prof. Dr. Hans Wanner on the occasion of his 70th birthday

depression in the surface of the mother thallus. By its relatively large isidia *P. pastillifera* can be distinguished macroscopically from the closely related and morphologically very similar *P. tiliacea* (Hoffm.) Ach., another greyish, foliose species which bears much smaller, globose to cylindrical, black isidia on the central, older parts of the thallus.

The present study aims to investigate the formation of the button-shaped isidia of *P. pastillifera* and the development of juvenile thalli after detachment of the isidia from the mother thallus.

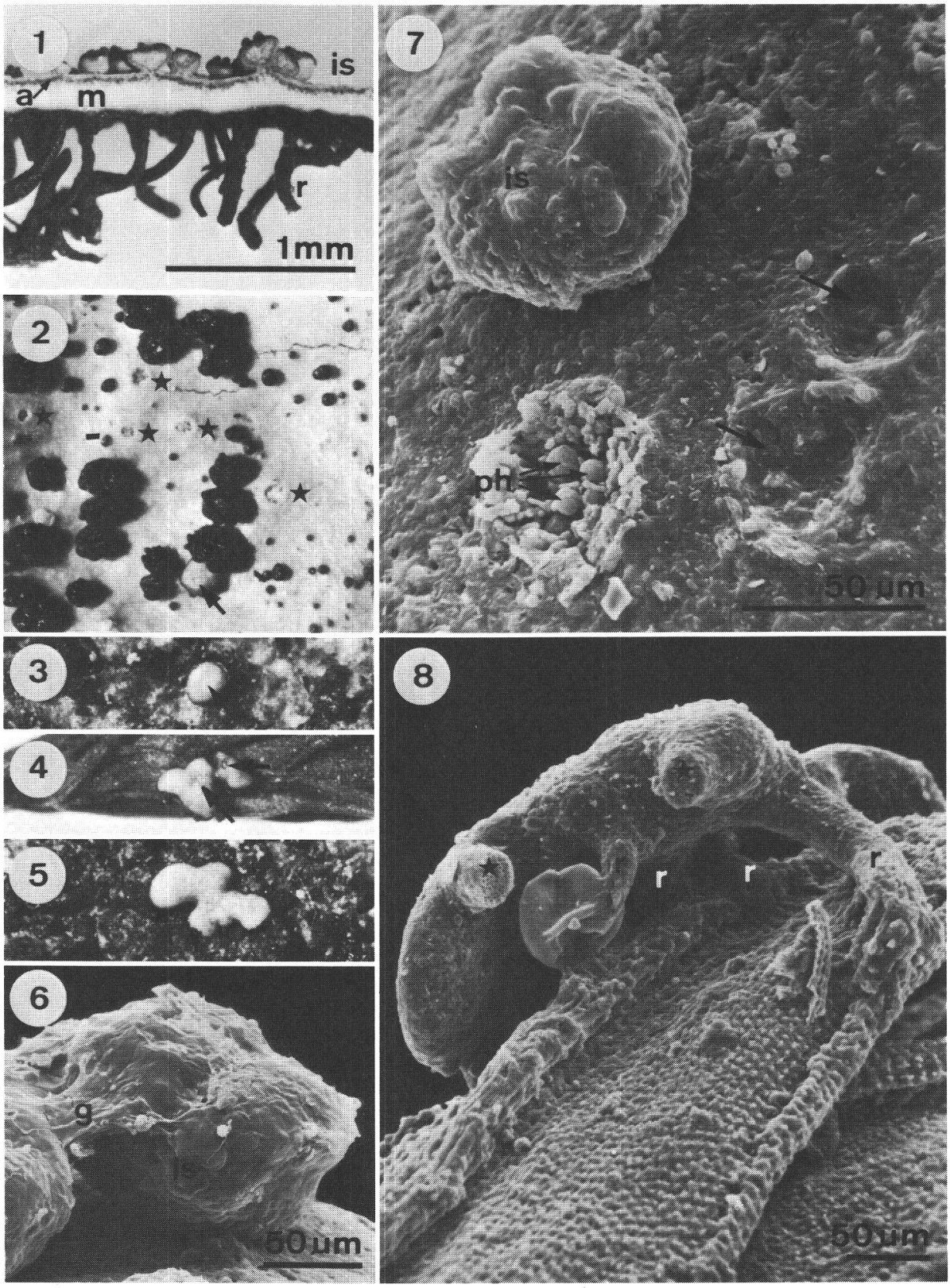
Materials and methods

Fresh thalli of *P. pastillifera* and *P. tiliacea* were collected on *Acer pseudoplatanus* at the border of the Klöntalersee GL, 850 m altitude, October 1986.

Light microscopy. The external morphology of the thalli was investigated and photographed with a Zeiss Tessovar. Semithin sectioning. About 0.5–1 µm thick sections of the isidia-bearing central parts of the thalli were fixed with a mixture of 1.5% acrolein and 1.25% glutaraldehyde in phosphate buffer, pH 7.1, for 2 h at room temperature. The thallus fragments were evacuated in the fixing solution with a water aspirator until they sank. After dehydration in a graded series of ethanol the material was infiltrated with a 1 : 1 mixture of ethanol and Historesin (without accelerator), a methacrylate manufactured by LKB, Bromma. After infiltration with pure Historesin for 4 h and short evacuation the material was embedded in pure methacrylate (accelerator added) using the small plastic covercles of tablet glasses as molds and an insect needle for the precise orientation of the specimens. Polymerized blocks were mounted on beam capsules with Technovit. Serial 1–2 µm thick sections were cut with a dry glass knife on a Reichert OM U3 ultramicrotome. The sections were picked up with a pair of tweezers and transferred to water drops on a clean microscope slide where they floated for 5 min. The slides were then dried on a hotplate at 70 °C for 10 min. Staining of the sections was performed with Lee's methylene blue – basic fuchsin stain containing 12 ml of 0.13% aqueous methylene blue, 12 ml of 0.13% basic fuchsin, 21 ml of 0.2 M phosphate buffer at pH 7.5, and 15 ml of absolute ethanol. Dried slides were mounted with either Entellan (preferably) or Eukitt, and investigated with a Zeiss Photomikroskop II.

Scanning electron microscopy. Fully hydrated thallus fragments were fixed in the vapour of a 4% aqueous solution of osmium tetroxide for 4 h at room temperature, then dehydrated in a graded series of acetone and critical point dried. After mounting on specimen stubs with conductive silver print paint, and sputter-coating with a 80 : 20% alloy of gold and palladium the samples were examined in a Cambridge Stereoscan S 2.

Figs. 1–8. Light and scanning electron microscopy of isidium formation in *Parmelia pastillifera*. 1. Cross-section of the isidia-bearing part of the thallus. The button-shaped isidia (is) have a warty, pigmented upper and a smooth, greyish lower surface. a: algal layer of the mother thallus; m: medullary layer; r: rhizinae. 2. different developmental stages of isidia. Crater-shaped depressions in the thallus surface (*) originate from detached isidia. The arrow points to the umbilicus of a detached isidium which is adhering to the mother thallus with its warty, pigmented former upper surface. 3–5: Subsequent developmental stages of juvenile thalli on bark (3, 5) or bryophytes (4). The arrows point to the umbilicus. Same magnification in Figs. 1–5. 6. SEM micrograph of an isidium: the viscous, gelatinous material (g) of two neighbouring isidia is confluent. 7. SEM micrograph of the thallus surface with an isidium with warty upper surface, a fresh, crater-shaped depression with exposed phycobiont cells (ph) and two depressions which are already closed by a gelatinous material (arrows), all three originating from detached isidia. 8. SEM micrograph of a juvenile thallus (same developmental stage as in Fig. 4) developing on bryophytes. Rhizinae (r) are anchoring the thallus on and raise it above the substrate by elongation. Two of the peripheral rhizinae are broken off (*).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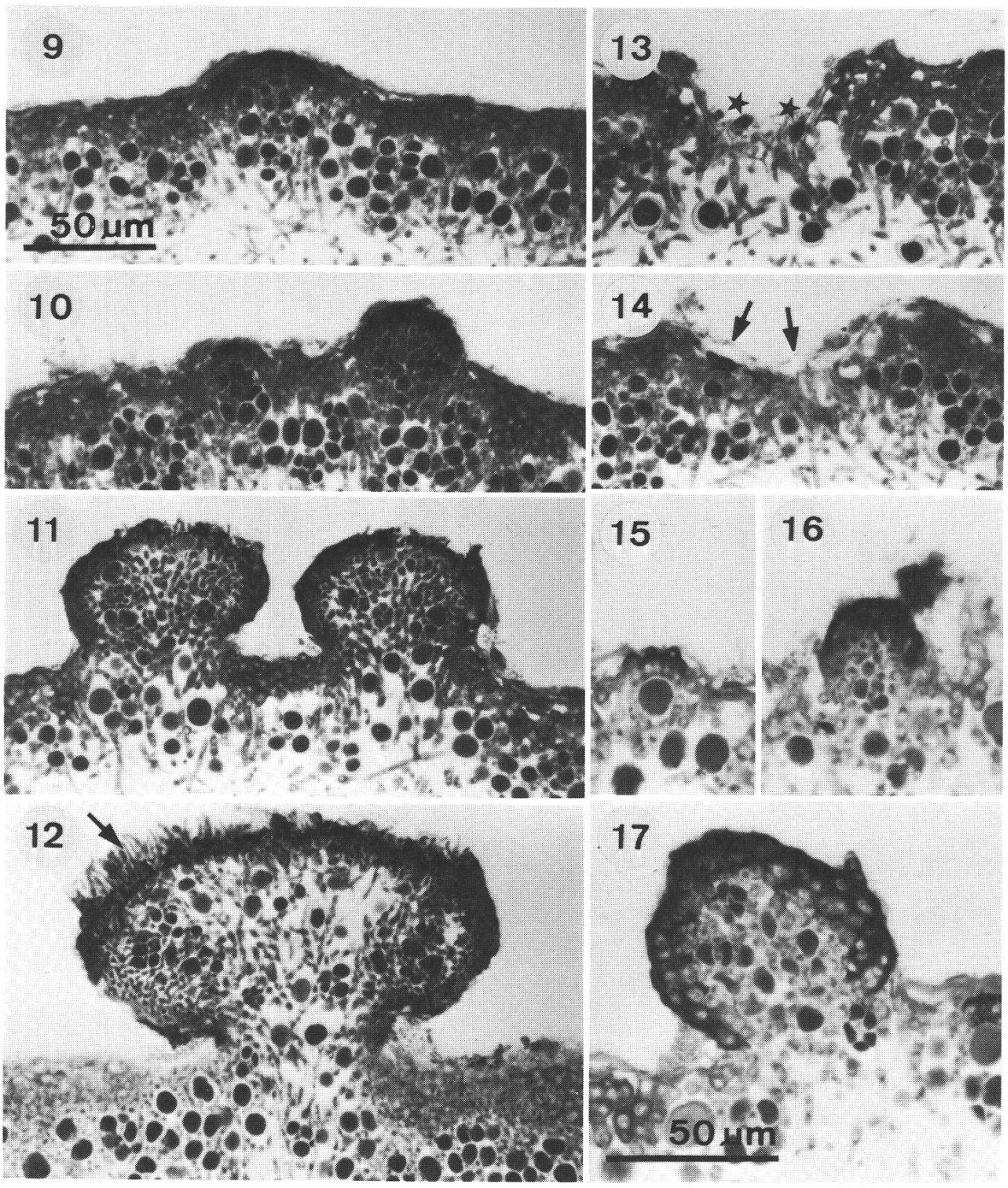

Fig. 9–17. Light micrographs of semithin sections showing subsequent developmental stages of isidium formation in *Parmelia pastillifera* (9–12) and *P. tiliacea* (15–17). 12. A mature, dorsiventrally differentiated isidium of *P. pastillifera*, showing an internal stratification. Aplanosporangia-bearing phycobiont cells occur mainly in the lower part. The arrow points to hyaline outgrowths of the pigmented cortical hyphae which will form rhizinae. 13. A crater-shaped depression in the thallus surface shortly after the breaking off of an isidium. Exposed phycobiont cells die off (*). 14. An older depression in the thallus surface which became closed by a gelatinous, probably mycobiont-derived material (arrows). 17. A mature, globose, internally non-stratified isidium of *P. tiliacea*. Same magnification in Figs. 9–14, and 15–17, respectively.

Results

In cross-sections of the central part of the thallus of *P. pastillifera* the button-shaped isidia look like minute thalli which develop on the mother thallus in an inversed position (Fig. 1). The warty, pigmented upper surface of the isidia resembles the lower, rhizinae-bearing surface of the mother thallus, whereas the lower, smooth surface of the isidia has the same greyish colour as the upper surface of the mother thallus. After breaking off, a crater-shaped depression is seen not only in the thallus surface (Figs. 2, 7, 13) but also in the isidium itself (Figs. 2–3). Both thalline depression and isidial umbilicus are soon getting closed by a, probably, mycobiont-derived gelatinous material (Figs. 7, 14). Phycobiont cells which were exposed at the surface of the depression die off (Figs. 7, 13).

In the vicinity of isidia-bearing mother thalli and even on the mother thallus itself numerous detached isidia were found (Figs. 2–3), all of which adhered to the substrate by means of a viscous material covering the warty, pigmented former upper, now lower surface (Fig. 6). Detached isidia can be easily recognized by their shape and mainly by their central umbilicus (Figs. 2–4). After landing on a suitable substrate such as bark (Figs. 3, 5) or bryophytes (Figs. 4, 8) the isidia are anchored on and then raised above the substrate by means of rhizinae which develop by elongation of the isidial warts (Fig. 8). Subsequently some areas of the disciform juvenile thallus start growing and thus form the first lobes (Figs. 4–5, 8).

The first developmental stage of isidium formation in *P. pastillifera* can be recognized from outside as a minute black dot on the thallus surface (Fig. 2). Each isidial primordium contains a group of growing hyphae, the uppermost peripheral ones of which become soon darkly pigmented, whereas the central ones are in very close contact with aplanosporangia-forming phycobiont cells (*Trebouxia* sp.) or young, developing aplanospores, respectively (Figs. 9–10). The globose to cylindrical, basally constricted isidia of the closely related *P. tiliacea* start their development in a similar manner with a primordium which contains fairly often at the very beginning only one phycobiont cell (Fig. 15). Fully developed isidia of *P. tiliacea* contain densely packed, young phycobiont cells and contacting mycobiont hyphae in their central part and a peripheral cortical layer which is built up by mycobiont hyphae with strongly pigmented cell walls (Fig. 17). The same developmental stage is also reached in *P. pastillifera* (Fig. 11), but in this species the developmental process proceeds until the isidium has attained a surprising degree of external and internal differentiation. Soon after bulging out of the thallus surface the vertical growth of the isidial primordium is slowed down, but horizontal development sets in, leading to a lens- or button-shaped outline of the isidium (Figs. 11–12). Phycobiont cells can be found in the whole isidium, but it is mainly in the basal part where numerous aplanosporangia develop, leading to the formation of an algal layer (Fig. 12). The hyphae of the central part of the isidium are loosely interwoven, whereas those of the pigmented upper surface form hyaline outgrowths (Fig. 12) and secrete a viscous, mucilaginous material (Fig. 8). The warts of the isidial surface are composed of bundles of hyaline outgrowths and represent prospective rhizinae which will elongate after getting in contact with an appropriate substrate (Fig. 8).

Discussion

Of all isidia-bearing lichen taxa so far investigated the isidia of *P. pastillifera* are unique in reaching a high degree of external and internal differentiation on the mother thallus in an inversed position. The clavate to spathuliform isidia of *P. exasperatula* Nyl., a brown, foliose species, develop also on the mother thallus into minute, dorsiventrally organized and internally stratified thalli which are, however, in the same position as the mother thallus (Rosendahl 1907). The scutelliform isidia of different tropical foliicolous lichens show, like their crustose, non-stratified mother thalli, no internal differentiation, as can be concluded from published data (Santesson 1954, Vezda 1975).

The thalli of foliose and fruticose species of lichen-forming Ascomycetes represent the most complex vegetative structures occurring in the fungi (Poelt 1986). The foliose Parmeliaceae are among the highest evolved groups of lichens, as can be concluded from morphological and anatomical criteria, especially from the mycobiont-phycobiont relationship by means of the very peculiar intraparietal haustoria (Tschermak 1941, Honegger, 1986). From a cell biological point of view, differentiation and pattern formation in a highly regulated system comprising two genetically different partners, none of which is forming meristema, appears particularly interesting. However, our knowledge of regulatory mechanisms involved in pattern formation in lichens is extremely limited (Honegger 1987). Isidium formation on subsenescent parts of the thallus is interesting because the cell turnover rates of most of the phycobiont cells in this non-growing zone are apparently slowed down, whereas the few phycobiont cells of the isidial primordium multiply repeatedly. This points to an activator-inhibitor system, the molecular basis of which is not understood (Honegger, 1987). In addition, it is difficult to imagine why the mycobiont of *P. pastillifera* develops its dorsiventrally organized isidia in an inversed position.

My sincere thanks are due to Prof. H. R. Hohl for critically reading this manuscript, and to Miss M. Pröschel for doing all the darkroom work.

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