The catapyrenioid lichen genera (*Ascomycota*, *Verrucariales*) in North America
1. Introduction and *Catapyrenium* s. str.

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Abstract: A monographic study of the catapyrenioid lichen genera in North America, from arctic Canada to temperate Mexico, is presented in a series of four papers. Catapyrenioid genera are characterized by a squamulose or squamulose-areolate thallus, perithecia lacking interascal filaments and hymenial algae, and simple or one-septate ascospores. Altogether 36 species belonging to seven genera are treated: *Catapyrenium* (4 spp.), *Clavascidium* (3 spp.), *Heteroplacidium* (5 spp.), *Involucropyrenium* (1 sp.), *Neocatapyrenium* (2 spp.), *Placidiopsis* (4 spp.), and *Placidium* (17 spp.). Keys to genera and species are presented and the circumscriptions of the genera are discussed. For each species a detailed description and accounts on ecology and distribution are provided. Distribution dot maps of more common species are supplied.

Zusammenfassung: In einer vierteiligen Artikelserie wird eine monographische Studie über catapyrenioide Flechten Nordamerikas, vom arktischen Kanada bis zur gemäßigten Zone Mexikos, vorgelegt. Catapyrenioide genera sind durch einen schuppigen oder areoliert-schuppigen Thallus, Perithecien ohne interascale Filamente und Hymenialalgen sowie durch ein- oder zweizellige Ascosporen gekennzeichnet. Insgesamt werden 36 Arten aus sieben Gattungen behandelt: *Catapyrenium* (4 spp.), *Clavascidium* (3 spp.), *Heteroplacidium* (5 spp.), *Involucropyrenium* (1 sp.), *Neocatapyrenium* (2 spp.), *Placidiopsis* (4 spp.), and *Placidium* (17 spp.). Bestimmungsschlüssel zu den Gattungen und Arten werden angeboten. Der Umfang der Gattungen wird diskutiert. Jede Art wird ausführlich beschrieben, Anmerkungen zu Ökologie und Verbreitung werden beigefügt. Für die häufigeren und weiter verbreiteten Arten werden Punktverbreitungskarten vorgelegt.

Catapyrenioid genera are characterized by a squamulose or squamulose-areolate thallus, perithecia lacking interascal filaments and hymenial algae, and simple or one-septate ascospores. A historical review on the early systematics of the catapyrenioid lichens was provided by BREUSS (1990). Up until the 1980s they have been mainly considered part of *Dermatocarpon* ESCHW. (e.g., THOMSON 1984). In the following years the generic name *Dermatocarpon* was restricted to the umbilicate and leafy members, and *Catapyrenium* FLOT. was brought back into use for the non-umbilicate species with crustose and squamulose habit. HARADA (1993) added three new genera:

Neocatapyrenium H. HARADA, *Scleropyrenium* H. HARADA, and *Dermatocarpella* H. HARADA. BREUSS (1990) distinguished six informal infrageneric groups of *Catapyrenium s. lat*. based on the presence or absence of an involucrellum, the type of attachment organs, exciple pigmentation, ascus shape, structure of the upper cortex, and differentiation of tissues. Following the general tendency towards narrower generic circumscriptions, BREUSS (1996) raised these groups to generic rank: The *cinereum*-group became *Catapyrenium* s. str., the *imbricatum*-group became *Heteroplacidium* BREUSS, for the *lachneum*-group the genus *Placidium* A. MASSAL. was resurrected, the *rhizinosum*-group was included in *Neocatapyrenium,* for the *virescens*-group the genus *Anthracocarpon* BREUSS was established, and the *waltheri*-group became *Involucropyrenium* BREUSS. The author added *Clavascidium* BREUSS for species similar to *Placidium* but differing in having clavate (vs. cylindrical) asci and reduced *Dermatocarpella* to synonymy with *Placidium*. Subsequent phylogenetic analyses (GUEIDAN & al. 2007, GUEIDAN & al. 2009, PRIETO & al. 2012) are largely in accordance with the morphologically and anatomically defined concepts of BREUSS (1996), with one major modification: PRIETO & al. (2012) found that there are two separated clades within *Placidium s. lat.* corresponding to species with and without rhizines and combined the rhizinate species to *Clavascidium* (with the exception of *Placidium arboreum*, see under this species).

A world-wide key was provided by BREUSS (2010). Currently the catapyrenioid lichens comprise 9 genera with 87 species.

Material and methods

The work on catapyrenioids of North America was started in the late 1990s with emphasis on the arid southwest and, little by little, extended until recently to cover the whole continent from Arctic Canada to temperate Mexico. The study is mainly based on herbarium material from the following institutional herbaria: ASU, B, BM, CANL, COLO, DUKE, FH, G, GZU, KANU, LD, LI, M, MICH, MIN, MSC, MUB, NDSU, NY, OSC, S, SBBG, SFSU, STU, U, UBC, UC, UCR, UPS, US, UTEP, W, WIS, and the private collections of ANDRÉ APTROOT, CHARIS BRATT, PIETER VAN DEN BOOM, IRWIN M. BRODO, GUNNAR DEGELIUS, RICK DEMMER, COLIN E. FREEBURY, KERRY KNUDSEN, RONALD ROBERTSON, HEATHER T. ROOT, ROGER ROSENTRETER, TOBY SPRIBILLE, DAPHNE STONE, SHIRLEY TUCKER, ROMAN TÜRK, ANTONIN VĚZDA, and VOLKMAR WIRTH. Material that has been transferred to an institutional herbarium is cited accordingly. Additional material was collected by the author during fieldwork in Alaska (2013), Alberta (1995), Arizona (1997 and 2000), Baja California (1997/98), British Columbia (1994), and California (1997 and 2000) and is now stored in LI. Fieldtrips in Arizona and Baja California were undertaken in the course of the Sonoran Desert Lichen Flora project organized by T. H. NASH III and the finds are included here with taxonomic adjustments. Altogether, approximately 3500 specimens have been studied. External morphological features were examined with a WILD-M7A stereomicroscope. Anatomical characters were observed with a ZEISS Axiolab transmission microscope. Free-hand sections with a razorblade were made in all cases and examined in tap water, partly pretreated with lactophenol cottonblue. Squash preparations were used for ascus and spore analyses. Measurements of anatomical structures refer to dimensions in tap water and are given in µm, measurements recorded under the dissecting microscope refer to dried material and are given in mm. Spore and conidia measurements given include the normal size range with the extremes within parentheses. Collecting dates are uniformly given in the form (D)D.(M)M.YYYY. Site data in m (meters) or ft (feet) refer to elevations above sea level. The distribution maps are based on the specimens examined only, if not stated otherwise; localities proximate to each other are merged into one dot.

Checklist of the North American catapyrenioid species (36)

***Catapyrenium* FLOT.**
cinereum (PERS.) KÖRB.
daedaleum (KREMP.) B. STEIN
psoromoides (BORRER) R. SANT.
squamellum (NYL. ex HASSE) J. W. THOMSON
***Clavascidium* BREUSS**
lacinulatum (ACH.) M. PRIETO
pseudorufescens (BREUSS) M. PRIETO
umbrinum (BREUSS) BREUSS
***Heteroplacidium* BREUSS**
compactum (A. MASSAL.) GUEIDAN & CL. ROUX
congestum (BREUSS & MCCUNE) BREUSS
phaeocarpoides (NYL.) BREUSS
transmutans K. KNUDSEN, BREUSS & KOCOURK.
zamenhofianum (CLAUZADE & CL. ROUX) GUEIDAN & CL.ROUX
***Involucropyrenium* BREUSS**
waltheri (KREMP.) BREUSS
***Neocatapyrenium* H. HARADA**
disparatum BREUSS
simulans (BREUSS) BREUSS
***Placidiopsis* BELTR.**
cinerascens (NYL.) BREUSS
minor R. C. HARRIS
oreades BREUSS
pseudocinerea BREUSS
***Placidium* A. MASSAL.**
acarosporoides (ZAHLBR.) BREUSS
andicola (BREUSS) BREUSS
arboreum (SCHWEINITZ ex MICH.) LENDEMER
californicum BREUSS
chilense (RÄSÄNEN) BREUSS
fingens (BREUSS) BREUSS
imbecillum (BREUSS) BREUSS
lachneum (ACH.) B. DE LESD.
lesdainii BREUSS
michelii A. MASSAL.
norvegicum (BREUSS) BREUSS
pilosellum (BREUSS) BREUSS
podolepis (BREUSS) M. PRIETO
rufescens (ACH.) A. MASSAL.
squamulosum (ACH.) BREUSS
subrufescens (BREUSS) BREUSS
yoshimurae (H. HARADA) BREUSS

Thallus

The most common growth form in catapyrenoid lichens is the squamulose thallus. Some species with squamules dividing by cracks form a thallus intermediate between crustose-areolate and squamulose (*Heteroplacidium compactum*, *H. zamenhofianum*). Crustlike thalli of adjoining, small, thin squamules fully adnate to the substrate are typically found in *Catapyrenium cinereum* and *Involucropyrenium waltheri*. Several *Placidium* species develop rather large, almost leafy squamae up to 10 mm across or even more (*P. chilense*, *P. rufescens*). The majority of species form medium-sized (3–6 mm), scattered to contiguous squamules. These may be fixed to the substrate by the entire undersurface or may have slightly uplifted margins. Several species have wavy squamules which are free from the substrate in a broad marginal zone and fixed only by their central parts (*Placidium rufescens*, *P. lachneum*, forms of *Clavascidium lacinulatum*). In some species the squamules are clustered to form compact, roughly circular patches or mounds or cushion-like aggregates up to several centimeters wide (*Heteroplacidium congestum*, *Neocatapyrenium disparatum*). In other species the thallus is composed of ± imbricate squamules (*Placidium imbecillum*, *P. rufescens*). In some species rosette-like thalli are formed with elongate, radiating lobes along the margin of the thallus (*Catapyrenium daedaleum*, *Placidium norvegicum*). Almost bullate squamules are found in *Placidium acarosporoides* and *P. lesdainii*. The individual squamules are mostly roundish to lobate in outline. Finely notched-incised squamules are characteristic for *Catapyrenium cinereum*.

Fig. 1. Specimen of *Placidium californicum* with a thick and strongly cracked epinecral layer. Width of the photograph 13 mm.

The coloration of the thallus does not vary much through the genera treated as no specific secondary substances are produced. Epruinose species are in shades of brown, often with a grayish or greenish tinge. The variation of the color in each species seems to depend largely on light exposition. In sunny sites the hyphal walls of the uppermost cortex layer are darker pigmented.

The upper surface is mainly smooth but may appear minutely rugulose in species with *cinereum*-type upper cortex. It is mostly dull, more rarely slightly glossy. In *Neocatapyrenium disparatum* it is distinctly scabrid due to the uneven thickness of the upper cortex. In *Catapyrenium cinereum* the squamules are usually densely covered by whitish gray pruina. *Catapyrenium daedaleum*, *C. psoromioides*, *Neocatapyrenium disparatum*, and *N. simulans* are slightly pruinose. In *Placidium* species a pruina is very rare and probably environmentally induced; in some specimens of *P. californicum* the epinecral layer is very thick and deeply furrowed giving them a whitish, cracked appearance (Fig. 1).

In *Catapyrenium cinereum* and, less conspicuously, in *Placidium andicola* the squamules are black-edged.

Thallus-anchoring structures

Most species are attached to the substratum over the whole or most of the lower surface by rhizohyphae arising from the medulla or the lower cortex. The rhizohyphae are more or less densely intricate to form a hypothalline weft extending for several millimeters into the soil. In several *Catapyrenium* species, *Involucropyrenium waltheri*, and *Placidiopsis pseudocinerea* they form a conspicuous, dark, spongy mat below the squamules. In *Catapyrenium cinereum*, *C. daedaleum* and *C. psoromoides* the hypothalline mat extends beyond the margin of the thallus. In several *Placidium* species the rhizohyphal weft is confined to the central part of the underside and lacks in a more or less broad zone along the margins. In *Catapyrenium squamellum*, *Heteroplacidium phaeocarpoides*, *H. zamenhofianum* and *Placidium podolepis* the rhizohyphae form hapter-like tufts or bundles. *Neocatapyrenium disparatum* is anchored to the substratum mainly by the basal ends of the squamae and has sparse rhizohyphae; *N. simulans* is anchored by rhizines and lacks rhizohyphae. Related species with (corticated) rhizomorphs deeply penetrating into rock fissures are absent in North America.

All *Clavascidium* species have rhizines that emerge from the lower surface and – in addition to a moderately dense hypothallus – penetrate the substrate. Rhizines are here defined as fascicles of roughly parallel running, more or less firmly cohering, colorless or brown hyphae. They vary from simple to ramified and anastomosing. Their main strands are 30–150 µm thick and up to several millimeters long. A unique feature within the catapyrenioid lichens is the brush-like anchoring structures of *Placidium arboreum* that support the squamae like stilts (Fig. 2). Stipe-like anchoring organs are developed in *Heteroplacidium compactum*, *H. transmutans* and *Placidium acarosporoides*.

Anatomy

All catapyrenioid lichens develop internally stratified thalli with main subdivisions into upper cortex, photobiont layer, medulla, and lower cortex with various tissue

types. In small-squamulose, thin species the algal cells are filling almost the entire thallus. In *Heteroplacidium* the thalli are entirely (sub)paraplectenchymatous and the tissues weakly differentiated.

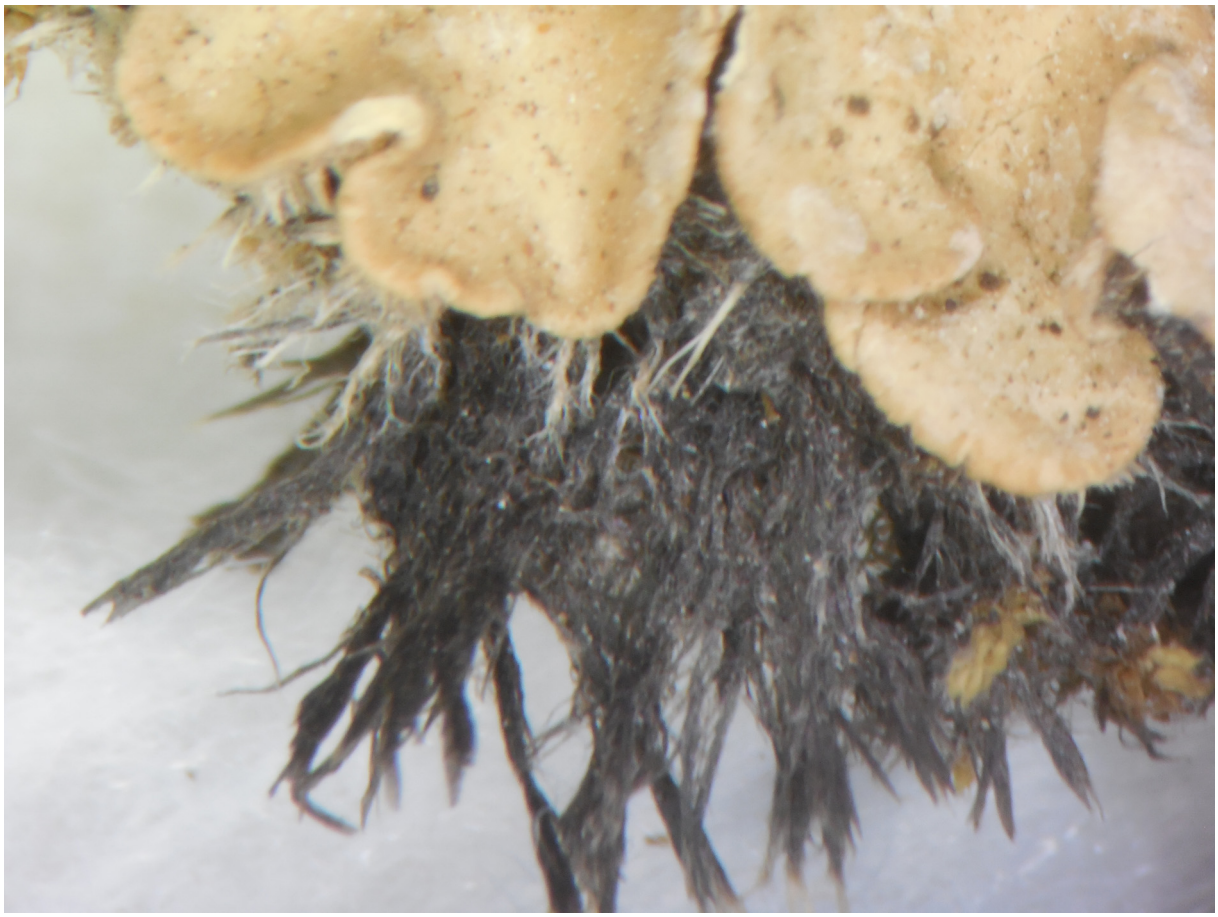


Fig. 2. Brush-like attaching organs of *Placidium arboreum*. Width of the photograph 6 mm.

Upper cortex

There are three main types of upper cortex developed in American species. The terminology follows GUEIDAN & al. (2007).

- The *cinereum*-type pseudocortex is thin (10–30 µm) and uneven in thickness and therefore poorly differentiated from the photobiont layer. It is composed of small (4–8 µm in diameter), roundish-angular cells with equally thick walls throughout the whole cortex. As the uppermost cells are not level with each other there is a certain degree of roughness seen under the dissecting microscope. This type of cortex is developed in *Catapyrenium*, *Involucropyrenium* and *Placidiopsis*.
- The *lachneum*-type eucortex is thicker (20–80 µm) and clearly delimited from the algal layer; in a vertical section of the thallus the border between these layers forms a sharp, straight line. The cortical cells are larger (c. 7–15 µm), angular, and tightly conglutinated, with relatively thin walls and large lumina, the walls gradually thickening upwards. The upper thallus surface is usually smooth. This type occurs in the genera *Clavascidium* and *Placidium*.
- The *nigrescens*-type eucortex is somewhat thinner and formed by smaller cells (3–9 µm) but constitutes a well-defined layer of even thickness well delimited from the

photobiont layer. Cell walls are equally thick throughout the cortex or slightly thickening upwards. This type is developed in *Heteroplacidium*.

The cortex of *Neocatapyrenium disparatum* is intermediate between types 2 and 3.

The uppermost cell layer of the cortex is usually brown, often in form of pigment caps on the outer cells. Crystalline deposits on or in the cortex are lacking in all catapyrenioid lichens.

Epinecral layer

The upper cortex is usually overlain by an amorphous epinecral layer which is formed by disintegration of the uppermost layer of the cortex and consists of dead, collapsed cortical cells. In *Catapyrenium*, *Placidiopsis* and *Neocatapyrenium* the dead cells form a scurfy surface of the squamules appearing as grayish white pruina. In *Placidium* the dead cortical cells become ± gelatinized, thus forming a continuous layer on the upper surface of the squamules giving them a smooth or fairly glossy apperance. Its thickness varies from almost absent to 50 µm. In some specimens it is deeply cracked to form a pyramid-like or trapezoid pattern, most often observed in *Clavascidium lacinulatum* (Fig. 3).

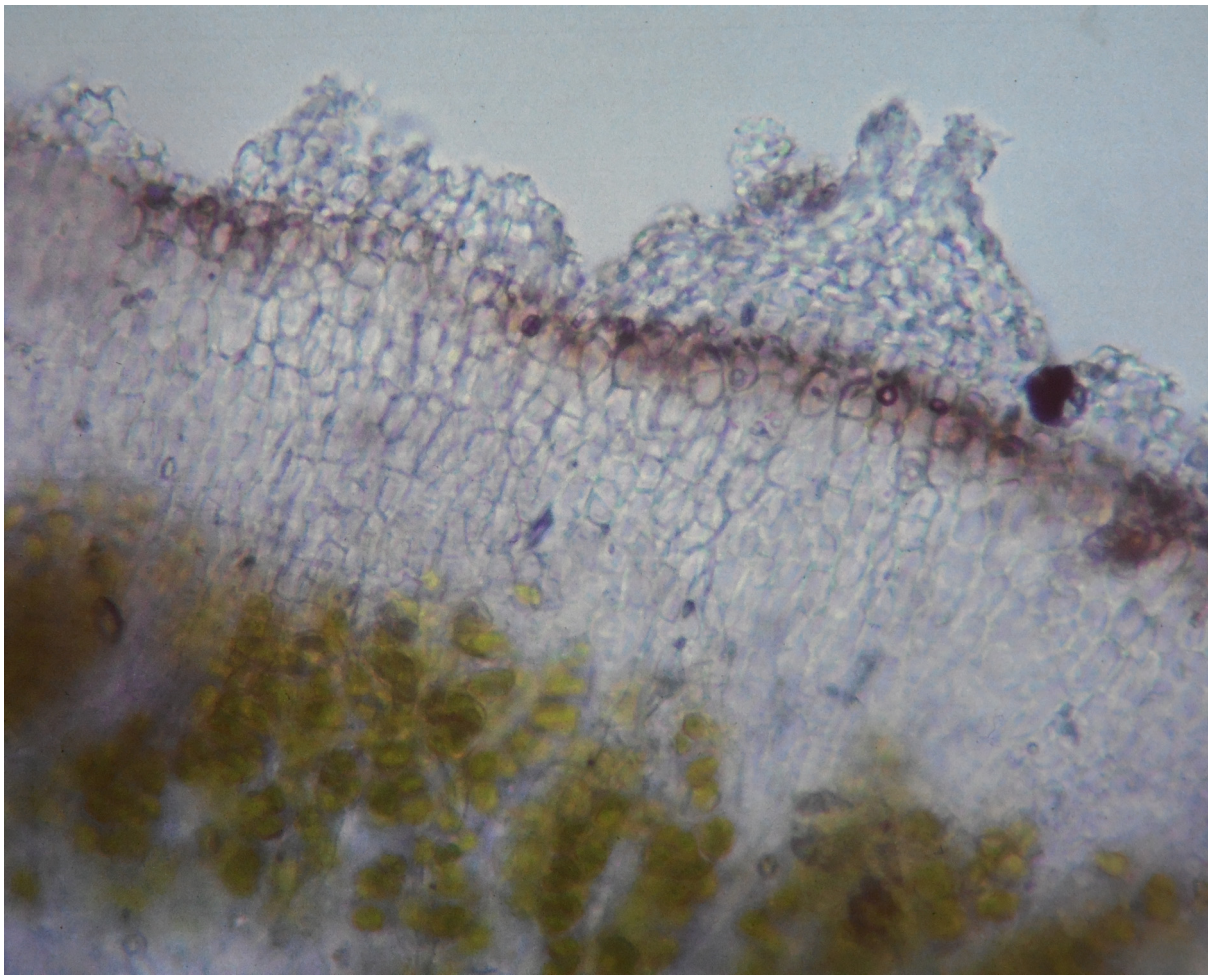


Fig. 3. Pyramid-like pattern of the epinecral layer in a specimen of *Clavascidium lacinulatum*.

Photobiont layer

In species with small, thin squamules the algal cells are filling almost the entire part of the thallus. In larger and thicker species, the algal cells form a continuous layer in the upper part of the squamules. In the genera *Catapyrenium* and *Placidiopsis* the algal layer is unevenly delimited against both the upper cortex and the medullary tissue. In the remeining genera the upper border of the algal layer is even, but its lower border is uneven with photobiont cells protruding more or less far into the medulla.

The photobionts belong to the trebouxiophycean genera *Myrmecia* (in *Clavascidium*, *Placidium*, and *Heteroplacidium*) and *Diplosphaera* (in *Catapyrenium*, *Placidiopsis*, and *Neocatapyrenium*; THÜS & al. 2011).

Medulla

Three types are present among catapyrenioid lichens:

- The prosoplectenchymatous (filamentous) medulla is built of long-celled, densely interwoven hyphae forming a cottony layer with rather large interhyphal spaces. A few shorter hyphal compartiments may be inflated to form globular cells, but these are barely noticeable in microscopic cross sections.

The prosoplectenchymatous type is typical for *Placidium arboreum*, *P. chilense*, *P. imbecillum*, *P. lachneum*, *P. rufescens*, *P. subrufescens*, *Catapyrenium simulans*, *Clavascidium pseudorufescens*, *Neocatapyrenium disparatum*, and *N. simulans*. In these species the medulla is usually at least 100 µm high, in *Placidium chilense*, *P. lachneum*, and *P. rufescens* it may be up to 300 µm thick.

- The mixed-type medulla has many globular cells that can readily be seen in cross section, but the development of the medullary tissue from an irregular hyphal network is not totally obscured and there are spaces between the hyphae. The mixed type is found in the majority of the catypyrenioid taxa.
- In the (sub)paraplectenchymatous or cellular medulla the globular cells are so numerous and tightly arranged that no filamentous parts are visible and the interhyphal spaces are very small. The cellular medulla type is found in *Catapyrenium cinereum*, *C. squamellum*, *Involucropyrenium waltheri*, and *Placidium lesdainii*.

Illustrations of medullary types are provided by BREUSS & BRATT (2000) and PRIETO & al. (2012). Though intermediate forms exist that cannot be be attributed to one of these types with certainty the construction of the medulla is important for species charcterization. Especially in thin specimens the attribution to a certain construction type may be difficult.

Crystalline deposits in the medulla are lacking in all catapyrenioid lichens.

Lower cortex

In most species there is a (sub)paraplectenchymatous lower cortex developed (Fig. 4), with cells roundish to subangular depending on their density and mutual pressure; interhyphal spaces are small or lacking. In species with a medulla of the mixed type the lower cortex is not clearly demarcated but develops gradually from the medullary tissue by a tighter arrangement of the globular cells. In species with a filamentous medulla the lower cortex is sharply delimited, appearing as a continuous layer of even

thickness, up to 90 µm high. A special form of lower cortex is developed in *Placidium lachneum*. In this species the cortex is composed of angular cells which are conglutinated in vertical rows (vs. the irregularly arranged cells of the cortex of other species). In tiny interhyphal spaces, if present at all, brown pigment is deposited, occassionally giving the cortex a brown-spotted appearence in microscopic section. The lowermost cell layer bears a black pigment cover.

In *Catapyrenium cinereum*, *Involucropyrenium waltheri*, and *Placidiopsis pseudocinerea* a lower cortex is visible as a small-celled, dark-pigmented paraplectenchyma. *Catapyrenium daedaleum* and *C. psoromoides* lack a lower cortex; in these species the medullary tissue merges gradually into a dark mat of rhizohyphae (Fig. 5). *Clavascidium umbrinum* has a fairly thick brown basal layer of mainly horizontally oriented filamentous hyphae with varying numbers of globular cells.

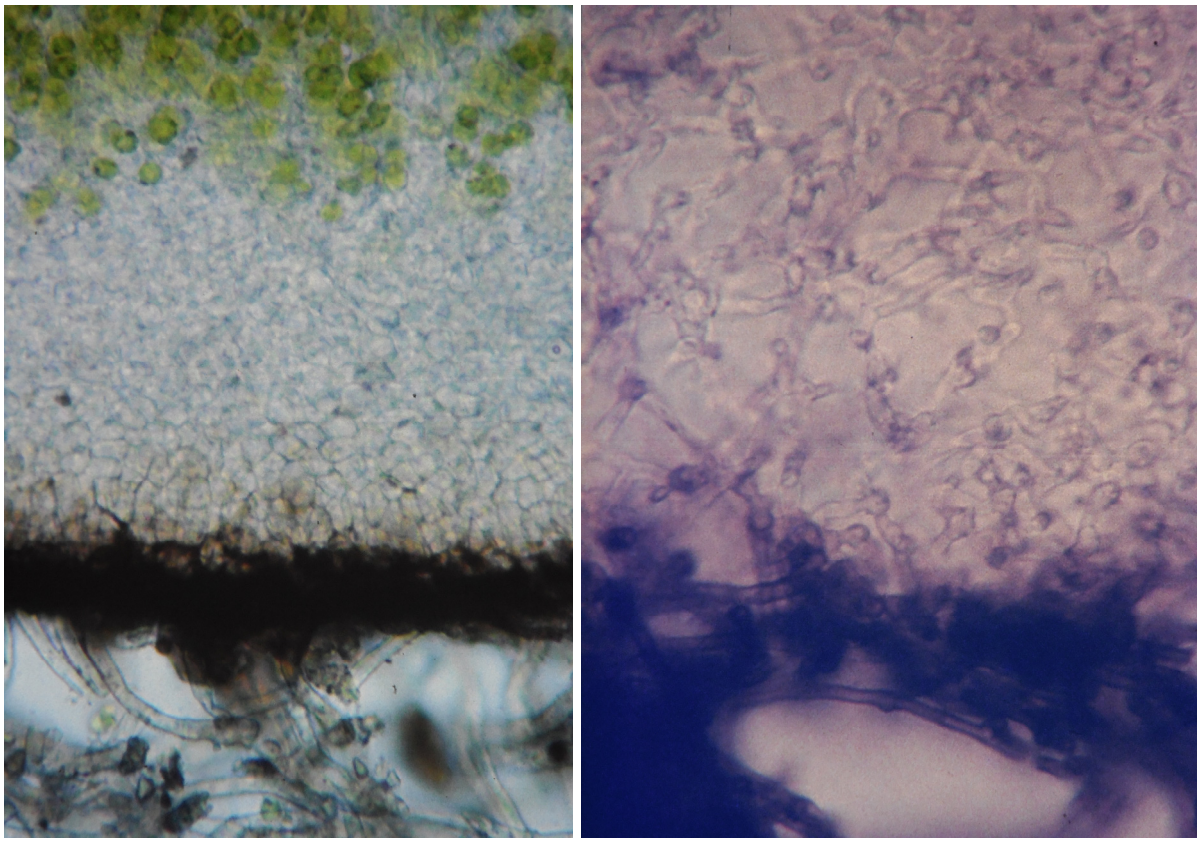


Fig. 4 (left). Paraplectenchymatous lower cortex of *Placidium* species. – Fig. 5 (right). *Catapyrenium psoromoides*: medullary tissue merging into the rhizohyphal web.

Pycnidia

Pycnidia are known from all catapyrenioid genera except for *Catapyrenium s. str*. and *Placidiopsis*. They are frequent in most species but may be easily overlooked. Their construction type and position on the thallus squamules is of taxonomic value. Two types can be distinguished:

The most common type is the *Dermatocarpon*-type (*Xanthoria*-type according to VOBIS 1980), which is found in *Clavascidium*, *Heteroplacidium*, and *Placidium*. It is built of a paraplectenchymatous tissue of isodiametric cells 5–7 µm in diameter and contains several cavities. The conidia are produced by the cells bordering the cavities.

There is no well-differentiated wall; the pycnidia are separated from the surrounding tissue by polygonal or tangentially slightly elongated cells of the same size as in the internal tissue. And there are no well-differentiated ostioles; the conidia are released through fissures, which – in case of laminal pycnidia – are visible as small dents or irregular openings on the upper surface of the thallus. The cortex around their openings is often darker pigmented and they are easily confused with the ostioles of perithecia, which are, however, mostly larger and more circular. Pycnidia of this type grow in three dimensions so that they are almost spherical. They may reach diameters of 450 µm or rarely more. They may be either laminally immersed in the thallus or marginal and then appear as knoblike or globular projections.

The rarer pycnidial type is the *Endocarpon*-type (or *Staurothele*-type), which occurs in *Neocatapyrenium* and was found once in an (extra-American) *Involucropyrenium* species. This pycnidium has a single central cavity – though sometimes irregularly expanded – which is bordered by radially oriented conidiophores. It has a thin wall of slightly elongated cells, and the conidia are released through an apical pore that is hardly visible at the surface of the thallus. This pycnidial type grows mainly in vertical direction and is usually less than 150 µm broad. It is always laminally immersed in the squamules.

The position of the pycnidia is highly specific. PRIETO & al. (2010) reported on pycnidia in both laminal and marginal positions in one extra-American species and in one specimen of *Placidium pilosellum*. These observations may represent extraordinary exceptions, but the following explanation seems more appropriate: Originally the pycnidia have been developed marginally in the rounded inward curve between two projecting lobes and then enclosed by the touching margins of the expanding lobes.

Conidia

In all species the conidia are hyaline, simple, and thin-walled. Their outer forms and sizes are of taxonomic value as was earlier shown by BREUSS (1990), though differences are subtle in some cases. Two shapes can be distinguished: oblong-ellipsoidal and cylindrical (bacilliform). The oblong-ellipsoidal conidia are less than 5 µm long and about 1.5–2 µm thick. The cylindrical conidia are not necessarily longer but thinner; the shortest ones are c. 4 µm long, in several species they measure 5–7 µm (e.g., *Placidium fingens*, *P. lachneum*, *P. yoshimurae*), in *Placidium norvegicum* up to 8 µm; the longest ones are 10–14 µm (in *Heteroplacidium transmutans*).

Perithecia

In most samples perithecia are numerous and easy to study. In the genus *Involucropyrenium*, where they originate from initials within the hypothallus, they are situated between the squamules. In all other catapyrenioid genera the perithecia develop within the photobiont layer. They are completely immersed in the thallus with only their apices showing as black dots or mounds on the thallus surface.

The perithecia are (sub)globose to broadly pyriform. In *Clavascidium* and *Placidium* they are pyriform when young and display a pronounced growth in horizontal directions to develop an almost spherical shape with maturity. In *Involucropyrenium* and *Catapyrenium* species they are (sub)globose from early stages on.

An involucrellum is lacking in all genera except for *Involucropyrenium* (with *I. waltheri* as the only species occurring in North America).

The excipulum is formed by several layers of strongly conglutinated, tangentially elongate cells with narrow lumina and in most species it is 25–35 µm thick. Thinner exciples are diagnostic for *Heteroplacidium zamenhofianum*, *Placidiopsis minor*, and *Placidium michelii*. In most species the exciples are colorless except for the ostioles and largely remain colorless during maturity, but frequently become yellowish or pale yellowish brown with age, with darker pigmentation only in overmature or decaying perithecia. Dark brown to black perithecia are diagnostic for *Placidium michelii* and *Clavascidium lacinulatum* var. *atrans*. In *Catapyrenium, Heteroplacidium*, and *Placidiopsis* exciples are either pale or dark. In *Catapyrenium cinereum* the pigmentation of the exciples starts in mature perithecia so that pale and dark fruiting-bodies can be found within the same squamules.

Perithecium sizes are not necessarily correlated with sizes and thickness of the squamules. In the genera *Placidium* and *Clavascidium* perithecia may reach up to 500 µm in diameter so that they are completely embedded within the squamules only in species with thick thalli. In thin thalli they cause conspicuous bulges of the lower side – a feature that is useful in determination of *Placidium* species.

Interascal filaments are lacking. Sterile hyphae in the ostiolar region are here referred to as “periphyses” without taking their genesis into consideration. Periphyses are of limited importance for species determination. They are mostly simple or sparingly branched, and their lengths range from c. 15 µm in *Catapyrenium squamellum* up to 30–50 µm in *Placidium* species. The apical cell is somewhat swollen in some species.

The hymenial gel reacts KJ+ blue.

Asci

The asci are either clavate or cylindrical. Clavate asci with biseriately arranged spores are found in most catapyrenioid genera. Cylindrical asci with uniseriately arranged spores are generally rare in Verrucariaceae and only found in *Placidium* and some *Clavascidium* species. The shape of asci is best observed in early developmental stages because during maturity the cylindrical ones may slightly broaden to display a somewhat irregular arrangement of spores. In BREUSS (1996) the shape of the asci was used for separating *Placidium* from the remaining genera, especially to distinguish *Placidium* from *Clavascidium*. In the current delimitation of *Placidium* as the result of phylogenetic analyses both ascus types are present, although taxa with distinctly clavate asci are mainly found within *Clavascidium* (PRIETO & al. 2012).

The asci are bitunicate, with a non-amyloid wall but surrounded by a thin amyloid sheet. They are usually not or only slightly thickened at the apex. Only in one genus (*Placidiopsis*) the ascus wall is apically thickened – but also non-amyloid – and contains a more or less distinct ocular chamber.

Ascospores

There are 8 spores per ascus in all catapyrenioid species. The ascospores are 1-septate in *Placidiopsis* and simple in the remeining genera, hyaline, without a perispore or

ornamentation and (except for *Placidium californicum*) thin-walled. Their shapes range from narrowly ellipsoidal to broadly ellipsoidal or subglobose, rarer are (sub)fusiform or clavate spores. The largest ascospores are found in *Placidium norvegicum*, *P. rufescens*, *Catapyrenium cinereum*, and *C. daedaleum*; their lengths may exceed 22 µm. *Placidiopsis minor* has the smallest spores (8–10 × 4–5 µm).

Chemistry

Spot tests are negative in all species. No secondary products are known to occur in catapyrenioid lichens.

Ecology

The majority of catapyrenioid species grow on soil or on rock. Only two species (*Catapyrenium psoromoides*, *Placidium arboreum*) are mainly corticolous, occasionally occuring on mossy boulders. *Placidium fingens* was found growing both on earth and bark. Most species grow on calciferous substrata. The majority of the epilithic members grow on limestone, only a few preferably on acidic rock like granite (*Placidium acarosporoides*, *P. lesdainii*), others are less substrate-specific and occur on both calcareous and non-calcareous rocks (e.g., *Placidiopsis minor*, *Placidium podolepis*). Similarly, the majority of terricolous species prefer calciferous soils. *Placidiopsis pseudocinerea* and *Placidium lachneum* grow on calcium-rich as well as on calcium-poor earth. *Clavascidium* species often colonize sandy ground and even fine-textured soils such as gypsiferous and silty loam soils, their rhizines firmly anchoring the squamules in the unstable substratum. *Placidiopsis cinerascens* was found on serpentine soil. *Heteroplacidium congestum* often colonizes saline soils.

Two species are parasitic in an early stage of development (*Heteroplacidium transmutans* on *Acarospora socialis*, and *H. zamenhofianum* on *Staurothele* spp.), but become autonomous in older stages. A third species of *Heteroplacidium* (*H. compactum*) seems to be a facultative parasite on various crustose lichens. *Placidium fingens* has been found growing on homoiomerous lichens (*Scytinium* sp.) on twigs in a part of its distribution area.

Most catapyrenioid lichens grow in open, often sun-exposed situations. Many species are especially common in arid or semi-arid habitats, where they are important components of biological soil crusts (ROSENTRETER & BELNAP 2003), accompanied by species of *Endocarpon*, *Fulgensia* (*Gyalolechia*), *Heppia*, *Peltula*, and *Psora*.

The second center of species diversity within catapyrenioids are the alpine and tundra-like habitats, where they grow on bare gaps between dwarf shrubs, on gravelly soil, pockets of earth on rock ledges, and in rock crevices.

Distribution

Most species of catapyrenioid lichens have their main distribution in the temperate region. The distributions of *Clavascidium lacinulatum* var. *lacinulatum*, *Placidium pilosellum*, and *P. squamulosum* var. *squamulosum* may be regarded as cosmopolitan; these taxa are not only the most widespread catapyrenioids but also the most frequent ones.

Many species have their main ranges in the Holarctic but have also been reported from occurrences in the Southern Hemisphere: *Catapyrenium psoromoides*, *Clavascidium umbrinum*, *Heteroplacidium compactum*, *H. phaeocarpoides*, *H. zamenhofianum*, *Placidiopsis cinerascens*, *Pl. oreades*, *Placidium fingens*, *P. imbecillum*, *P. michelii*, *P. rufescens*, and *P. yoshimurae*.

The arctic-alpine circumpolar element is represented by *Involucropyrenium waltheri*, *Placidiopsis pseudocinerea*, *Placidium lachneum*, and *P. norvegicum*. Arctic-alpine bipolar species are *Catapyrenium cinereum* and *C. daedaleum*.

Disjunct distribution patterns are shown by *Heteroplacidium congestum* (western North America and Spain), *Placidium acarosporoides* (western North America and South Africa), and *P. subrufescens* (California and Mediterranean Europe).

Placidium andicola, *P. chilense*, *P. podolepis*, and *P. squamulosum* var. *argentinum* occur in both North and South America.

North American endemics are *Catapyrenium squamellum* (southwestern North America and Jamaica), *Clavascidium lacinulatum* var. *atrans* (United States and Mexico), *Cl. l.* var. *erythrostratum* (North America), *Cl. l.* var. *latisporum* (Mexico), *Clavascidium pseudorufescens* (Baja California Sur), *Heteroplacidium transmutans* (southern California), *Neocatapyrenium disparatum* (Texas), *N. simulans* (Mexico), *Placidiopsis minor* var. *minor* (North America including Greenland), *Placidium arboreum* (North America), *P. californicum* (western North America), and *P. lesdainii* (Baja California).

Key to genera

1 Ascospores 2-celled ..... ***Placidiopsis***

1* Ascospores simple 2

2 Perithecia situated between the squamules, with an involucrellum. Squamules small (< 1.5 mm) and thin ..... ***Involucropyrenium***

2* Perithecia embedded in the squamules, without involucrellum 3

3 Squamules fixed by their elongate basal ends or by rhizines only, lower side naked, no rhizohyphal web. Pycnidia of *Endocarpon*-type .... ***Neocatapyrenium***

3* Squamules attached with a rhizohyphal web, hyphal tufts or rhizines originating from the lower side, or by central peduncles. Pycnidia, if present at all, of *Dermatocarpon*-type 4

4 Upper cortex of *cinereum*-type, composed of small, roundish-angular cells, thin (10–30 µm) and unevenly delimited from the algal layer ..... ***Catapyrenium***

4* Upper cortex not of *cinereum*-type, well differentiated, composed of small to large, roundish-angular to polygonal cells, thin to thick, sharply and evenly delimited from the algal layer 5

5 Walls of cortical cells almost equally thick throughout the cortex; tissue below photobiont layer (sub)paraplectenchymatous. Asci clavate, spores biseriate ..... ***Heteroplacidium***

5* Walls of cortical cells gradually thickening upward. Tissue below photobiont layer filamentous or with a varying number of inflated cells. Asci clavate or cylindrical 6

6 Squamules fixed to the substratum by a rhizohyphal weft (brush-like hyphal bundles supporting the squamae like stilts in one species: *P. arboreum*). Asci cylindrical at least when young, with uniseriately arranged spores ... ***Placidium***

6* Squamules fixed by a rhizohyphal felt and additional rhizines which penetrate the substratum. Asci mainly clavate from early stages on ..... ***Clavascidium***

Catapyrenium FLOT.

Botanische Zeitung 8 (1850): 361.
Type species: *C. cinereum* (PERS.) KÖRB.

T h a l l u s : composed of irregularly arranged squamules or rosulate, attached by a rhizohyphal weft or tufts of hyphae. Individual squamules about 1–5 mm wide, rounded or lobed or finely incised. Upper surface brownish or greenish gray or brown, dull, smooth or minutely scabrose, often whitish pruinose.

A n a t o m y : upper cortex paraplectenchymatous, formed by isodiametric rounded-subangular cells 5–8 µm in diam., poorly delimited from the algal layer, with or without an amorphous epinecral layer. Photobiont layer about 50–100 µm high, unevenly delimited against upper cortex and medulla, photobiont *Diplosphaera* with cells 4–10 µm in diam. Medulla of intricately interwoven hyphae which are filamentous or divided into spherical cells. Lower cortex of more closely packed globular medullary cells to paraplectenchymatous or lacking. Rhizohyphae colorless or brown, forming a loose or dense hypothallus or gathered together to form tufts or rhizines.

P e r i t h e c i a : laminally immersed within the squamules, subglobose, up to 300 µm broad. Involucrellum lacking. Excipulum hyaline or pale yellowish brown to brown-black, ostiolum always blackish.

P e r i p h y s e s : simple or sparingly branched.

A s c i : clavate, thin-walled, non-amyloid, apically not or slightly thickened, without ocular chamber.

A s c o s p o r e s : 8 in ascus, biseriately arranged, simple, ellipsoidal, ovate to clavate or subfusiform, colorless, thin-walled, smooth, without gelatinous sheath.

C o n i d i o m a t a : lacking.

Short characterization:

- Squamules comparatively small, attached by a rhizohyphal weft or tufts of rhizohyphae.
- Cortex a *cinereum*-type pseudocortex.
- Asci clavate, spores biseriate.
- Conidiomata lacking.

Catapyrenium dactylium BREUSS, characterized by the formation of dactyloid outgrowths with apically immersed pycnidia, was tentatively assigned to this genus on account of anatomical features (BREUSS 2000) but has to be excluded according to molecular analyses: PRIETO & al. (2010b) found it to be sister of *Placopyrenium caeruleopulvinum* (THOMSON) BREUSS and, together with *Placopyrenium stanfordii* (HERRE) K. KNUDSEN, it belongs to a well-supported separate clade.

Catapyrenium encompasses 6 species, 4 of which occur in North America.

Key to *Catapyrenium* species

1 Squamules ascending, olive- or brownish green, epruinose, thin, with finely crenate margins, attached by tufts of very thin (c. 2.5–3 µm) rhizohyphae. Ascospores narrowly ellipsoidal, 15–20 × 5–6 µm ..... ***C. squamellum***

1* Squamules loosely to firmly adnate, ± pruinose, thickish, lobate, attached by a dense rhizohyphal weft, rhizohyphae thicker (3–5 µm). Ascospores broader .. **2**

2 With a black paraplectenchymatous lower cortex. Squamules finely notched-incised to deeply incised, usually densely pruinose, dark-rimmed. Ascospores oblong ovoid to clavate, 17–23 × 6.5–8.5 µm ..... ***C. cinereum***

2* Without a paraplectenchymatous lower cortex, rhizohyphal weft gradually emerging from the medullary tissue. Squamules irregularly rounded and lobed, usually slightly pruinose **3**

3 On soil or terricolous mosses. Thallus often rosette-forming, marginal lobes broadly roundish and thickish. Pruina fine, diffuse, on inner parts of thallus. Asci 75–85 × 17–20. Ascospores c. 17–22 × 6–8 µm, oblong ovoid to clavate .. .. ***C. daedaleum***

3* On bark or over saxicolous mosses. Thallus irregular, with patchy pruina especially on distal parts of lobes. Asci 55–65 × 13–16 µm. Ascospores c. 13–17 × 5.5–7 µm, ellipsoidal to fusiform ..... ***C. psoromoides***

The species

***Catapyrenium cinereum* (PERS.) KÖRB.**, Syst. Lich. Germ. 1855: 325.

Endocarpon cinereum PERS., Neue Annal. Bot. 1 (1794): 28. For generic combinations see BREUSS (1990: 45).

Endocarpon hepaticum ACH., Kgl. Vetensk.-Akad. Nya Handl. 1809: 156. – Type: Lapponia, WAHLENB. (H-ACH no. 853 – lectotype, selected by BREUSS 1990: 48).

Verrucaria polythecia ACH., Lich. Univ. 1810: 288. – Type: Helvetia (H-ACH no. 852 upper specimen – holotype).

Lichen tephroides ACH., Lich. Suec. Prodr. 1798: 18 nom. illeg.

Dermatocarpon cinereum (PERS.) TH. FR. var. *fuscescens* VĚZDA, Acta Mus. Sil., ser. A, 10 (1961): 3. – Type: CSSR, Tatra Magna, supra lacum Zelené pleso, c. 1600 m, ad terram humosam, 9.1960 A. VĚZDA (hb. VĚZDA – holotype).

T h a l l u s : Squamules dispersed or more often adjacent, exceptionally slightly overlapping, forming small patches or flat crusts to 3–4 cm across. Individual squamules (0.5–)1–3 mm wide, at least isolated ones or those along the thallus margin finely notched-incised to deeply divided into tongue-shaped lobes, fully adnate to the substratum, flat or weakly convex, mostly grayish pruinose except for the margins which are ± distinctly dark-rimmed, rarely bare throughout and then grayish brown to brown, occasionally olivaceous, dull, with rounded or rather acute flanks, often densely pitted with the dark ostioles of the perithecia.

A n a t o m y : Thallus about 150–300 µm thick. Upper cortex barely more than 20 µm high, amorphous layer almost lacking to thick (up to 50 µm), algal cells usually filling most of thallus thickness, with only a thin alga-free medullary tissue of densely packed globular cells. Lower cortex paraplectenchymatous, composed of 2–4 layers of

(sub)angular cells 8–11 µm in diam., with black-brown walls. Rhizohyphae (3.5–) 4–4.5(–5) µm, densely interwoven to form a conspicuous dark spongy mat.

P e r i t h e c i a : usually abundant, embedded in the squamules, with the ostiolar regions somewhat projecting and showing as small dark mounds, subglobose, 200–250(–300) µm broad. Excipulum initially hyaline, becoming brown to blackish at maturity.

P e r i p h y s e s : 20–30 µm long and 2.5–3.5 µm thick, with slightly swollen apical cells (up to 5 µm).

A s c i : broadly clavate, about 60–70 × 16–22 µm.

A s c o s p o r e s : (15–)17–23(–25) × (6–)6.5–8.5(–9.5) µm, mostly ± clavate, rarer fusiform to ellipsoidal.

Icon.: BREUSS 1990: 169, BREUSS & HANSEN 1988: 102, DIEDERICH & BRÜCKER 2022: 164, DOBSON 2018: 130, HARADA 1993: 126, MCCUNE 2017a: 145, MCMULLIN 2023: 94–95, MOBERG & al. 2017: 60, PUNTILLO 1996: tav. 10, SCHEIDEGGER & al. 2023: 169, STENROOS & al. 2016: 128–129, THOMSON 1984: 211 sub *Dermatocarpon cinereum*, 1987: 29, VAN HALUWYN & al. 2012: 91, VUST 2011: 65, WIRTH & al. 2013: 330, WITTMANN & TÜRK 1990: 45. Anatomy: HARADA 1993: 117, 119 & 127. – When comparing the illustrations cited one gets a good impression of the variability of the species (see below).

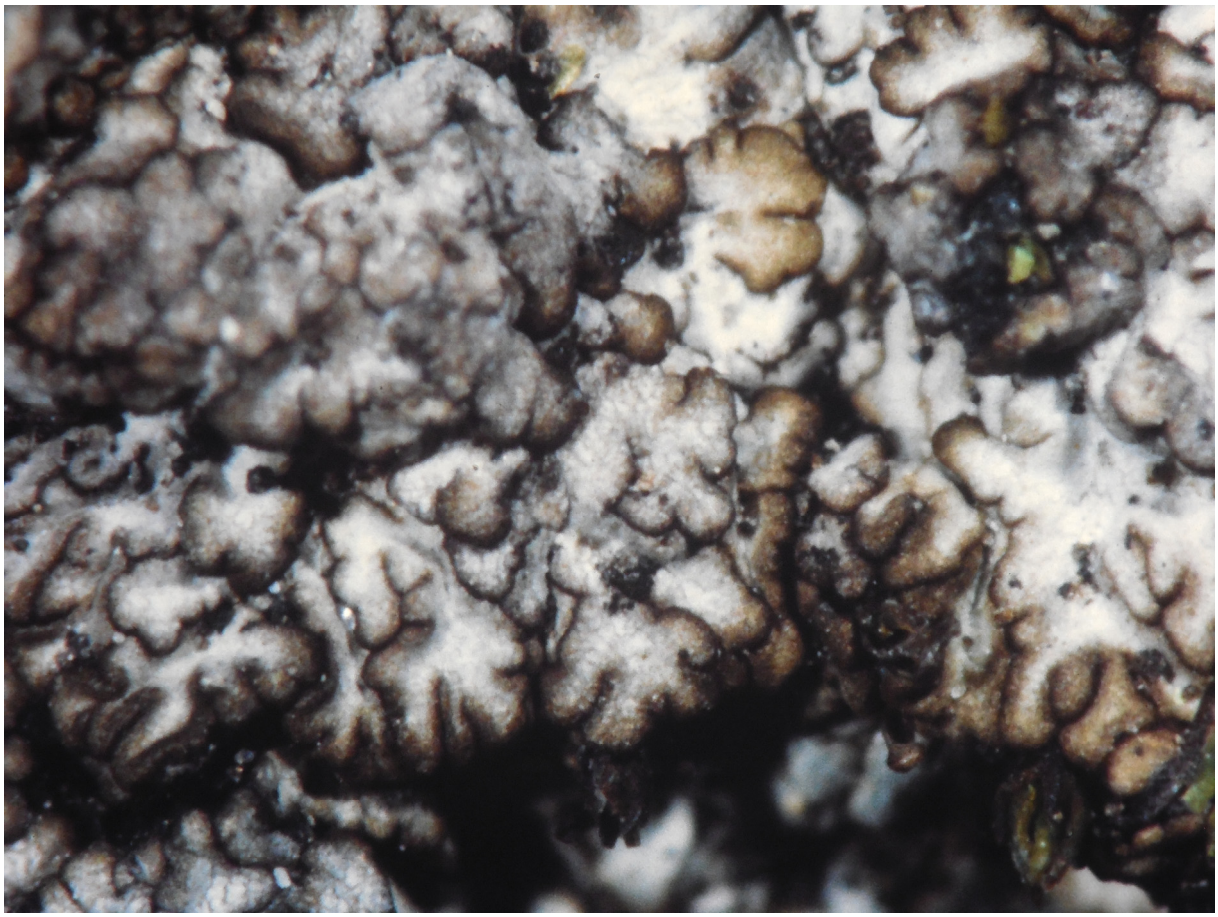


Fig. 6: *Catapyrenium cinereum*: typically lobed specimen. Width of the photograph 10 mm.

Characterization: Easily recognized by its small, finely notched-incised to lobulate, dark-rimmed squamules which are usually densely whitish gray pruinose except for the very margins (Fig. 6), and the black lower cortex with dark rhizohyphae forming a conspicuous dark spongy hypothallus. At first sight *Involucropyrenium waltheri* looks similar and was not recognized as a separate species by THOMSON (1989), but its perithecia are situated between the squamules and are surrounded by an involucrellum. *Placidiopsis pseudocinerea* is anatomically identical with *C. cinereum* but differs in having 2-celled ascospores; its squamules are usually not as finely and deeply incised as in *C. cinereum*.

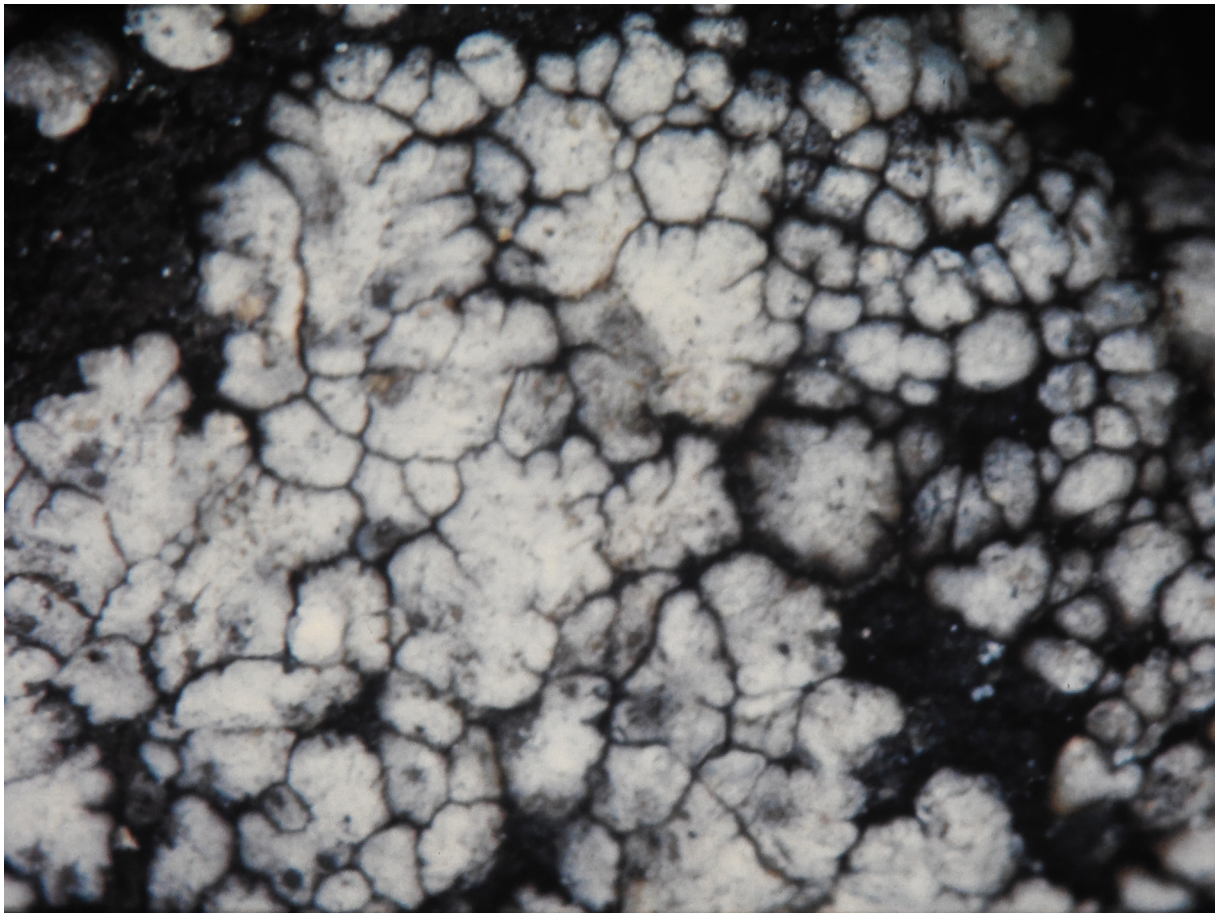


Fig. 7. *Catapyrenium cinereum*: crust-like thallus of densely adjoining squamules. Width of the photograph 6 mm.

Variability: There is some variation in the formation of lobes or notches and in pruinosity. Most specimens are finely notched, at least isolated squamules or squamules at the thallus margins, others are cut deeply and sharply. If squamules are densely crowded to form a subcontinuous crust the central ones often are less incised and rather angular in shape giving the thallus a chinky areolate appearance (Fig. 7). In rare cases the thallus consists of convex, almost granular areoles. While the majority of samples of *Catapyrenium cinereum* are distinctly pruinose and therefore have a gray or even whitish coloration, there are others that are barely or not at all pruinose and have a grayish hue or are brown, respectively. Both the types of *Endocarpon hepaticum* and of *Dermatocarpon cinereum* var. *fuscescens* represent epruinose forms of *Catapyrenium cinereum*. Erroneously the epithet “*hepaticum*” has widely been misapplied to

brown-squamulose catapyrenoids presently known as *Placidium*, mainly *P. squamulosum*. In hb. Turner (BM) there is a specimen labelled "*Endocarpon hepaticum* Dr. ACHARIUS 1809" which indeed represents *Placidium squamulosum*, but it is not in full accordance with the diagnosis of *Endocarpon hepaticum* and without any locality information.

Ecology and distribution: *Catapyrenium cinereum* grows on humus soils and over mosses in open places on ± calciferous ground mainly in arctic and alpine regions. It has a wide circumpolar distribution in the Holarctic with rather few occurrences in the Southern Hemisphere: southernmost South America (Tierra del Fuego), southeastern Australia (New South Wales), and New Zealand (BREUSS 1993, 1995, 2001). The North American distribution ranges from Alaska and arctic Canada southward along the mountains to Colorado and northernmost New Mexico with scattered occurrences in the east (Map 1). There is a report from Ontario by MCMULLIN (2023). Its altitudinal range is from near the sea level in the arctic to mountain tundras in southern parts. For Greenland localities see BREUSS & HANSEN (1988).

Map 1. North American distribution of *Catapyrenium cinereum*.

Specimens examined:

CANADA: ALBERTA: Bertha Lake Trail, area surrounding Bertha Lake, Waterton Lakes National Park, 5.8.1963 G. W. SCOTTER 4756 (CANL). – Summit of Plateau Mt., 50 mi N of Coleman, alpine area, 8000 ft, 15.8.1969 C. M. WETMORE 18644 (MIN). – Rocky Mts.: Rock Lake area, c. 3 km E of Rock Lake, 53°28’ N, 118°13’ W, dry forested limestone cliff, 30.7.1995 O. BREUSS 11314 (LI); Cardinal River Divide, c. 20 km S of Cadomin, 52°53’ N, 117°14’ W, c. 2000 m, calcareous alpine tundra, 1.8.1995 O. BREUSS 11379, 11405, 11412 (LI). – Jasper National Park: Maligne Canyon, 52°52’ N, 118°01’ W, c. 1100 m, limestone, 2.8.1995 O. BREUSS 11482 (LI); Bald Hills at NW end of Maligne Lake, 52°44’ N, 117°40’ W, top of hill, calc. and acid rock, 2.8.1995 O. BREUSS 11513 (LI). – Banff National Park: Bow Range, near Upper Victoria Glacier above Lake Louise, alpine zone, 51°24’ N, 13.7.1950 H. A. IMSHAUG 6889 (MICH); Bow Range, Mt. Rundle near Banff, base of limestone cliffs, 7000 ft, 9.7.1950 H. A. IMSHAUG 6607 (MICH); N of Mosquito Creek Campground, 1820 m, 10.8.1979 R. ROSENTRETER 2216 (MIN). **BRITISH COLUMBIA:** Haines Triangle, 18 km N of confluence of Tatshenshini and Alsek Rivers, open heath, 59°44’ N, 137°45’ W, 1100–1400 m, 22.7.1992 T. GOWARD, W. B. SCHOFIELD & G. GODFREY 92-476 (UBC). – Taku River, Sinwa Mtn., limestone, open tundra, 58°52’ N, 133°20’ W, 1420–1520 m, 11.7.1982 T. GOWARD & O. CESKA 82-667A (UBC). – Coastal Mountain Range, N of Vancouver, Garibaldi Mts., Whistler Mt., 50° 07’ N, 122° 58’ W, 1800–2000 m, 22.8.1994 O. BREUSS 10575 (LI). – Wells Gray Provincial Park, Trophy Mtn. Recreation Area, 51° 46’ N, 119° 54’ W, 1900–2000 m, 24.8.1994 O. BREUSS 10668 (LI). **CANADIAN ARCTIC ARCHIPELAGO:** Southampton Island, near the camp at Coral Harbor and toward the granitic ridge, 16.8.1959 J. W. THOMSON (WIS). **NEW BRUNSWICK:** Grand Manan Island, Swallow Trail, 9.1898 without collector (FH). **NORTHWEST TERRITORIES:** Mackenzie District: on clay frost boil area near cabin N of Bloody Falls, 30.7.1962 J. W. THOMSON & J. A. LARSEN (WIS). – Central Mackenzie Mts., Keele River Region, above Keele River, 1600 ft, 64°13’ N, 127°32’ W, 27.6.1971 G. W. SCOTTER 14896 (WIS). **NUNAVUT:** District of Franklin, King Christian Island, 78° N, 102° W, on silty soils, 7.7.1979 L. C. BLISS 1 (CANL). – Keewatin District, south end of Dubawnt Lake, 62°43’ N, 101°30’ W, 1.8.1963 J. W. THOMSON, J. A. LARSEN & K. G. FOOTE 14321a (WIS). – Mackenzie District, Coppermine, 67°45’ N, 113°38’ W, 1.8.1962 J. W. THOMSON & J. A. LARSEN 12886 (WIS). **QUEBEC:** Riviere du Loup, 14.8.1880 C. G. PRINGLE (FH). **SASKATCHEWAN:** E of Hwy 167, N of Meridian Creek, limestone cliff, 300 m, 54°32’ N, 102°07’ W, 10.6.1984 J. D. JOHNSON 7593 (CANL). **YUKON TERRITORY:** Goatherd Mt., Kluane National Park, 4000 ft, 60°17’ N, 137°56’ W, 5.8.1972 G. W. SCOTTER 20279 (CANL).

U.S.A.: **ALASKA: Anchorage Co:** Chugach State Park, Flattop Mtn. just SE of urban Anchorage, timberline and alpine tundra at Blueberry Hill, 2500–2800 ft, 13.8.2013 O. BREUSS 32336 (LI). – **Bering Sea:** Pribilof Islands: St. Paul Island, 1880 T. H. BEAN (US). – **Chugach Co.:** Prince William Sound, College Fjord, sea level to 400 ft, 61°15’ N, 147°45’ W, 26.8.1957 L. & T. VIERECK (COLO). – **Denali Co.:** Mt. McKinley National Park, moist tundra, NW slope to summit of Mt. Eielson (Copper Mt.), 3500–5500 ft, 25.7.1956 W. A. WEBER & L. A. VIERECK (COLO). – **Juneau Co.:** Juneau, Mt. Roberts, path to Gold Ridge, c. 800 m, 7.8.2013 O. BREUSS 32265 (LI). – **Lake and Peninsula Co.:** Lake Clark National Park: slopes and flats above Turquoise Lake, alpine tundra with noncalc. boulders and outcrops, 990 m, 10.7.2014 R. ROSENTRETER 18525, 18526 (SRP); alpine tundra, saddle on ridge near headwaters of Johnson River, 770 m, 17.7.2014 MCCUNE 35507, NELSON, ROSENTRETER, TØNSBERG & WALTON (OSC). – **North Slope Co.:** western Brooks Range, De Long Mts., dwarf shrub tundra, SW of Copter Peak, watershed of Kugururok River, Noatak National Preserve, 729 m, 68°27.628’ N, 161°27.091’ W, 27.6.2004 R. ROSENTRETER 15782 (SRP, LI). – **Southeast Fairbanks:** near Fielding Lake Campsite, 1.5 mi off road from mile 200 of Richardson Hwy, 63°12’ N, 145°40’ W, 3100–3960 ft, on terrace slope, 4.8.1967 J. W. THOMSON & T. AHTI 18220 (WIS). **COLORADO: Boulder Co.:** Rocky Mts. National Park, Wild Basin, vicinity of Thunder Lake and NE slope of Tanima Peak, 10500–10900 ft, 11.–12.8.1961 R. A. ANDERSON 1683 (COLO, PRA-V); SW corner of the county, alpine tundra, Continental Divide, summit of Rollins Pass, 11800 ft, 22.7.1960 S. SHUSHAN & R. A. ANDERSON with *Involucropyrenium waltheri* (COLO). – **Clear Creek Co.:** Mt. Evans, vicinity of Summit Lake, 12700 ft, 1.8.1953 W. A. WEBER & E. DAHL (COLO); McClellan Ridge just above Santiago Mine, tundra slope, c. 12500 ft, 2.10.1954 W. A. WEBER (COLO); 4 mi W of Bergen Park, E of Squaw Pass, c. 27 mi W of Denver, 39°41’20’’ N, 105°25’45’’ W, 2685 m, mixed woods with *Pinus contorta* and *Populus tremuloides*, 20.8.1977 S. SHUSHAN 10230 (WIS). – **Costillo**/Huerfano/Las Animas Cos.: summit of Trinchera Peak, Sangre de Cristo Range, 13546 ft, 37°18’ N, 7.8.1952 H. A.

IMSHAUG 12181B (MICH). – **El Paso Co.:** Pikes Peak, Front Range, 38°50’ N, 4.8.1952 H. A. IMSHAUG 11946 (MICH); summit of Pikes Peak, 14100 ft, 1.8.1955 S. Shushan (COLO); Pikes Peak just S of Teller Co., 38°50’ N, 105°02’ W, 4150 m, 10.8.1984 T. H. NASH 25801 (ASU). – **Garfield Co.:** Flat Tops Wilderness, alpine area below cliffs leading to Derby Peak, c. 100 m W of Stillwater Reservoir, Hooper Lake Trail, 40°00’ N, 107°07’15’’ W, c. 3600 m, 20.6.1992 T. H. NASH 31529 (ASU); Flat Tops Wilderness, south end of Blair Mtn., overlooking Elk Lakes, 39°46’ N, 107°25’ W, c. 3415 m, 24.6.1992 T. H. NASH 31889 (ASU). – **Grand Co.:** Rocky Mts. National Park: Never Summer Mts., Red Mtn., Hells Hip Pocket, talus and subalpine forest, 10400–11000 ft, 9.8.1962 R. A. ANDERSON 3220 (COLO); Never Summer Mts., Mt. Richthofen, 11200–12000 ft, 16.8.1962 R. A. ANDERSON 3395 (COLO). – **Gunnison Co.:** Virginia Basin, Elk Mts., 12000 ft, 5.7.1952 H. A. IMSHAUG 10627 (MICH); summit ridge of White Rock Mt., Elk Mts., 38°59’ N, 13000 ft, 13.7.1952 H. A. IMSHAUG 11023 (ASU, MICH); ibid. 12800 ft, 13.7.1952 H. A. IMSHAUG 10982 (MICH); trail from Gothic through Virginia Basin to summit of Virginia Ridge, 9600–11000 ft, 30.6.1955 W. A. WEBER & LINNA WEBER (COLO). – Gunnison/Chaffee Cos.: Sawatch Mts., summit ridge above Cottonwood Pass, 12700 ft, 38°51’ N, 31.7.1952 H. A. IMSHAUG 11645 (MICH); Sawatch Mts., Lake Pass, 12225 ft, 39°00’ N, 1.8. 1952 H. A. IMSHAUG 11817 (MICH). – Gunnison/Pitkin Cos.: Elk Mts., summit of Mt. Belleview, 12500 ft, 39°01’ N, 4.7.1952 H. A. IMSHAUG 10531 (MICH); East Maroon Pass, Elk Mts., 11850 ft, 39°01’ N, 7.7.1952 H. A. IMSHAUG 10667, 10692 (MICH). – **Lake**/Pitkin Cos.: Sawatch Mts., Independence Pass, 39°07’ N, 12100 ft, H. A. IMSHAUG 11580 (ASU, MICH). – **Larimer Co.:** Rocky Mts. National Park: Front Range, Trail Ridge Road, 12000 ft, 40°24’ N, 16.7.1952 H. A. IMSHAUG 11247A (MICH); Trail Ridge, in saddle E of Toll Memorial, 11920–12000 ft, 29.6.1963 R. A. ANDERSON 3952 (COLO); Trail Ridge Road 0.4 mi E of Rock Cut, alpine tundra area, 12000–12300 ft. 3.6.1967 C. M. WETMORE 15853 (MIN); Trail Ridge Road at Toll Memorial (NW of Sundance Mt.), in alpine tundra N of memorial, 3700 m, 4.8.1984 C. M. WETMORE 53505 (MIN); Fall River Canyon, 1 mi W of Endovalley Campground, near Chasm Falls along Fall River and N-facing talus, 8900–9400 ft, 5.6.1962 R. A. ANDERSON 1997 with *Catapyrenium daedaleum* (COLO); NE slope of Flattop Mtn., 11600–12000 ft, 19.7.1962 R. A. ANDERSON 2776 (COLO); Mummy Range, Mt. Chiquita, alpine tundra, 11600–12400 ft, 25.7.1962 R. A. ANDERSON 2919 with *Catapyrenium daedaleum* (COLO); Mummy Range, NW slope of Mt. Chapin, 11800–12400 ft, 18.8.1962 R. A. ANDERSON 3511 (COLO); Longs Peak, 11800 ft, wet ground, N-exp., 15.9.1989 W. KIENER 9155 (COLO); alpine sod, off the Ute trail, 12355 ft., 8.8.2014 R. ROSENTRETER (SRP). - Larimer Co., Grand Co. line, Continental Divide, 1–2 mi NW of Mt. Ida, 11500–12150 ft, 6.8.1962 R. A. ANDERSON 3107 with *Catapyrenium daedaleum*, 3113, 3112 (COLO). – **Ouray Co.:** Blue Lake Pass, San Juan Mts., c. 12500 ft, 38°00’ N, 21.8.1954 H. A. IMSHAUG 16993 (MICH). – **Park**/Summit Cos.: east end of Hoosier Ridge, c. 11 mi N of Fairplay, tundra, c. 13000 ft, 8.7.1956 S. SHUSHAN & H. A. IMSHAUG (COLO, S). – **Rio Blanco Co.:** White River National Forest, c. 2 km along trail from South Fork Campground to Spring Cave, 107°29’30’’ W, 39°51’ N, pinyon pine and oak woodland, c. 2360 m, 21.6.1992 T. H. NASH 31784 with *Placidium lachneum* (ASU). – **Routt Co.:** timberline, south ridge of Mt. Zirkel, Park Range, E of Slavonia above Gold Creek, 11300 ft, 28.7.1956 S. SHUSHAN (COLO). – **San Miguel**/Dolores Cos.: summit of Black Face, San Miguel Mts., 12100 ft, 37°50’ N, 24.8.1954 H. A. IMSHAUG 17136 (MICH). – **Summit Co.:** N-facing slope of North Star Mtn. S of Quandary Peak, near Blue Lake Reservoir, 11750–12750 ft, 8.7.1969 R. A. ANDERSON 7069 (COLO); Blue Lakes, head of Monte Cristo Creek, 11800 ft, steep irrigated talus slope just above the dam, on north-facing slope of North Star Mtn., alpine, 3.9.1969 W. A. WEBER, O. ALMBORN & R. ANDERSON (COLO). – Summit/Park Cos.: ridge NE of Hoosier Pass, Park Range, 13000 ft, 39°22’ N, 8.7.1956 H. A. IMSHAUG 18958 (MICH). **IDAHO: Clark Co.:** Skull Canyon, SE of Lone Pine, on limestone cliffs and calc. soil, Mountain mahogany, *Cercocarpus ledifolius* and black sagebrush, *Artemisia nova* habitat, 44°09’ N, 112°54’ W, 1800 m, 31.7.1999 R. ROSENTRETER 13907, H. MAYRHOFER & C. DAVIS (SRP, LI). – **Custer Co.:** bench below Leatherman Pass, near Pass Lake, Lost River Range, 10000 ft, 44°05’ N, 29.7.1954 H. A. IMSHAUG 16573, 16576 (MICH). – **Lemhi Co.:** Lemhi Mts., alpine ridge line, windswept dry open ridge top, alpine habitat, 44°23’ N, 113°15’ W, c. 3050 m, on calc. soil, 29.7.1999 R. ROSENTRETER 13869, H. MAYRHOFER & C. DAVIS (SRP, LI). **MICHIGAN: Chippewa Co.:** Drummond Island, scattered *Thuja* with exposed limestone pavement and low juniper, E side of Big Shoal Cove, 45°57’ N, 83°37’ W, 2.10.1976 H. A. IMSHAUG 59944, 59946B, 59952 (MICH). **MONTANA: Beaverhead Co.:** Pioneer Mts., subalpine limestone ridge between Sheep Mtn. and Black Lion Mtn., at head of Cannivan Gulch, broken krummholz *Pinus albicaulis*, 2680 m, 45°39’ N,

112°58’ W, 7.1993 B. McCune 20652 (OSC, with *Placidium lacinulatum*). – **Flathead Co.:** crest of Swan Range 4 km N of Swan Peak, 2340 m, 7.8.1978 B. McCune 9792 (OSC). – Flathead/Glacier Cos.: Rocky Mts., Garden Wall above Grinnell Glacier, 8000 ft, 8.8.1950 H. A. Imshaug 8840 (MICH); Rocky Mts., Glacier National Park, Reynolds Mt., 48°41’ N, 7700 ft, 1.8.1950 H. A. Imshaug 7780 (MICH); Glacier National Park, summit of Swiftcurrent Mt., 8300 ft, 48°47’N, 2.8.1950 H. A. Imshaug 7852, 7853 (MICH). – **Glacier Co.:** Rocky Mts., Glacier National Park: Siyeh Pass, 8200 ft, 17.8.1950 H. A. Imshaug 8993 (MICH); Lunch Creek, north side of Going-to-the-Sun Road, E of Logan Pass, 2100 m, 23.8.1984 A. DeBolt & P. Lesica 503 (WIS); False summit just E of Firebrand Pass, 48°24’ N, 113°21’ W, 1925 m, 7.1987 B. McCune 16861 (OSC); near lip of Lunch Creek cirque, 48°42’ N, 113°42’ W, 2165 m, 8.1989 B. McCune 17846 (LI, with *Placidium lachneum* var. *oleosum*); on prairie flats across hwy from Saint Mary Visitor Center, 1385 m, 48°44’ N, 113°26’ W, 7.1991 B. McCune 19254 (OSC). – **Lake Co.:** near Riddell Lake, N of Missoula, 7100 ft, alpine, 5.8.1982 R. Rosentreter 2807 (SRP, LI). – **Ravalli Co.:** Bitterroot Range, summit of Sweeney Peak, 2780 m, 46°39’ N, 114°13’ W, 4.7.1981 B. McCune 10990 (OSC). **Nevada: White Pine Co.:** 39°00’30’’ N, 114°03’30’’ W, trail to Terrace Lake, Snake Range N of Wheeler Peak, Humboldt National Forest, 3140 m, 7.1984 B. D. Ryan 11422 (ASU). **New Mexico: Taos Co.:** summit of Wheeler Peak, Sangre de Cristo Range, 13151 ft, 36°33’ N, 9.8.1952 H. A. Imshaug 12249, 12280 (MICH). **Oregon: Lane Co.:** Cascade Range, on ridge at head of Lookout Creek drainage, open area with scattered *Abies* and *Pseudotsuga* near Forest Route 1506 H. J. Andrews Experimental Forest, 44°12’ N, 122°07’ W, 1341 m, 10.1998 B. McCune 24273 (OSC). – **Wallowa Co.:** just E of Ice Lake, sparse *Pinus albicaulis*/*Abies lasiocarpa* forest, wind-swept grassy openings with rock outcrops and boulders, 2435 m, 45.228° N, 117.269° W, 7.–9.9.2005 R. Rosentreter 16074 with *Catapyrenium daedaleum* (SRP, LI); Wallowa Mts., Eagle Cap Wilderness, sparse *Pinus* forest, grassy openings, rock outcrops and boulders (limestone, marble, granite), near camp at Ice Lake, 2435 m, 45.228° N, 117.269° W, 7.–9.9.2005 B. McCune 27928 (OSC). **South Dakota: Lawrence Co.:** vicinity of Timon Campground, 4 mi WSW of Savoy, 11 mi W of Lead, in Limestone Plateau Region, near Little Spearfish Creek, 5600–5900 ft, 4.6.1960 R. A. Anderson (COLO, MICH). – **Meade Co.:** Black Hills, Stagebarn Canyon 1.5 mi W of US14 (11 mi NW of Rapid City), in shady valley, 3800 ft, 30.6.1961 C. M. Wetmore 10429 (BM, CANL, DUKE, MICH). – **Pennington Co.:** Black Hills, Ditch Creek Campground (18 mi NW of Custer), on west facing hillside, 6300 ft, 18.7.1960 C. M. Wetmore 7642 (MICH, US, WIS); Black Hills, on road to Rhodes Ranch (21 mi NE of Newcastle, Wyoming), 6500 ft, on steep W facing hillside, 20.7.1960 C. M. Wetmore 7874 (MICH). **Utah: Duchesne**/Summit Cos.: Uinta Mts., summit of Bald Mtn., 40°42’ N, 11.8.1954 H. A. Imshaug 16739 (MICH). – **Salt Lake**/Utah Cos.: Wasatch Mts., summit of Mt. Baldy, 40°34’ N, 11049 ft, 13.8.1954 H. A. Imshaug 16822 (MICH). – **San Juan Co.:** La Sal Mts., summit of Mt. Mellenthin, 12890 ft, 38°28’ N, 18.8.1954 H. A. Imshaug 16890, 16920 (MICH). **Vermont: Chittenden Co.:** Mt. Mansfield, Smuggler’s Notch, 14.10.1880 C. G. Pringle 640 (FH, UPS, US); Mt. Mansfield, C. G. Pringle (FH). **Washington: Clallam Co.:** Moose Lake Trail, Olympic Mts., 6200–6500 ft, 47°55’ N, 9.9.1954 H. A. Imshaug 17580 (MICH); Olympic National Park, Hurricane Ridge around Hurricane Hill, alpine meadow and rocky ridge, 5750 ft, 20.8.1969 C. M. Wetmore 19002 (MIN). – **Skagit Co.:** 48°47’ N, 121°14’30’’ W, Glacier Peak Wilderness, Plot 5 (5000 ft), off Green Mountain Trail, c. 1500 m, 8.10.1993 B. Ryan 30409b (ASU). **Wyoming: Albany Co.:** Medicine Bow Mts., summit of Medicine Bow Peak, 12000 ft, 41°22’ N, 4.7.1956 H. A. Imshaug 18868, 18916 (MICH). – **Crook Co.:** Black Hills, along Beaver Creek (10 mi SW of Sundance), on N facing slope in open pines, 4800 ft, 14.8.1961 C. M. Wetmore 11361 (MICH, MIN). – **Johnson**/Big Horn Cos.: Leaf Mt. near Powder River Pass, Big Horn Mts., 11000 ft., 44°12’ N, 18.7.1956 H. A. Imshaug (LI, MICH). – **Park Co.:** Beartooth Plateau, Cooke City to Red Lodge Hwy, dry rocky tundra of East Summit at head of Wyoming Creek, 3250 m, 21.8.1973 W. A. Weber (COLO); alpine tundra, calcareous ridge N of Clay Butte, near Beartooth Plateau, 3075 m, 44°57’ N, 109°38’ W, 7.1992 B. McCune 19787 (OSC). – **Sheridan Co.:** Big Horn Mts., above Owen Creek Campground, SW facing slope with pines, spruce and some fir, 8500 ft, 1.8.1965 C. M. Wetmore 12953 (COLO, MIN). – **Teton Co.:** Yellowstone National Park, near Divide trailhead just W of Craig Pass, along stream and N-facing slope with engelmann spruce, 8045 ft, 44°25’59’’ N, 110°43’56’’ W, 9.8.1998 C. M. Wetmore 81992 (MIN). – **Weston Co.:** Black Hills, along U.S.85 at Soldier Creek (20 mi NNW of Newcastle), on north facing slope, 5900 ft., 12.8.1961 C. M. Wetmore 11302 (LD, MICH, UPS).

Catapyrenium daedaleum **(KREMP.) B. STEIN**, in COHN, Kryptog.-Flora von Schlesien 2, 2 (1879): 312.

Endocarpon daedaleum KREMP., Flora 38 (1855): 66. For further generic combinations see BREUSS (1990: 59). – Type: [Germany,] Steinthal und Vorderberg zwischen Hochkalter und Kammerlinghorn, c. 5800–6000 ft, 1854 RAUCHENBERGER (M – lectotype).

Placidium cartilagineum β *terrestre* ARNOLD, Flora 41 (1858): 532. – Type: [Germany,] auf steinigem Boden bei der Espershöhle, Geilenreuth in Oberfranken, hb. KREMPELHUBER no. 479 (M – lectotype).

Lectotypes selected by BREUSS (1990): 59.

T h a l l u s : crowded-squamulose, often almost rosette-like and up to several centimeters across, more rarely consisting of dispersed squamules. Individual squamules 2–5 mm wide, roundish or weakly lobed or shallowly incised, thickish, fully adnate to the substratum or with slightly elevated margins, contiguous or weakly overlapping (Fig. 8), in the thallus center often aggregated crust-like, the outer ones slightly elongate and widening at the apices, often broadly spoon-shaped (Fig. 9). Upper side dull, minutely roughened, pale to medium brown, occasionally olivaceous, bare or slightly grayish pruinose, but bare towards the tips and the outermost squamules of rosettes always epruinose.

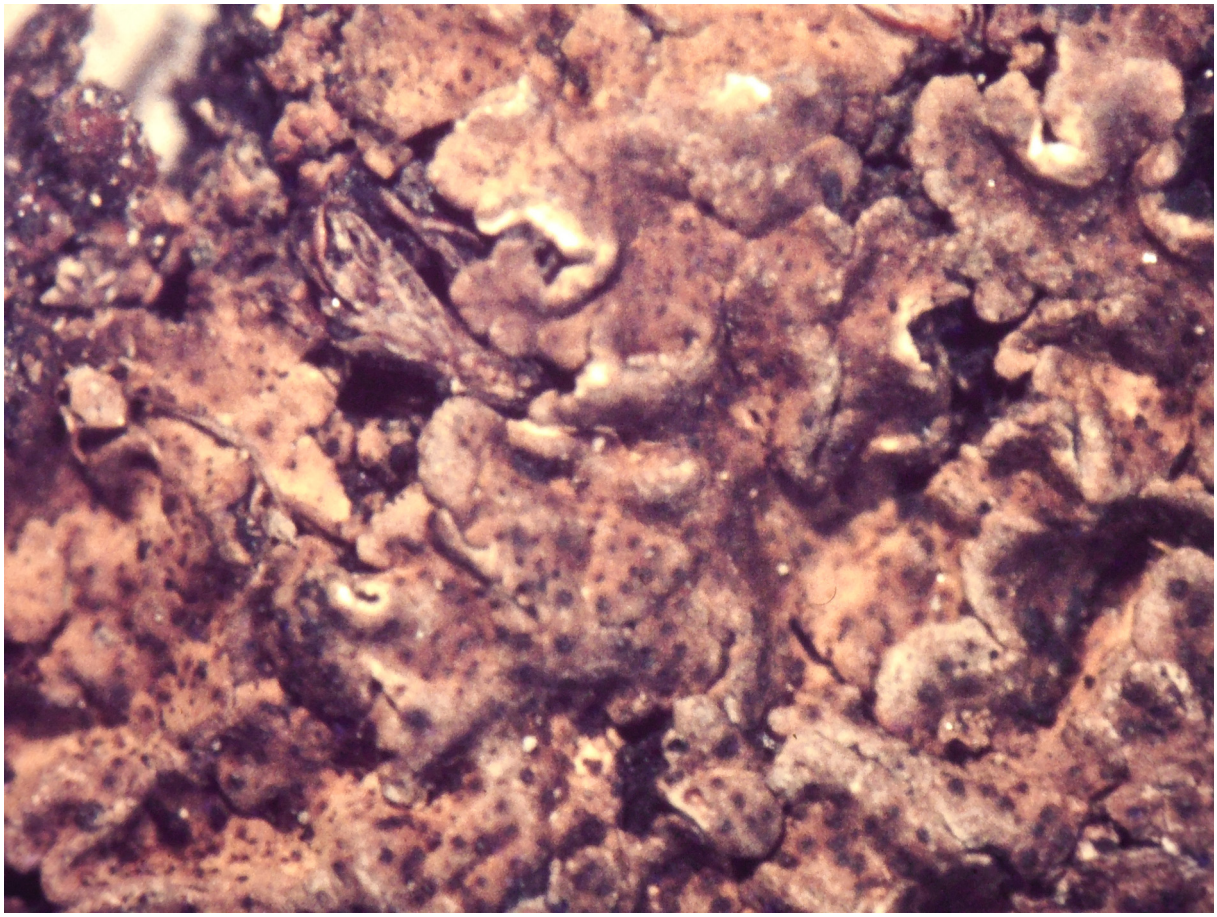


Fig. 8. *Catapyrenium daedaleum*: typical thallus. Width of the photograph 9 mm.

Fig. 9. *Catapyrenium daedaleum*: marginal lobes. Width of the photograph 6.5 mm.

A n a t o m y : Thallus 200–400 µm thick. Upper cortex 10–30 µm; epinecral layer very thin or lacking. Algal layer about 50–150 µm high. Alga-free medullary tissue mostly rather thick (– c. 150 µm), of intricated hyphae with varying amounts of interhyphal spaces and globular cells c. 6–8 in diam. Lower cortex lacking, the medulla developing gradually into an intricate web of brown rhizohyphae 3–4(–4.5) µm in diam.

P e r i t h e c i a : 200–250(–300) µm broad; excipulum c. 15–20 µm thick, colorless or slightly brownish, ostiolum dark brown.

P e r i p h y s e s : 15–25 µm long and 2–3 µm thick, mostly simple, terminal cell not or slightly thickened.

A s c i : broadly clavate, about 75–85 × 17–21 µm.

A s c o s p o r e s : mostly oblong-ovoid to lacriform, rarer regularly ellipsoidal or subfusiform, (15–)17–22 × (5–)6–8(–9) µm.

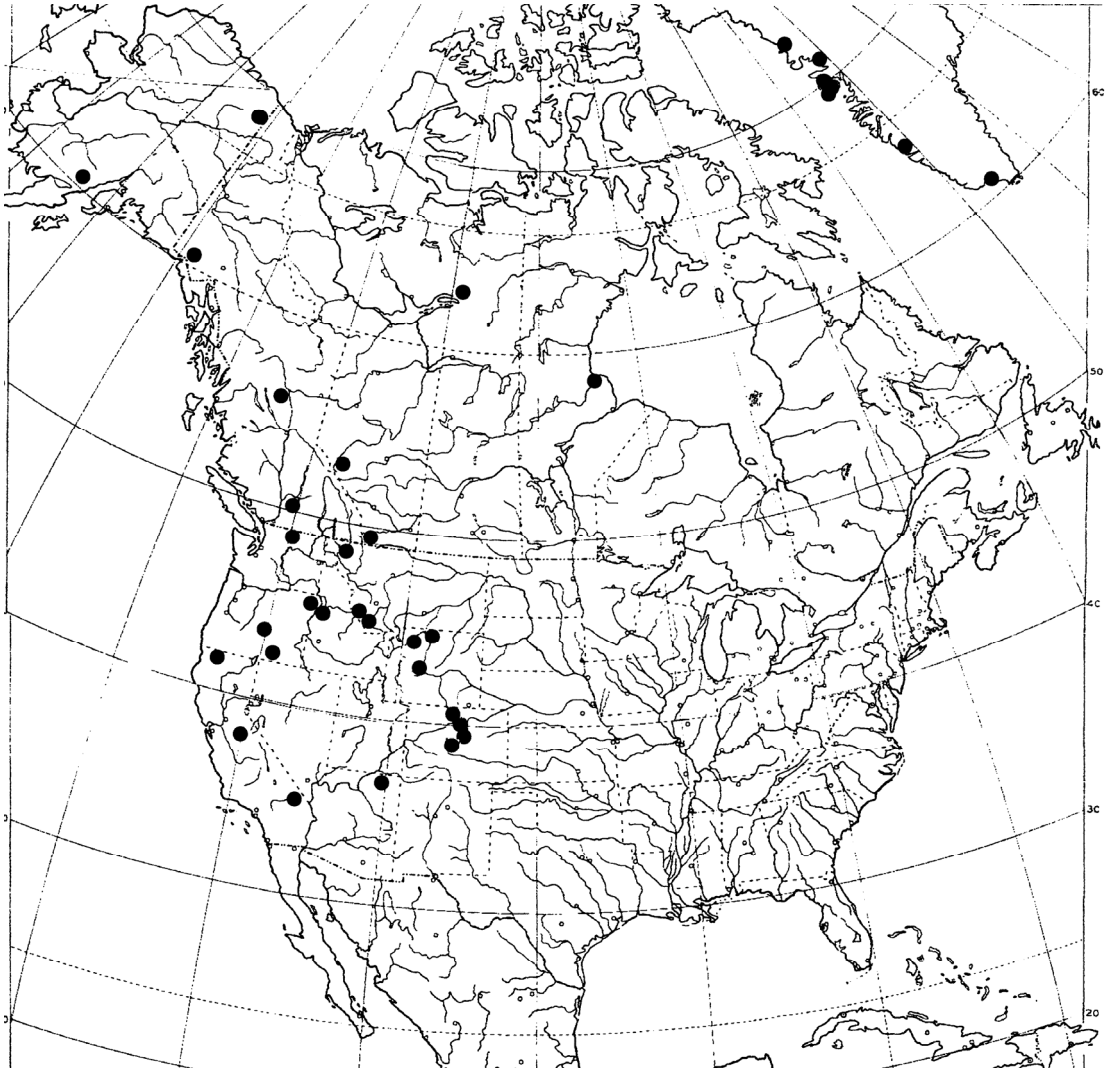
Icon.: BREUSS 1990: 169, DIEDERICH & BRÜCKER 2022: 165, MOBERG & al. 2017: 61, STENROOS & al. 2016: 129, THOMSON 1989: 191, VAN HALUWYN & al. 2012: 91. Anatomy: MCCUNE 2017b: 170.

Characterization: *Catapyrenium daedaleum* is characterized by irregularly rounded, thickish squamules lacking a lower cortex, with medullary hyphae merging into the dark hypothallus. In herbarium material the species was often found misidentified as *C. cinereum*, but this latter species has thinner, finely notched-incised and dark-rimmed

squamules with a paraplectenchymatous lower cortex. Specimens of *C. daedaleum* with a densely cellular medulla may appear to have a lower cortex as in *C. cinereum*, but the cortical cells are less closely packed and roundish rather than polygonal and do not form a distinctly delimited cortical layer. And contrary to *C. cinereum*, the exciples of *C. daedaleum* are not entirely dark even in mature stages.

There may be difficulties in the distinction from closely related *Catapyrenium psoromoides*, which is mainly corticolous but may rarely occur on other substrata. It primarily differs in size and shape of its spores, in the form of lobation and in the development of pruina (see under this species).

Ecology and distribution: *Catapyrenium daedaleum* grows on earth, humus and mosses over calcareous ground. It is mainly arctic-alpine with a wide circumpolar distribution. It is bipolar with Southern Hemisphere occurrences in the Andean cordillera southwards to Tierra del Fuego and on several Antarctic islands (BREUSS 1995, ØVSTEDAL & LEWIS SMITH 2001). In North America its distribution ranges from the Arctic southward along the mountain chains to California and Arizona. It has roughly the same distribution as *Catapyrenium cinereum* but seems to be rarer and there are no collections from the east (Map 2). For records from Greenland see BREUSS & HANSEN (1988).



Map 2. North American distribution of *Catapyrenium daedaleum*.

Specimens examined:

CANADA: ALBERTA: Waterton Lakes National Park, Bertha Lake Trail, base of trail to International Boundary turnoff, 5.8.1963 G. W. SCOTTER 4699 (WIS). – Rocky Mts., Cardinal River Divide, c. 20 km S of Cadomin, 52°53’ N, 117°14’ W, c. 2000 m, calcareous alpine tundra, 1.8.1995 O. BREUSS 11429 (LI). – *Picea-Abies* forest on calcareous bedrock above Whitehorse Creek, c. 4 km S of Cadomin on Hwy 40, 1600 m, 52°58’ N, 117°20’ W, 8.1995 B. MCCUNE 22515 (OSC). **BRITISH COLUMBIA:** Hozameen Ridge, 1900 m, Manning Park, 49°01’ N, 121°00’ W, Engelmann Spruce and Subalpine Fir Zone, 13.7.1985 T. GOWARD (CANL). – Northern Rocky Mts., Peace River Basin, Robb Lake, 56°54’ N, 123°48’ W, N-facing slope on south side of lake, 2.–3.8.1977 I. M. BRODO & P. HAMILTON 22208 (CANL). – Above Slide Lake, Blue River, OHA, 5600 ft, 15.10.1979 T. GOWARD & S. GOWAN 79-1427 (UBC). **MANITOBA:** W of Hudson Bay, Churchill, 10.8.1950 J. W. THOMSON 3602 (CANL, WIS). **NORTHWEST TERRITORIES:** Artillery Lake, on top of the east slope of Rat Lodge, west side of lake, 63°15’ N, 106° W, 17.7.1962 J. W. THOMSON & J. A. LARSEN 12315 (WIS). **YUKON TERRITORY:** Kluane Lake, 61°03’ N, 138°30’ W, mile 1064 Alaska Hwy, Sheep Mtn. above campground, 5000 ft, 22.7.1967 J. W. THOMSON & T. AHTI 21758 (WIS).

U.S.A.: ALASKA: Lake and Peninsula Co.: Lake Clark National Park, trail to Tanalian Falls from Port Alsworth, 160 m, 9.7.2014 R. ROSENTRETER 18453 (SRP); Lake Clark National Park, Marble Cliffs and talus by shore of Lake Clark c. 30 km NE of Port Alsworth, W of Hatchet Point, 80 m, 14.7.2014 R. ROSENTRETER 18788 (SRP). – **North Slope Co.:** on gravel pavement of airstrip near Mancha Creek and Firth River, 68°40’ N, 141° W, 8.8.1958 A. J. SHARP (WIS). **ARIZONA: Navajo Co.:** north side of Black Mesa across from Navajo National Monument, 2140 m, 36°32’30’’ N, 110°30’30’’ W, 18.7.1983 T. H. NASH 21095 (ASU, LI). **CALIFORNIA: Inyo Co.:** 37°26’ N, 44°30’ W, Eastern Brook Lakes Watershed, Sierra Nevada Mts., along Creek Rd., 10600 ft, E of largest lake, 6.1985 B. D. RYAN 12648 (ASU). – **Mariposa Co.:** Josemite Valley, 1867 H. N. BOLANDER (FH). – **Siskiyou Co.:** The Lieutenants near Private Lake, Siskiyou Mts., 1790 m, 41°52.701’ N, 123°36.245’ W, rock crevice, rocky ridgetop, 6.2003 B. MCCUNE 27010 (OSC). **COLORADO: Boulder Co.:** Gregory Canyon, between Flagstaff Mtn. and Green Mtn., c. 4 mi SW of Boulder, c. 7000 ft, 15.5.1956 W. A. WEBER 9592 (COLO, WIS). – **Jefferson Co.:** Bull Gulch, outer foothills of Front Range between Plainview and Colorado Springs, c. 7500 ft, 9.9.1962 W. A. WEBER & R. A. ANDERSON 36343 (COLO). – **Larimer Co.:** Grand Co. line, Continental Divide, 1–2 mi NW of Mt. Ida, 11500–12150 ft, 6.8.1962 R. A. ANDERSON 3107 with *Catapyrenium cinereum* (COLO). - Rocky Mts. National Park: South Lateral Moraine, open Ponderosa forest, 8100–8500 ft, 17.7.1962 R. A. ANDERSON 2646 (COLO); Lumpy Ridge, near the Twin Owls on trail to Gem Lake, 1.5 mi N of Lake Estes, 8100–8500 ft, 27.–28.8.1962 R. A. ANDERSON 3636 (COLO); Fall River Canyon, 1 mi W of Endovalley Campground, near Chasm Falls along Fall River and N-facing talus, 8900–9400 ft, 5.6.1962 R. A. ANDERSON 1997 (COLO with *Catapyrenium cinereum*, WIS); Battle Mtn., NE of Longs Peak, 11600–12000 ft, 18.7.1962 R. A. ANDERSON 2666 (COLO); Mummy Range, Mt. Chiquita, alpine tundra, 11600–12400 ft, 25.7.1962 R. A. ANDERSON 2919 with *Catapyrenium cinereum* (COLO). – **Park Co.:** Wheeler Lake, head of Platte Gulch, N of Mt. Lincoln, 12300 ft, tundra, 3.7.1954 W. A. WEBER & S. SHUSHAN (COLO). **IDAHO: Idaho Co.:** Seven Devils Mts., ridgetop above Seven Devils Lake, with scattered *Pinus albicaulis*, 2630 m, 45°26’ N, 116°31’ W, 8.1990 B. MCCUNE 18591 (OSC). **MONTANA: Beaverhead Co.:** Badger Pass on Montana Route 278, 2030 m, mixed *Artemisia tridentata*-grassland, 6.8.1981 B. MCCUNE 11664 (WIS, OSC); Pioneer Mts., Comet Mtn., c. 3100 m, near summit, granitic alpine area, 45°27’ N, 113°03’ W, 7.1993 B. MCCUNE 20982 (OSC). – **Lincoln Co.:** Murphy Lake, 48°44’15’’ N, 114°51’20’’ W, on moss-covered bare mineral soil along path to wildlife viewing platform, 915 m, 4.7.2001 T. SPRIBILLE 1038 (hb. Spribille). – **Ravalli Co.:** Bitterroot Range, summit of El Capitan, 46°01’ N, 114°21’ W, 3043 m, 18.8.1983 B. MCCUNE 13106 (US, WIS). **OREGON**: **Lake Co.:** N of Christmas Valley, Derrick’s Cave area, old lavabed with *Pinus ponderosa* and *Juniperus occidentalis*, near 43°31’13.614’’ N, 120°52’0.390’’ W, c. 5000 ft, 15.5.2010 D. STONE 7929.30 (hb. Stone); E of Adel and N of Hwy 140, High Lakes ACEC, high desert with sparse *Juniper occidentalis*, heavily grazed bunchgrass between *Artemisia* shrubs, 42.178° N, 119°694° W, 5940 ft, on soil between rocks along low cliffs, 7.6.2013 D. STONE 8849.9 (hb. Stone). – **Wallowa Co.:** just E of Ice Lake, sparse *Pinus albicaulis* and *Abies lasiocarpa* forest, wind-swept grassy openings with rock outcrops and boulders, 2435 m, 45.228° N, 117.269° W, 7.–9.9.2005 R. ROSENTRETER 16074 (SRP, LI). **WASHINGTON: Okanogan Co.:** Cascade Mts, Okanogan Range, summit of Windy Peak, 8345 ft, 48°55’ N, 17.8.1955 H. A. IMSHAUG 18690B (LI, MICH). **WYOMING: Big Horn Co.:** Big

Horn Mts., Bald Mtn., 3100 m, 44°47' N, 107°50' W, 2.8.1983 V. WIRTH, J. ELIX, T. NASH & R. WIRTH 21387 (STU-Wirth). – **Fremont Co.:** Wind River Range, Shoshone National Forest, Stough Pass, c. 3150 m, 42°41' N, 109°01' W, 24.7.1983 V. & R. WIRTH (STU-Wirth). – **Park Co.:** Beartooth Plateau, Cooke City to Red Lodge Hwy, dry rocky tundra of East Summit at head of Wyoming Creek, 3250 m, 21.8.1973 W. A. WEBER 57617 (COLO).

***Catapyrenium psoromoides* (BORR.) R. SANT.**, Lichenologist 12/1 (1980): 106.

Verrucaria psoromoides BORR. in HOOKER & SOWERBY, Engl. Bot., Suppl. 1 (1831): 2612. – Type: (Great Britain), on elm at Hurstpierpoint and on ash at Beeding, Sussex, BORRER (K – holotype).

Dermatocarpon daedaleum var. *corticola* H. MAGN., Bot. Not. 108 (1955): 297. – Type: [Sweden,] Västergötland, par. Skallsjö, Drängsered, at base of *Fraxinus*, 17.9.1933 A. H. MAGNUSSON no. 14123 (UPS – holotype).

Placidium cartilagineum α *muscicolum* ARNOLD, Flora 41 (1858): 532. – Type: [Germany,] auf Dolomitfelsen gegenüber der Stämpfer Mühle in Oberfranken, 6/55 ARNOLD no. 182 (M – lectotype, selected by BREUSS 1990: 66).

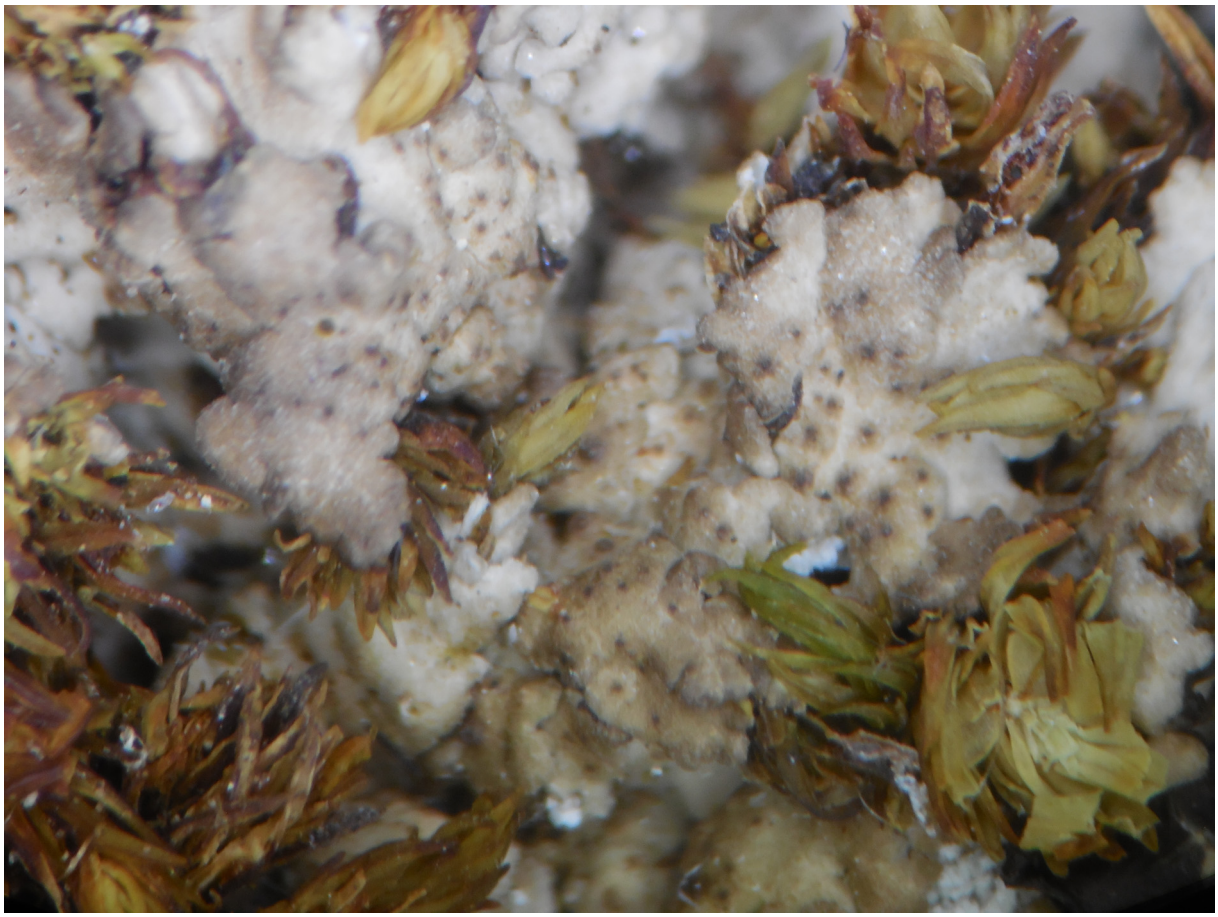


Fig. 10. *Catapyrenium psoromoides*, thallus. Width of the photograph 6 mm.

T h a l l u s : composed of irregularly arranged, slightly overlapping to imbricate squamules, ± rosulate if well developed. Individual squamules c. 1.5–3 mm wide, roundish or weakly divided, loosely to rather firmly attached. Upper surface grayish or greenish brown, dull. Marginal squamules somewhat elongate, often with spotted pruina on distal parts, central squamules usually epruinose. Lower side filamentous-felted, dark centrally, whitish marginally.

A n a t o m y : Squamules (150–)200–300(–350) µm thick. Upper cortex 10–30 µm, amorphous layer 5–20 µm. Algal layer about 50–80 µm high. Alga-free medullary tissue c. 50–100 µm high, of rather loose hyphae with many globular cells 6–8 µm in diameter and distinct interhyphal spaces. Lower cortex lacking, with medullary hyphae merging into the blackish brown rhizohyphal web. Rhizohyphae 3–4 µm in diam., colorless only along margins, darkening inwards.

P e r i t h e c i a : 150–200 µm broad. Excipulum c. 20 µm thick, colorless or slightly brownish yellow except for the dark apex, more rarely darkening throughout.

P e r i p h y s e s : 20–30 µm long and 2.5–3.5 µm thick, usually simple, terminal cell often somewhat swollen (–5 µm).

A s c i : clavate, about 55–65 × 13–16 µm.

A s c o s p o r e s : elongate ellipsoidal or subfusiform, occassionally oblong-ovoid, (12–)13–17(–19) × (5–)5.5–7(–7.5) µm, partly pseudoseptate (with plasma-bridges dissolving in K).

Icon.: BRATLI & al. 2010: 10, HARADA 1993: 126, MCCUNE 2017a: 143, MOBERG & al. 2017: 61, PRIETO & al. 2010a: 640, STENROOS & al. 2016: 130, SWINSCOW & KROG 1988: 34. Anatomy: HARADA 1993: 128, PRIETO & al. 2010a: 641.

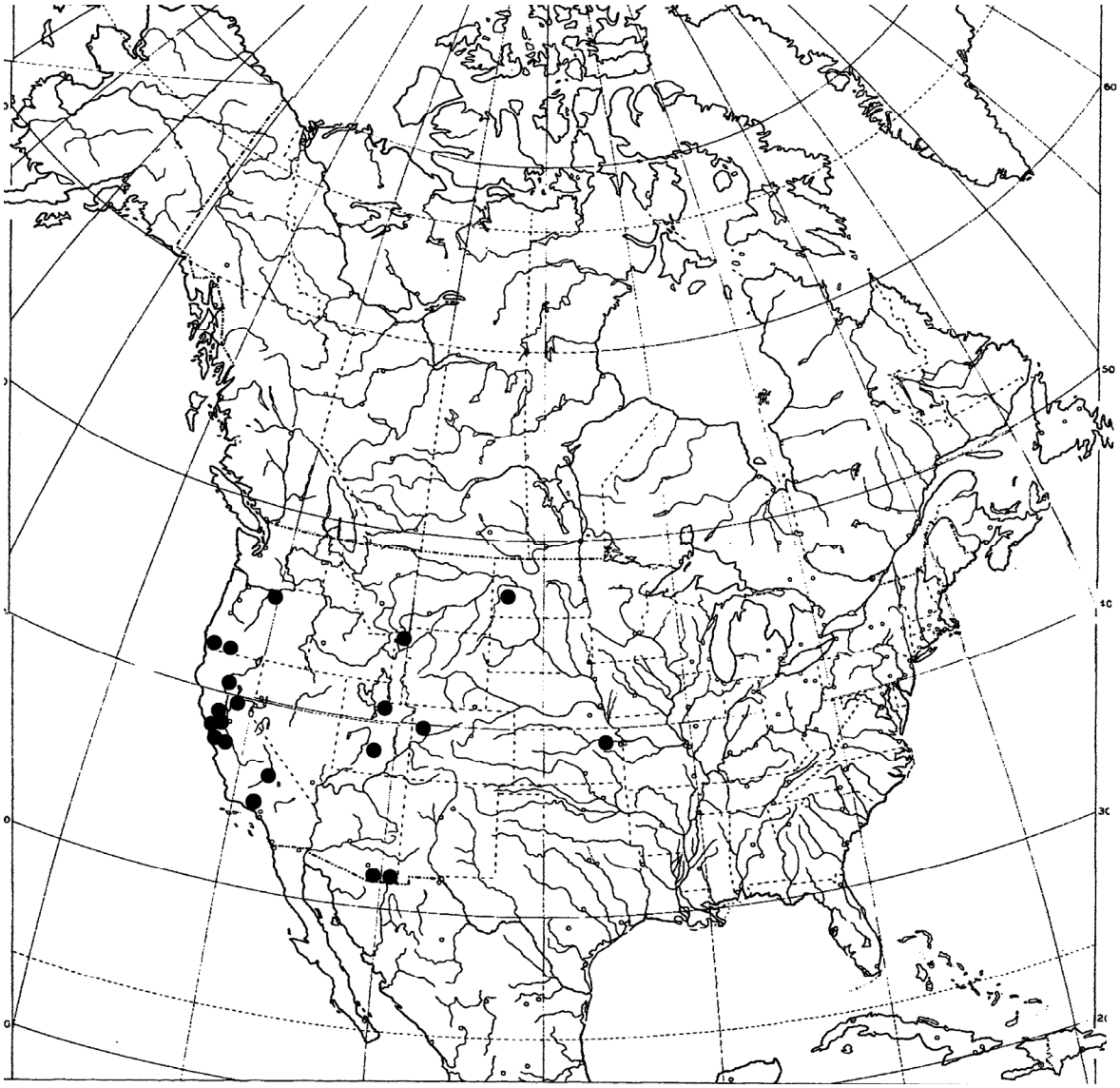
Characterization: *Catapyrenium psoromoides* is closely allied to *C. daedaleum*, from which it differs in several microscopical features. The asci are significantly smaller (55–65 × 13–16 µm vs. 75–85 × 17–20 µm in *C. daedaleum*), the ascospores are also smaller (mostly less than 18 µm long vs. 17-22 µm in *C. daedaleum*) and of different shape: they are mainly regularly ellipsoidal to subfusiform vs. oblong-clavate (i.e. with one end clearly narrower than the other) in *C. daedaleum* (see BREUSS 1990, figs. 2 & 3). The terminal cells of the periphyses are often swollen up to 5 µm wide (in *C. daedaleum* 2–3 µm). Morphologically, *Catapyrenium psoromoides* differs from *C. daedaleum* in having thinner and more divided thalli with narrower and not spoon-shaped marginal squamules/lobes (Fig. 10). A useful distinguishing character is the pruina in defined patches mostly on distal parts of lobes in *Catapyrenium psoromoides*, whereas *C. daedaleum* – if not bare at all – has a thin, diffuse, not fleck-like, pruina in central parts of the thallus. Specimens with very small squamules occurring on earth may be confused with *C. squamellum*, which differs in having narrower ascospores.

Ecology and distribution: *Catapyrenium psoromoides* is mainly corticol and one of the very few bark-inhabiting catapyrenioid lichens, but it also occurs on mossy boulders. It is usually found directly on bark or over mosses thereon, mainly on *Quercus*, rarely on *Cupressus* and *Juniper* or decomposing conifer wood, in open forests. It is widely distributed in the warm-temperate zone but not common. There are records from Europe, East Africa (Tansania), Japan, and New Zealand. In North America it is found in the western half of the United States, with most collections from California (Map 3).

Specimens examined:

U.S.A.: ARIZONA: Cochise Co.: Chiricahua Mts., Cave Creek Canyon, between Herb Martyr Reservoir and Wym Falls, on oak, 26–29.10.1963 WEBER, VAARAMA & KHANNA (COLO). – **Santa Cruz Co.:** Santa Rita Mts., spring below Josephirce Saddle, 31°42’ N, 110°51’30’’ W, on boulder face among *Hedwigia*, 7000 ft, 5.10.1981 T. H. NASH 18567 (ASU). **CALIFORNIA: Butte Co.:** on bark of

Quercus douglasii at Visitor Center, 2.4.1976 D. TOREN 2832 with *Placidium fingens* (SFSU). – **Fresno Co.:** foothills c. 55 km SE of Fresno, grassy landscape with few trees, on *Quercus douglasii*, 36°46' N, 119°10' W, 600 m, 29.4.1986 R. MOBERG 6821 (UPS). – **Lake Co.:** on bark of *Quercus douglasii*, on the end of Hell's Peak Road, 26.4.1975 D. TOREN 1801 with *Placidium fingens* (SFSU); Hell's Peak, on bark of *Quercus douglasii*, 4.1975 L. SIGAL, with *Placidium fingens* (ASU). – **Los Angeles Co.:** Santa Monica Gebirge, auf Erde unter Moos, 1897 H. E. Hasse sub *Verrucaria squamella*, ex hb. Hasse 792 (W). – **Napa Co.:** Glen Ellen, 25.4.1946 C. L. BROWN 389 (UC). – **San Mateo Co.:** Santa Cruz Mts., foothills 4 mi from Mayfield, 300 ft, on *Quercus lobata*, 4.6.1904 A. C. HERRE (533)792 (FH), 533 (W). – **Santa Clara Co.:** on bark of *Quercus douglasii*, road from Frank Raines



Map 3. North American distribution of *Catapyrenium psoromoides*.

Park to Livermore just south of the Alameda Co. line, 27.3.1976 D. TOREN 2812 (CANL, SFSU with *Placidium fingens*). – **Sonoma Co.:** 1 mi N of Santa Rosa, 6.1946 C. L. BROWN 444 (UC); Sonoma Valley Park, c. 1 mi S of Glen Ellen, oak woodland on S-facing slope, on roadside cypress, 20.3.2000 R. ROBERTSON 3363 (hb. Robertson, LI). – **Tehama Co.:** dry exposed site, with oaks, Forest Inventory and Analysis Plot 4012224, 110 m, c. 40°13' N, 122°26' W, 30.7.2003 M. CASTEEL 12 (OSC). – **Tulare Co.:** Sequoia National Park, west end of Little Baldy Saddle, on E-facing slope to valley with fir and rock and some pine, 7100 ft, 16.5.1984 C. M. WETMORE 50930 (MIN); Sequoia National Park, ridge S of Little Baldy, on E-facing slope of ridge in fir and pine forest with some incense cedar, 6800 ft, 19.5.1984 C. M. WETMORE 51099 (LI, MIN). **COLORADO: Rio Blanco Co.:** valley of Piceance

Creek, between Little Hills Experiment Sta. and Rio Blanco, 6000–6700 ft, base of a *Juniperus osteosperma* tree overgrowing *Leskea tectorum*, 16.5.1959 W. A. WEBER & S. SHUSHAN (COLO, LI). **KANSAS: Pottawatomie Co.:** 0.2 mi S, 2.25 mi E of Laclede, along southside of Emmert Rd., 39.34320° N, 96.17770° W, 1150 ft, edge of rocky mixed oak–hickory forest along road, on *Quercus macrocarpa*, 26.6.2008 C. A. MORSE 17478 (KANU). **NORT DAKOTA**: **Billings Co.:** Theodore Roosevelt National Park, S-Unit, Buck Hill (6.5 mi E of Medora), on N-facing hillside with juniper and few ash, 2700 ft, 26.7.1982 C. M. WETMORE 45209 (MIN). **OREGON**: **Curry Co.:** Oak Flat, from Gold Beach take Gold Beach – Agness Rd. c. 25 mi along Rogue River, right on gravelled Oak Flat Rd. to end, picnic area on river, 10.1996 S. TUCKER 34949 (SBBG). – **Gilliam Co.:** Lonerock, rocky hillslope, 1132 m, 45.13118° N, 119.902° W, on earth, 28.10.2009 H. T. ROOT 2762 (OSC). – **Jackson Co.:** *Quercus garryana* woodland, above confluence of Forest Creek and Poormans Creek, Applegate River drainage, 3.4 km NNW of Ruch, 42.26685° N, 123.02983° W, on *Quercus*, 4.2008 B. MCCUNE 29563 (OSC). **UTAH: Sevier Co.:** FIA Plot (State-County-Plot) 49-41-1, 6965 ft, on moss in crack of tree, 15.10.2009 M. CROSS & D. STONE 7911.18 (OSC). – **Summit Co.:** Wasatch-Cache National Forest, Hole in the Rock Spring, 40°56’37’’ N, 110°09’40’’ W, N-facing canyon in foothills of Uinta Mts., 2591 m, on mossy decomposing conifer wood, 10.8.1989 C. NEWBERRY 704 (WIS). **WYOMING**: **Park Co.:** Yellowstone National Park, Upper Terrace Loop 1 mi SW of Mammoth, valley with douglas fir and flats with juniper on limestone rocks, 7000 ft, on juniper, 20.7.1998 C. M. Wetmore 80931 (MIN).

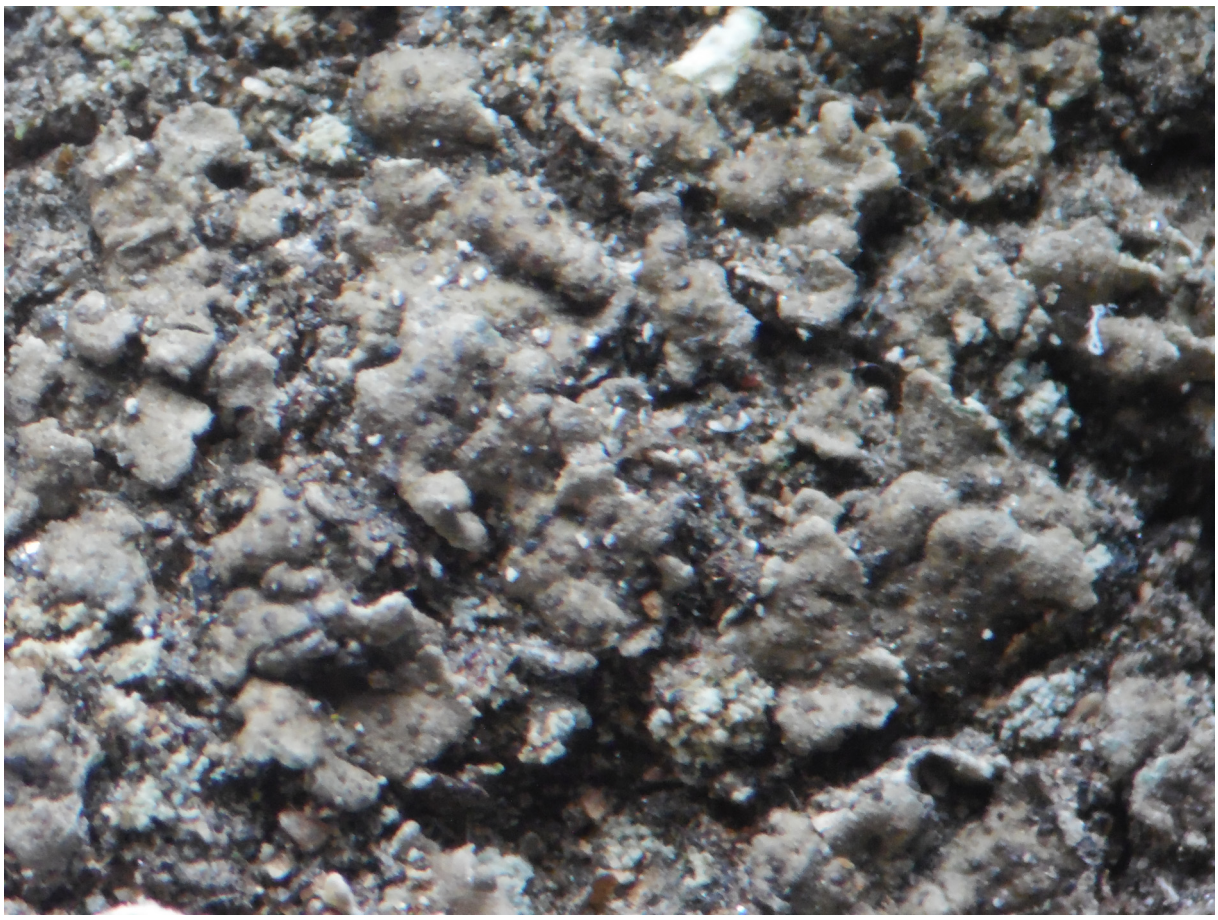


Fig. 11. *Catapyrenium squamellum*, thallus. Width of the photograph 8 mm.

Catapyrenium squamellum (NYL. ex HASSE) J.W.THOMSON

Verrucaria squamella NYL. in HASSE, Bull. Torrey Bot. Club 24 (1897): 449. – Type: On shaded earth among moss near Santa Monica (Calif.), February 1897, H. E. HASSE (FH – holotype).

T h a l l u s : of very small, loosely aggregated squamules. Individual squamules 1–2 mm wide, adnate to more often raised from the substrate, with finely divided margins (Fig. 11). Upper surface olive-green or brownish green, bright green when wet, underside pale to brownish.

A n a t o m y : Thallus 180–250 µm thick. Upper cortex 15–20 µm. Amorphous epinecral layer lacking. Photobiont layer filling most of the thallus, algal cells 5–8 µm in diam. Medulla thin, composed of tightly packed globular cells 5–8 µm diam., without a delimited lower cortex. Rhizohyphae hyaline or brownish, 2.5–3 µm in diam., mainly aggregated to form hapter-like bundles.

P e r i t h e c i a : 150–200 µm broad; excipulum 15–20 µm thick, colorless or brownish.

P e r i p h y s e s : c. 15 µm long and 2 µm thick.

A s c i : narrowly clavate, 50–60 × 12–15 µm.

A s c o s p o r e s : narrowly ellipsoidal, (13–)15–20(–22) × (4.5–)5–6 µm.

Icon.: THOMSON 1987: 30.

Characterization: The species is recognized by small, loosely aggregated, ± ascending squamules attached by tufts of very thin rhizohyphae and comparatively long and slender ascospores. It may be confused with small-squamulose specimens of *Catapyrenium psoromoides*, which sometimes occur on moss or earth cover over rock. This latter species has thicker squamules covered by an amorphous layer, a distinct filamentous medullary tissue, and broader ascospores (5.5–7 vs. 5–6 µm). It was found in a part of HASSE´s collections which contain mostly poor material of either *C. squamellum* or *C. psoromoides*. There are several packets of both these species likewise numbered as "792". HERRE´s (1910) report of *C. squamellum* (sub *Dermatocarpon*) from bark of *Quercus lobata* represents *Catapyrenium psoromoides*.

Ecology and distribution: *Catapyrenium squamellum* is a rare species. In over 120 years since HASSE´s original collections near Santa Monica in California only a handful additional occurrences have been found, all but one in western North America (Map 4); one sample is from the West Indies (Jamaica). The species was found growing among mosses over soil or acidic rocks, partly on newly exposed unstable soil banks. KNUDSEN (2006) reported on rich occurrences on soil crusts on vertical trail cuts in California´s San Mateo Wilderness Area that were wiped out by torrential rainstorms. Probably *Catapyrenium squamellum* is a pioneer species with a poor competitive capacity.

KERRY KNUDSEN (in litt.) communicated the data of an additional Californian record (Santa Cruz Co., UCSC campus, on a soil bank with moss, 15.3.2004 R. ROBERTSON 8718, hb. Robertson).

Specimens examined:

U.S.A.: ARIZONA: Santa Cruz Co.: Florida Saddle Trail above Forest Experiment Station, among mosses over acidic rock, 1400–2200 m, 3.9.1988 T. H. NASH 25310 (ASU). **CALIFORNIA: Los Angeles Co.:** Santa Monica, near Soldiers Home, earth among mosses, 1897 H. E. HASSE (UC); Santa Monica Mts., Sepulveda Cañon, H. E. Hasse 792 (FH); Santa Monica Gebirge, 1898, ex hb. H. E. Hasse 792 (W). – **Riverside Co.:** San Mateo Wilderness Area, Tenaja Canyon, 33°31'720'' N, 117°24'570'' W, 430 m, vertical bank of soil over granite in shade on north slope with moss,

18.3.2003 K. KNUDSEN 56 (LI, UCR); San Mateo Wilderness Area, Los Alamos Canyon, 33°31.897’ N, 117°23.975’ W, 458 m, mixed chaparral, soil bank with N-expos., 31.12.2003 K. KNUDSEN 754 (LI, UCR). **WASHINGTON: Douglas Co.:** NE of Wenatchee, N of Badger Mt., BLM lands, 47.528224° N, 120.05198° W, 1042 m, on soil, 22.9.2013 D. STONE, A. HARDMAN, J. PONZETTI, M. RUSSEL & K. BECK (SRP).

Map 4. North American distribution of *Catapyrenium squamellum*.

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References

BRATLI, H., JØRGENSEN, P. M., HAUGAN, R., JOHNSEN, J. I., 2010: *Catapyrenium psoromoides* new to Norway. – Graphis Scripta **22**: 9–13.

BREUSS, O., 1990: Die Flechtengattung *Catapyrenium* (*Verrucariaceae*) in Europa. – Stapfia **23**.

BREUSS, O., 1993: *Catapyrenium* (*Verrucariaceae*) species from South America. – Pl. Syst. Evol. **185**: 17–33.

BREUSS, O., 1995: The genus *Catapyrenium* (*Verrucariales*) in the Southern Hemisphere. – Cryptog. Bot. **5**: 177–183.

BREUSS, O., 1996: Ein verfeinertes Gliederungskonzept für *Catapyrenium* (lichenisierte Ascomyceten, *Verrucariaceae*) mit einem Schlüssel für die bisher bekannten Arten. – Ann. Naturhist. Mus. Wien **98** B Suppl.: 35–50.

BREUSS, O., 2000: A peculiar new *Catapyrenium* species (Lichenized Ascomycetes, *Verrucariaceae*) from Mexico. – Linzer Biol. Beitr. **32**/2: 1053–1055.

BREUSS, O., 2001: *Catapyrenium*. – In: Flora of Australia Vol. 58A, Lichens 3. Melbourne: ABRS/CSIRO Australia: 160–161.

BREUSS, O., 2010: An updated world-wide key to the catapyrenioid lichens (*Verrucariaceae*). – Herzogia **23**(2): 205–216.

BREUSS, O., BRATT, C. C., 2000: Catapyrenioid lichens in California. – Bull. Calif. Lichen Soc. **7**: 36–43 (2001).

BREUSS, O., HANSEN, E. S., 1988: The lichen genera *Catapyrenium* and *Placidiopsis* in Greenland. - Pl. Syst. Evol. **159**: 95–105.

DIETRICH, M., BRÜCKER, W., 2022: Die Flechten im Kanton Uri des 19. Jahrhunderts, dokumentiert von ANTON GISLER (1820–1888). – Cryptogamica Helvetica **24**: 1–413.

DOBSON, F. S., 2018: Lichens. An illustrated guide to the British and Irish species. 7th revised edition. British Lichen Society, London.

GUEIDAN, C., ROUX, CL., LUTZONI, F., 2007: Using a multigene phylogenetic analysis to assess generic delineation and charcter evolution in *Verrucariaceae* (*Verrucariales, Ascomycota*). – Mycol. Res. **111**: 1145–1168.

GUEIDAN, C., SAVIĆ, S., THÜS, H., ROUX, CL., KELLER, C., TIBELL, L., PRIETO, M., HEIÐMARSSON, S., BREUSS, O., ORANGE, A., FRÖBERG, L., AMTOFT WYNNS, A., NAVARRO-ROSINÉS, P., KRZEWICKA, B., PYKÄLÄ, J., GRUBE, M, LUTZONI, F., 2009: Generic classification of the *Verrucariaceae* (*Ascomycota*) based on molecular and morphological evidence: recent progress and remaining challenges. – Taxon **58**(1): 184–208.

HARADA, H., 1993: A taxonomic study on *Dermatocarpon* and its allied genera (Lichenes, Verrucariaceae) in Japan. – Nat. Hist. Res. **2**(2): 113–152.

HERRE, A. W. C., 1910: The lichen flora of the Santa Cruz Peninsula, California. – Proc. Washington Acad. Sci. **12**(2): 27–269.

KNUDSEN, K., 2006: Notes on the lichen flora of California # 2. – Bull. Calif. Lichen Society **13**(1): 10–13.

MCCUNE, B., 2017a: Microlichens of the Pacific Northwest Volume 1: Key to the genera. – Corvallis: Wild Blueberry Media.

MCCUNE, B., 2017b: Microlichens of the Pacific Northwest Volume 2: Keys to the species. – Corvallis: Wild Blueberry Media.

MCMULLIN, R. T., 2023: Lichens. The Macrolichens of Ontario and the Great Lakes Region of the United States. – Buffalo: Firefly Books (U.S.) Inc.

MOBERG, R., TIBELL, S., TIBELL, L. (Eds.), 2017: Nordic Lichen Flora Vol. 6, *Verrucariaceae* 1. – Museum of Evolution, Uppsala University.

ØVSTEDAL, D. O., LEWIS SMITH, R. I., 2001: Lichens of Antarctica and South Georgia. A guide to their identification and ecology. – Cambridge University Press.

PRIETO, M, MARTÍNEZ, I., ARAGÓN, G., 2010a: The genus *Catapyrenium* s. lat. (*Verrucariaceae*) in the Iberian Peninsula and the Balearic Islands. – Lichenologist **42** (6): 637–684.

PRIETO, M, MARTÍNEZ, I., ARAGÓN, G., OTÁLORA, M. A. G., 2010b: Phylogenetic study of *Catapyrenium* s. str. (*Verrucariaceae*, lichen-forming Ascomycota) and related genus *Placidiopsis*. – Mycologia **102**(2): 291–304.

PRIETO, M, MARTÍNEZ, I., ARAGÓN, G., GUEIDAN, C., LUTZONI, F., 2012: Molecular phylogeny of *Heteroplacidium*, *Placidium*, and related catapyrenioid genera (*Verrucariaceae*, lichen-forming Ascomycota). – Amer. J. Bot. **99**(1): 23–35.

PUNTILLO, D., 1996: I licheni di Calabria. – Monografie XXII, Museo Regionale di Scienze Naturali, Torino.

ROSENTRETER, R., BELNAP, J., 2003: Biological soil crusts of North America. – Ecol. Stud. **150**: 31–50.

SCHEIDEGGER, C., KELLER, C., STOFER, S., 2023: Flechten der Schweiz. Vielfalt, Biologie, Naturschutz. – Bern: Haupt.

STENROOS, S., VELMALA, S, PYKÄLÄ, J., AHTI, T. (Eds.), 2016: Lichens of Finland. – Norrlinia **30**: 1–896.

SWINSCOW, T. D. V., KROG, H. 1988: Macrolichens of East Africa. – London: British Museum (Natural History).

THOMSON, J. W., 1984: American arctic lichens. 1. The Macrolichens. – New York: Columbia University Press.

THOMSON, J. W., 1987: The lichen genera *Catapyrenium* and *Placidiopsis* in North America. – The Bryologist **90**(1): 27–39.

THOMSON, J. W., 1989: Additions and a revised key to *Catapyrenium* in North America. – The Bryologist **92**(2): 190–193.

THÜS, H., MUGGIA, L., PÉREZ-ORTEGA, S., FAVERO-LONGO, S. E., JONESON, S., O´BRIEN, H., NELSEN, M. P., DUQUE-THÜS, R., GRUBE, M., FRIEDL, T., BRODIE, J., ANDREW, C. J., LÜCKING, R., LUTZONI, F., GUEIDAN, C., 2011: Revisiting photobiont diversity in the lichen family *Verrucariaceae* (Ascomycota). – Eur. J. Phycol. **46**(4): 399–415.

VAN HALUWYN, C., ASTA, J., BOISSIERE, J-C., CLERC, P., 2012: Guide des lichens de France. Lichens des sols. – Éditions Belin.

VOBIS, G., 1980: Bau und Entwicklung der Flechten-Pycnidien und ihrer Conidien. – Biblioth. Lichenol. **14**: 1–141.

VUST, M., 2011: Les lichens terricoles de Suisse. – Mémoire de la Société vaudoise des Sciences naturelles **24**: 1–352.

WIRTH, V., HAUCK, M., SCHULTZ, M., 2013: Die Flechten Deutschlands. Band 1.– Stuttgart: Ulmer.

WITTMANN, H., TÜRK, R., 1990: Die Flechten im Nationalpark Nockberge (Kärnten, Österreich). – Kärntner Nationalpark-Schriften Bd. **4**: 1–112.