Notes RBG Edinb. 44(3):581–599 (1987)

MUHRIA, A REMARKABLE NEW LICHEN GENUS FROM SCANDINAVIA

P. M. JØRGENSEN* & H. M. JAHNS**

ABSTRACT. A new monotypic lichen genus *Muhria,* with the species *M. urceolata* sp. nov., is described. The thallus is dimorphous and consists of areoles with a green photobiont on a basal mat of mixed blue-green photobionts, evidently forming a continuum. The apothecia originate in the blue-green part and develop mostly between the areoles. This has not previously been recorded in photosymbiodemes. However, both *Stereocaulon leucophaeopsis* and *S. tornensis* are shown to behave similarly. Although the ascocarp development is hemiangiocarpic, the genus has many characters including ascus structure, paraphyses and chemistry, in common with the Stereocaulaceae and is possibly a primitive representative of that family. A key to the crustose Stereocaulaceae of NW Europe is given.

INTRODUCTION

While studying the enigmatic lichen *Rinodina humilis* H. Magn., material of a lichen thought to be related to it, was kindly made available for study by L.-E. Muhr. It proved to be a very different, but highly interesting and obviously new species. As the species had certain characters suggesting affinities with the Stereocaulaceae, but apothecia of a most unusual appearance, it was sent to the junior author who is responsible for the ontogenetic part of this paper as well as the identification of the photobionts.

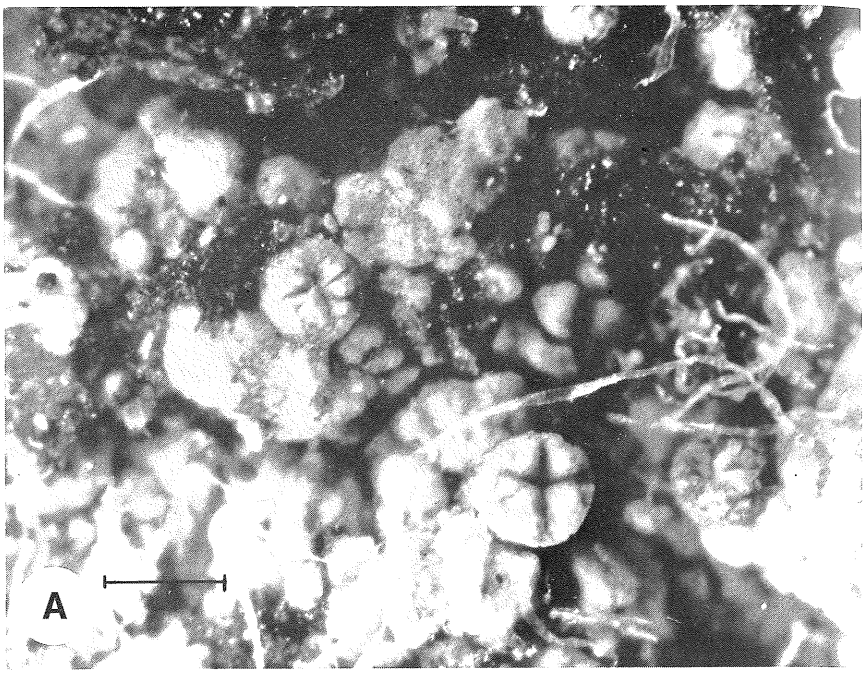
MATERIAL & METHODS

In addition to the material sent to us by Mr L.-E. Muhr, Karlskoga over the years, we have also studied specimens provided by Mr E. Timdal (O). We have also seen all material of the following taxa from the herbaria in BG, BM, E, GB, O and UPS: *Stereocaulon dactylophyllum* f. *sessile* Lamb (type: Sweden, Västergötland, Floby, i 1896, *C. Stenholm,* holo. GB; *Stereocaulon leucophaeopsis* (Nyl.) James & Purvis (type: Scotland, Mid Perth, Ben Lawers, ix 1871, *J. M. Crombie,* holo. BM, iso. UPS); *Stereocaulon tornensis* (H. Magn.) James & Purvis (type: Sweden, Torne Lappmark, Jukkasjärvi, Vassitjåkko towards Vassijaure, vii 1950, *E. Dahl,* holo. O, iso. UPS); *Stereocaulon vesuvianum* f. *sessile* (H. Magn.) Lamb (type: Sweden, Västergötland, Halleberg, 1893, *C. Stenholm,* holo. GB).

Sections of specimens were cut by freezing microtome and stained in lactophenol cotton blue. Lugol's iodine solution was used to study the apical structures of asci. For ontogenetic studies specimens were also studied by SEM. The chemistry was studied by standard thin layer chromatography (TLC) (White & James, 1985).

*Botanisk institutt, Universitetet i Bergen, Postboks 12, N-5027 Bergen, Norway.

**Botanisches Institut, J. W. Goethe-Universität, Postfach 111932 D-6000 Frankfurt am Main, West Germany.



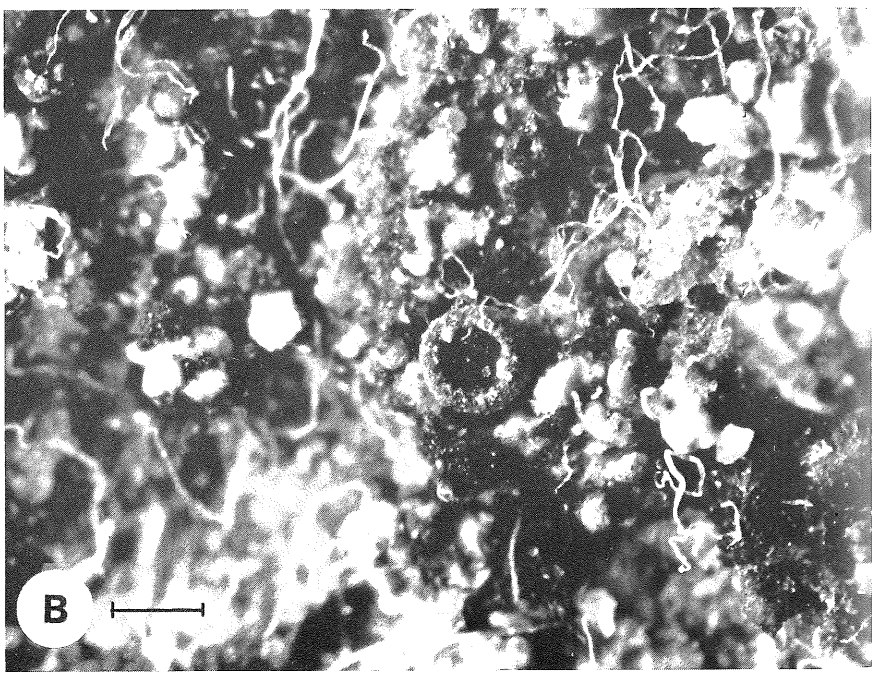
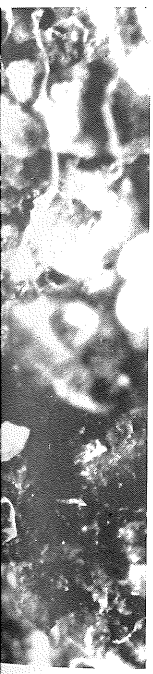


FIG. 1. *Muhria urceolata*: A, with young apothecia showing star-like openings; B, with fully opened, urceolate apothecium with white teeth on the margin. Note the association with black, *Stigonema*-tufts between the areoles. Scales = 0·5mm.





gs; B, with fully
ssociation with

DESCRIPTION

Muhria urceolata P. M. Jørg., **gen. et sp. nov.** Figs 1–10.

Thallus crustosus; ± areolatus, cinereo-viridus, irregulariter sorediosus, dimorphus, areolae photobionto viridi strato cyanobionto insidentes, atranoricum, chloratranoricum et acidum lobaricum continens. Apothecia brunneola ad 0·5mm diam. inter areolas exorientia, primo globosa, stellatim aperentia demum urceolata; asci lecanoralei sporis hyalinis, 1–3-septatis, 20–28 × 6–8μm. Pycnidia globosa, fusca, ad 0·2mm diam. inter areolas exorientia, conidia arcuata, 6–10 × 0·5–1μm.

Typus: Suecica, Wermelandia, Dalby, Gravbäcken, 6 viii 1981, *L.-E. Muhr* 4208 (holo. UPS; iso. BG, BM, CANL, CHR, GZU, H, M, PE, TNS, US, hb. Muhr, hb. Vězda).

Thallus crustose, grey-green, ± areolate, individual areolae convex, often confluent in small cracked crust-like patches, up to 5mm diam., dispersed over the substratum, upper surface ± irregularly erupting into coarse-grained, often crateriform soralia, resting on a hypothallus-like mat of cyanobacteria mainly *Microcystis* and *Stigonema*. Areoles up to 150μm thick; upper cortex poorly and irregularly developed, without lower cortex, but with a narrow, brownish pigmented zone towards the blue-green parts; photobiont protococcoid in clusters, individual cells ellipsoid to barrel-shaped, 9–12μm diam. *Apothecia* rare, developed between the areoles, pale to chestnut brown, initially globose with star-like opening, later urceolate with a distinct proper margin, to 0·5mm diam. *Proper exciple* paraplectenchymatic, to 60μm wide; subhymenial layers with brown upper parts, K+ intensifying, 20–30μm wide of dense, intricately interwoven hyphae resting on a more loosely organized, colourless, inverted cone-shaped tissue; hymenium I+ blue only in the vicinity of the asci, 90–110μm deep; paraphyses straight, simple or rarely branched, 1–1·5μm wide with enlarged, externally brown-pigmented apical cell to 3·5μm wide (Fig. 2b); asci cylindrical, 60–90 × 12–15μm, with a blue apical dome with a darker, central ring structure (Fig. 2a), 8-spored. *Spores* colourless, narrowly ellipsoid, 1–3-septate, 20–28 × 6–8μm (Fig. 2c). *Pycnidia* (Fig. 9) rare, formed between the areoles, brownish, to 0·2mm diam., producing filiform, arcuate, colourless conidia, 6–10 × 0·5–1μm, apically on short-celled conidiophores.

Chemistry. Atranorin, chloratranorin and lobaric acid (UV+ ice-blue) in the areoles and most probably the apothecia (see below).

Variation. *M. urceolata* is a rather variable species: the blue-green part is better developed in moist habitats, where the areoles are very scattered and also rarely sorediate. In more exposed, drier habitats the areoles are dominant, sometimes forming dense aggregations and are usually conspicuously sorediate.

Ecology. On acid, moist rocks or rock walls in the lowlands (up to 800m alt.), mainly in sheltered humid habitats such as ravines and woodlands. Associated species include *Aspicilia lacustris, Porpidia tuberculosa, Rhizocarpon hochstetteri* and *Trapelia placodioides*. A detailed description of the type locality is given by Muhr (1987). *Muhria* is also occasionally found in more exposed habitats, even in the moderately polluted outskirts of the city Karlskoga, but there it is obviously not well developed.

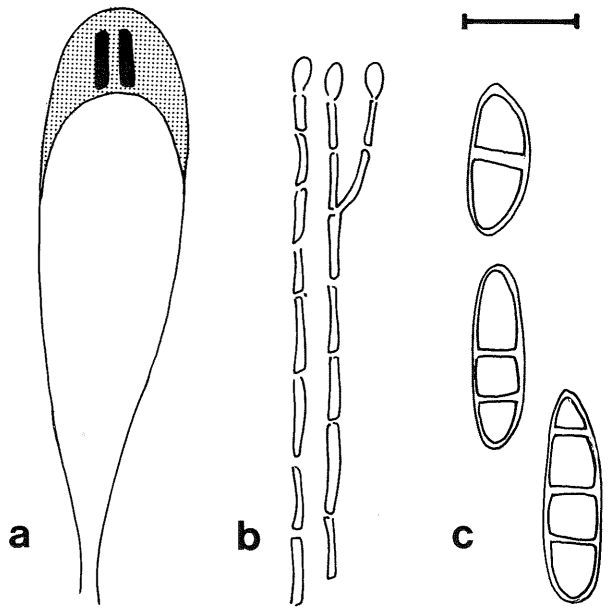


FIG. 2. *Muhria urceolata*. Sketches of: a, ascus, b, paraphyses; c, spores. Scale = 15μm.

Other specimens examined:
NORWAY. Akershus: Enebakk, between Bysætermose and Vangen, 27 iv 1986, *E. Timdal* 4544 (E, O). Oslo: Østmarka, 800m N of Sandbakken, 13 iv 1986, *E. Timdal* 4542 (O).
SWEDEN. Värmland: Bjurtjärn, 50km E of lake Svarttjärn, 11 ix 1979, *L.-E. Muhr* 1252 (hb. Muhr); Dalby, Gravbäcksravinen, 18 vii 1985, *L.-E. Muhr* 8069 (hb. Muhr); Färnebo, Änggruvorna SW of the old railway station, 21 ix 1985, *L.-E. Muhr* 8436 (hb. Muhr); N of the old railway station, 11 vi 1986, *L.-E. Muhr* 8915 (BG, GB, LD, hb. Degelius, hb. Muhr); Karlskoga, Karåsen, S of the barrage at the power station, 16 x 1981, *L.-E. Muhr* 4612 (hb. Muhr); W shore of lake Norrgryten, 24 viii 1979, *L.-E. Muhr* 1253 (hb. Muhr); Pottemyren, 10 ix 1979, *L.-E. Muhr* 1275 (hb. Muhr); Häsängen, 8 vi 1986, *L.-E. Muhr* 8900 (hb. Muhr); Norra Finnskoga, Havsvallen, 20 vii 1983, *L.-E. Muhr* 6449 (C, E, LE, LWU, MEL, hb. Muhr).

ANATOMY & ONTOGENY

The SEM and ontogenetic studies on *Muhria urceolata* revealed several interesting and unusual features. The thalline areoles have an irregular surface, composed of a strongly gelatinous layer in parts penetrated by pores (Fig. 3). Sections (Fig. 4) show that no clearly defined cellular cortex is present, but groups of two to three aligned hyphae grow vertically towards the surface forming the poorly defined, dense outer layer. The green photobiont is situated within the inner parts of the areoles. The lower cortex is absent and a continuum of hyphae connects to the layer of cyanobacteria underneath. This layer covers the surface of the substratum in an irregular way. The fungal hyphae penetrate into this diffuse, part crustose, part granular to fruticulose layer.

Colonies of the cyanobacterium *Microcystis* occur in the lowest parts of this layer. It is likely that the fungal hyphae are primarily in contact with

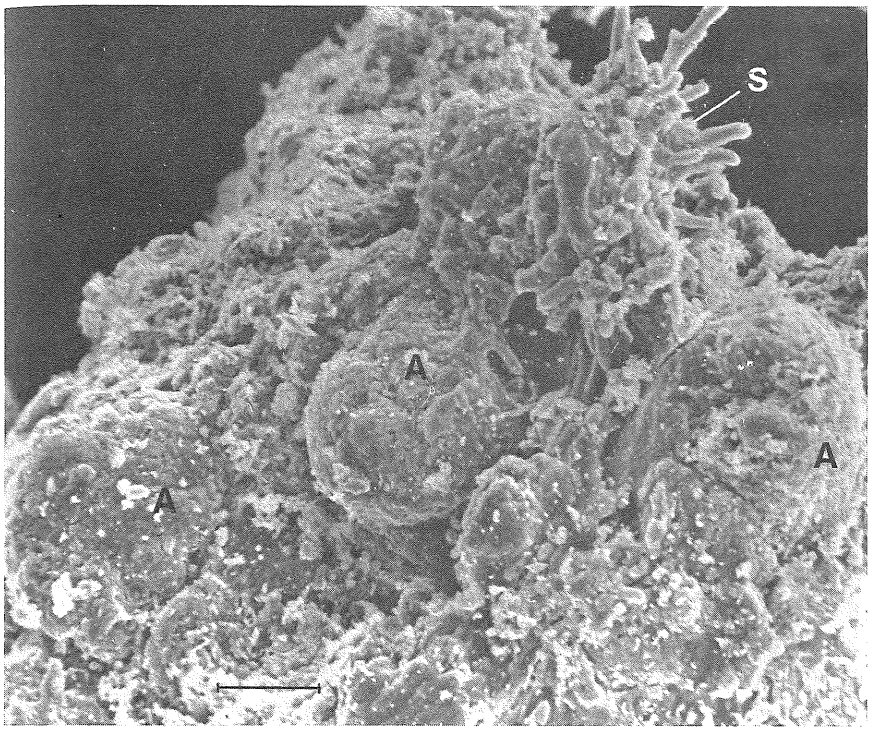


FIG. 3. *Muhria urceolata*. SEM photo of thallus. A = areoles with green photobiont. S = *Stigonema*. Scale = 100μm.

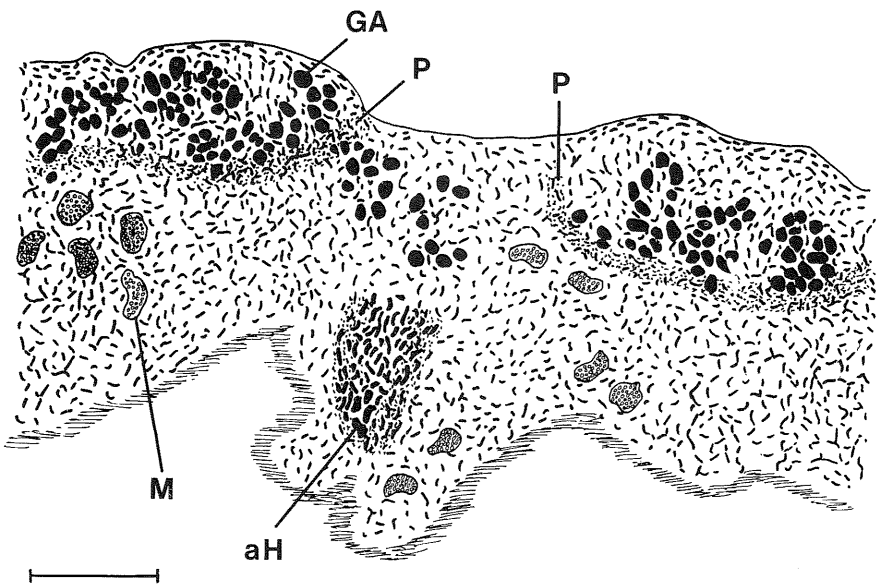


FIG. 4. *Muhria urceolata*. Section through thallus. aH = ascogenous hyphae, GA = green algae, M = *Microcystis*, P = pigmentation. Scale = 50μm.

this species, as this element of the blue-green layer is always found below the areoles with the green photobiont. Other cyanobacteria are also associated, usually covering the undifferentiated *Microcystis* layer (Fig. 3). Easily visible is *Stigonema* which forms dense fruticulose tufts, often surrounding the areoles. *Stigonema* is usually lichenized, the mycobiont overgrowing the photobiont branchlets until only the apices are visible, often eventually entirely incorporating them within the lichen thallus. The contact between *Stigonema* and the mycobiont is, however, less regular and frequent than that with *Microcystis*. It is also noteworthy that, in spite of this lichenization, no organized structures reminiscent of cephalodia are formed. *Gloeocapsa* is also frequently present on the upper surface of this cyanobacterial layer. However, it is only occasionally lichenized and rarely forms an integral part of the lichen thallus.

Most surprisingly, the development of the ascocarps does not start in the areoles with the green photobiont, but within the depths of the cyanobacterial layer among the *Microcystis*. The primordia are usually situated in the areas between the areoles, more rarely directly below them, and then penetrating through the areoles. Since the primordia are formed deep down in an undifferentiated tissue, it is very difficult to locate the earliest stages. Fig. 4 shows an aggregation of generative hyphae growing inverted cone-like towards the surface. In it the ascogenous hyphae can be observed, but the ascogones have already disappeared. The generative tissue is pigmented and therefore easily discernible from the loose tissue of the surrounding vegetative hyphae.

The ascocarp primordia grow upwards and widen. On reaching the surface they form globular protuberances. The surface of these are of the typical loose structure of growing tissues. Sections (Fig. 5A) exhibit the high degree of differentiation already reached. The origin of the primordia in the lower parts of the thallus is expressed by the inverted cone-like form of the generative tissue. The ascogenous hyphae have grown upwards and are situated centrally in the primordium, with only a few being left behind in the lower parts of the generative tissue.

In the outer parts of the primordium a thick proper exciple, consisting of cells with rather large lumina, is differentiated. This part of the primordium is not pigmented, while the inner parts of the inverted cone-like generative tissue are easily visible by their pigmented gelatine. Of particular importance is a zone in the upper part of the primordium where a loose convex structure is found; in it lies the earliest stage of a hymenium.

The globular protuberances become more or less stalked during the subsequent development (Fig. 5B). The exciple ceases to grow in the upper parts and accordingly becomes narrower. The longitudinal growth is particularly demonstrated by a layer of longitudinal hyphae situated just inside the exciple. The ascogenous hyphae gather in a flat layer and, at the same time through a concentration of other hyphae, the formation of the subhymenium begins. The layer of loose hyphae, the young hymenium, develops further and a central cavity (Fig. 5A) now appears covered inside by projecting proparaphyses. This is very typical of hemiangiocarpic development.

Subsequently, the shape of the developing apothecium becomes evident (Fig. 6A). The inverted cone-like, pigmented generative tissue is still discernible with a few, scattered remaining ascogenous hyphae enclosed. Outside this pigmented part, the longitudinal hyphae noted in the previous stage are still visible just inside the exciple which now encloses the young apothecium in an urceolate manner. The subhymenium is by now fully differentiated in the upper parts of the primordium, and also the hymenium is clearly visible. The part of the exciple constituting the roof of the internal cavity now breaks up and partly disappears. Paraphyses and young asci, which have grown into the cavity from below, are now visible. Marginal periphyses are developed, but they remain rather indistinct (Fig. 6A). This kind of apical opening is characteristic of hemiangiocarpic development and is also easy to observe externally by the apical star-like pattern on the globular protuberances (Fig. 7A & B).

This apical opening widens as the development continues and the apothecium attains an urceolate form (Fig. 7C). Remnants of the tissue that covered the hymenium can still be seen as white 'teeth' along the inner margin of the exciple (Fig. 1B). In the final stages the apothecium widens considerably and becomes plane with a distinct exciple above which the hymenium may eventually be elevated (Fig. 8). In this late stage it is very difficult to recognize the hemiangiocarpic origin of the apothecium, although most tissues present in the earlier stages are still there, except for the periphyses which are now completely included in the hymenium (Fig. 6B).

A few pycnidia have also been observed. Like the apothecia they are formed in the cyanobacterial part, starting their development in the *Microcystis* layer (Fig. 9A). The development starts with the pigmentation of the future pycnidial wall. The inner parts of the future pycnidium contain only very few hyphae. The fungal hyphae, from which the conidiophores are later formed, are very short-celled and are, most surprisingly, partly situated outside the future pycnidium. Very small pycnidia are formed as a result of the subsequent growth. They contain branched, short-celled conidiophores which produces filiform, arcuate conidia (Fig. 9B).

Discussion

Biological aspects

Muhria urceolata is a highly interesting and perplexing lichen biologically as well as taxonomically. The first superficial impression of it leads inevitably to the question: is this really one entity? There are three principle ways of explaining this unusual consortium of organisms. It is:

1. an areolate, sterile, ± sorediate lichen with a green photobiont growing upon a cover of cyanobacteria which is infested by a parasitic fungus producing ascomata.
2. an areolate, sterile, ± sorediate lichen with a green photobiont growing upon another fruiting lichen with cyanobacterial photobionts.
3. one dimorphous lichen species producing soralia in the green part and ascomata in the blue-green (cyanobacterial) part (i.e. a photosymbiodeme).

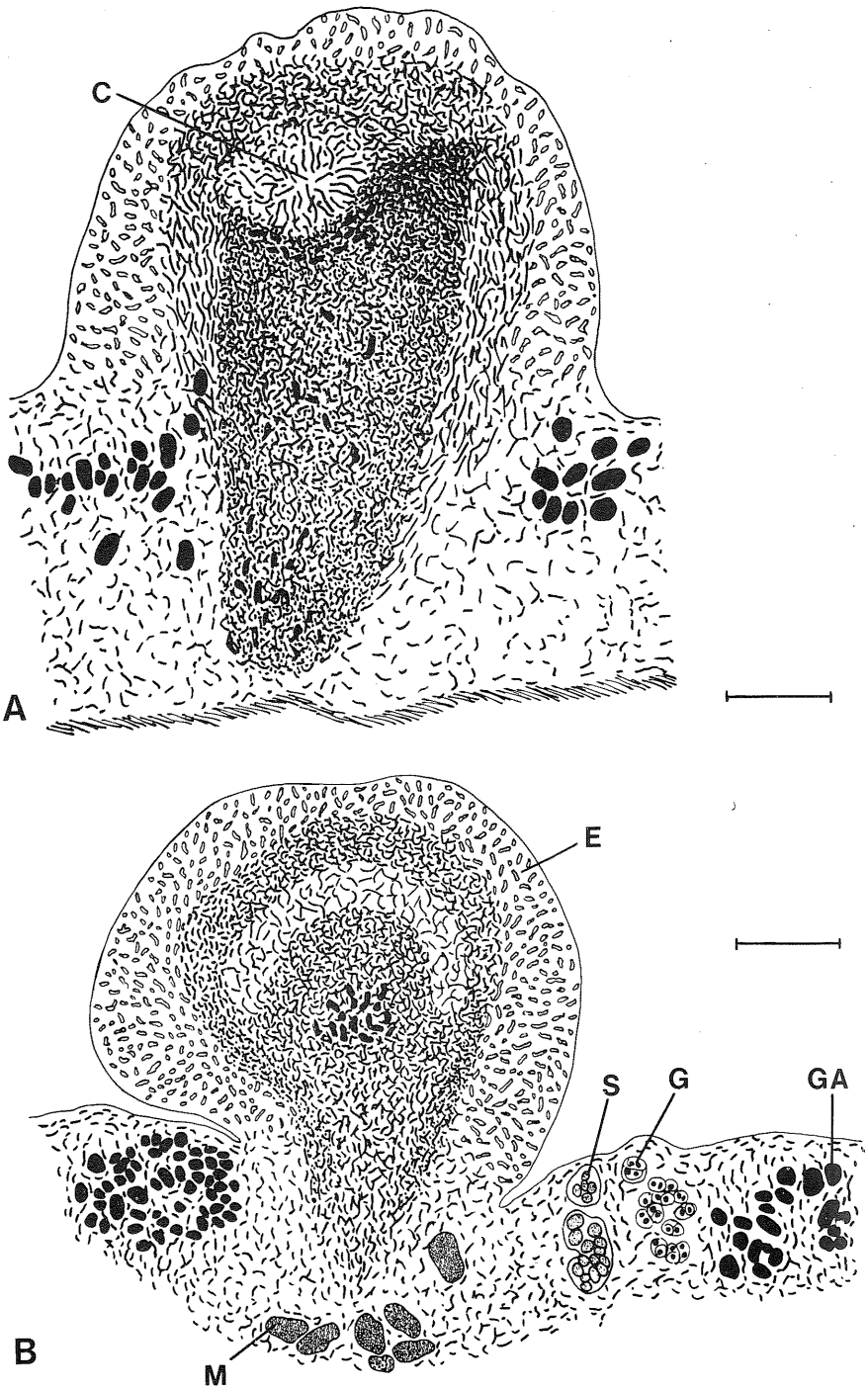


FIG. 5. *Muhria urceolata*. Young primordium growing up between the areoles with green algae: A, early stage where a central cavity (=C) is found; B, later stage. E=exciple, GA=green algae, G=*Gloeocapsa*, M=*Microcystis*, S=*Stigonema*. Scales=50μm.

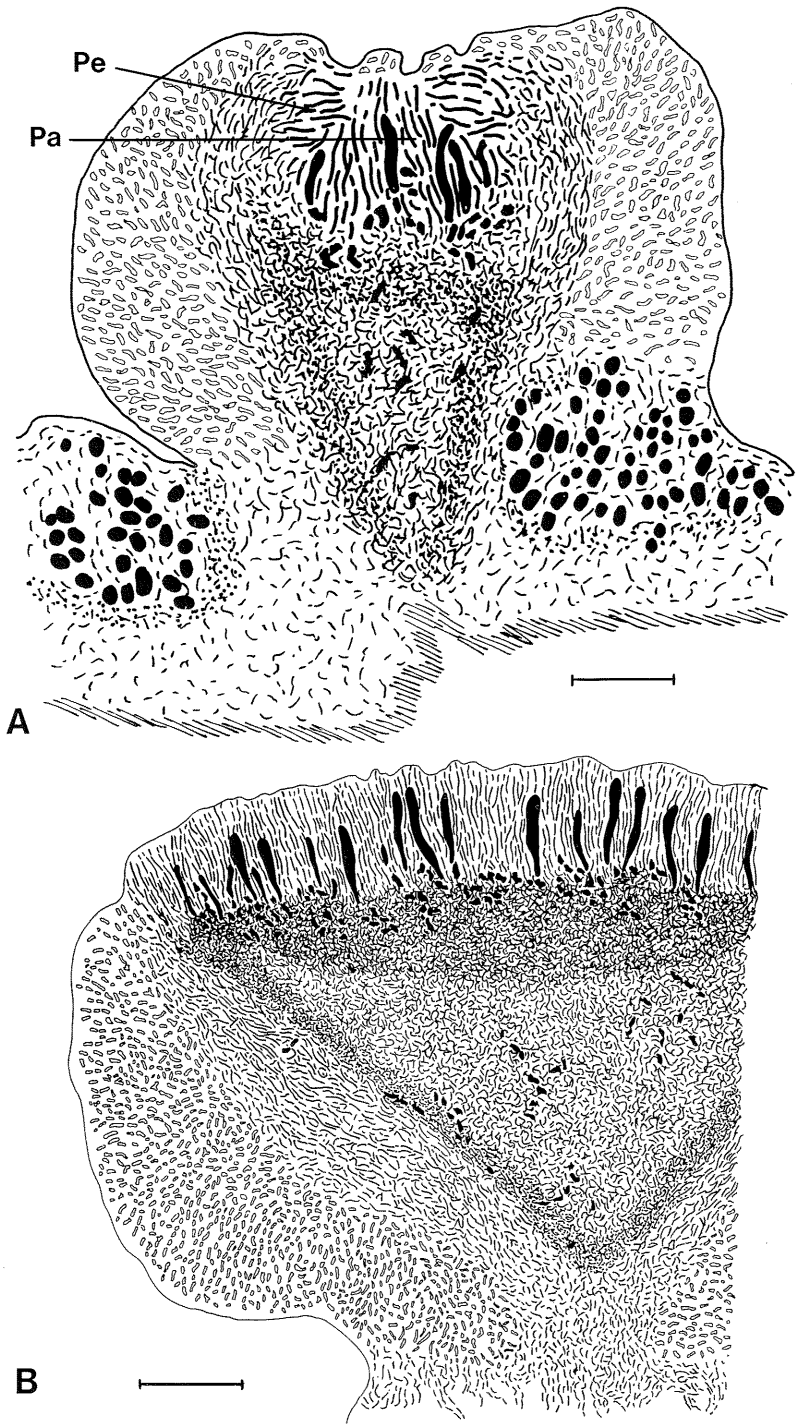
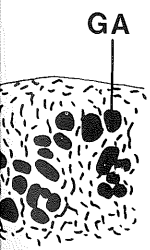


FIG. 6. *Muhria urceolata*: A, apothecium in the opening stage; B, fully developed apothecium. Pe = periphyses, Pa = paraphyses. Scales = 50μm.



bles with green
ge. E = exciple,
μm.

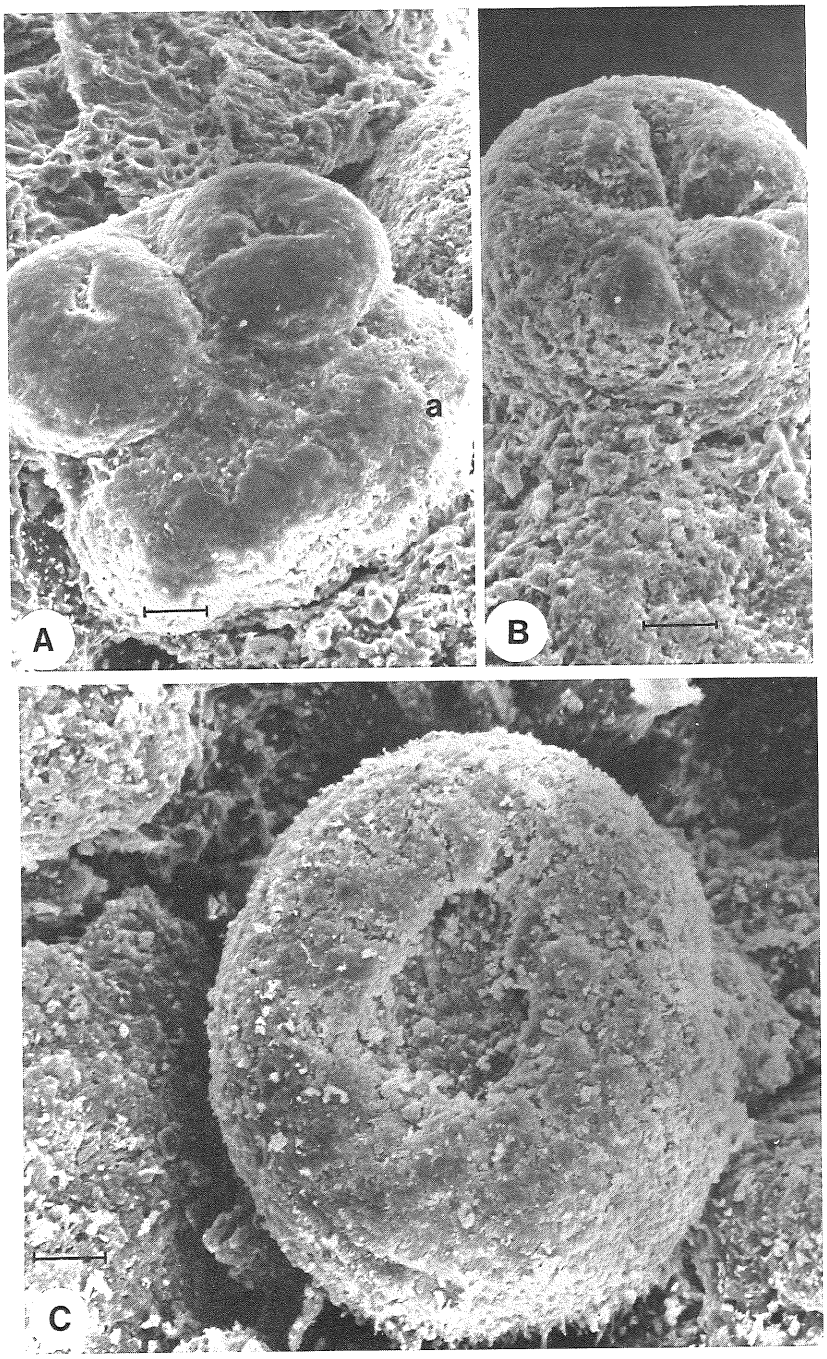
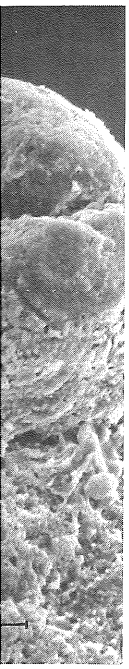
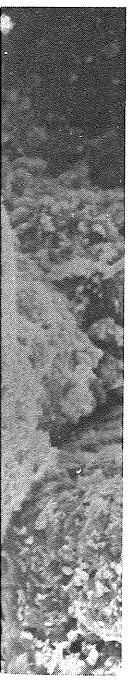


FIG. 7. *Muhria urceolata*. SEM photos of developing apothecia: A, young apothecia just about to open; also an example of the rare occasion when apothecia grow through the areoles (=a); B, a later stage, showing the star-like opening; C, completely opened apothecium. Scales = 50μm.





g apothecia just
ow through the
npletely opened

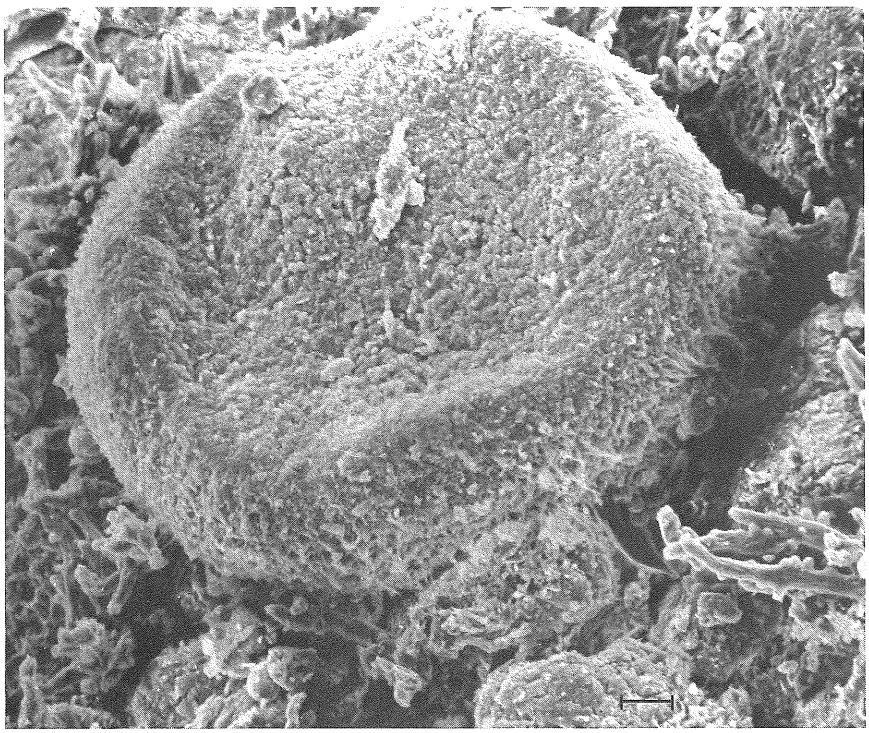


FIG. 8. *Muhria urceolata*. SEM photo of fully developed apothecium. Scale = 50μm.

The first alternative is obviously incorrect. The ascomata have the appearance of ordinary lichen apothecia and indeed the characters of the internal structures are known among lichens but not among fungal parasites of cyanobacteria. As discussed below the apothecia also contain lichen acids, substances not known to be produced by non-lichenized fungi, including parasites.

It is more difficult to distinguish between the two remaining alternatives. We have, however, observed a continuum of hyphae between the two parts, and it is easily seen how fungal hyphae from the areoles enclose *Stigonema* filaments. Indirect proof of the continuous contact between the apothecia and the green algal part was discovered when sections were studied in polarized light. Both the exciple and upper parts of the hymenium proved to contain crystals of the same kind as seen in the areoles, but not in the blue-green part. Unfortunately the rarity and the minute size of the apothecia prevented any detailed chemical analysis, but as these crystals dissolved when acetone was added, we believe they represent the lichen acids found in the TLC studies. It is also noteworthy that apothecia are only formed in the vicinity of the areolae and never where the cyanobacterial cover occurs alone.

We have accordingly concluded that alternative three is the correct interpretation of the consortium. *Muhria urceolata* represents, therefore,

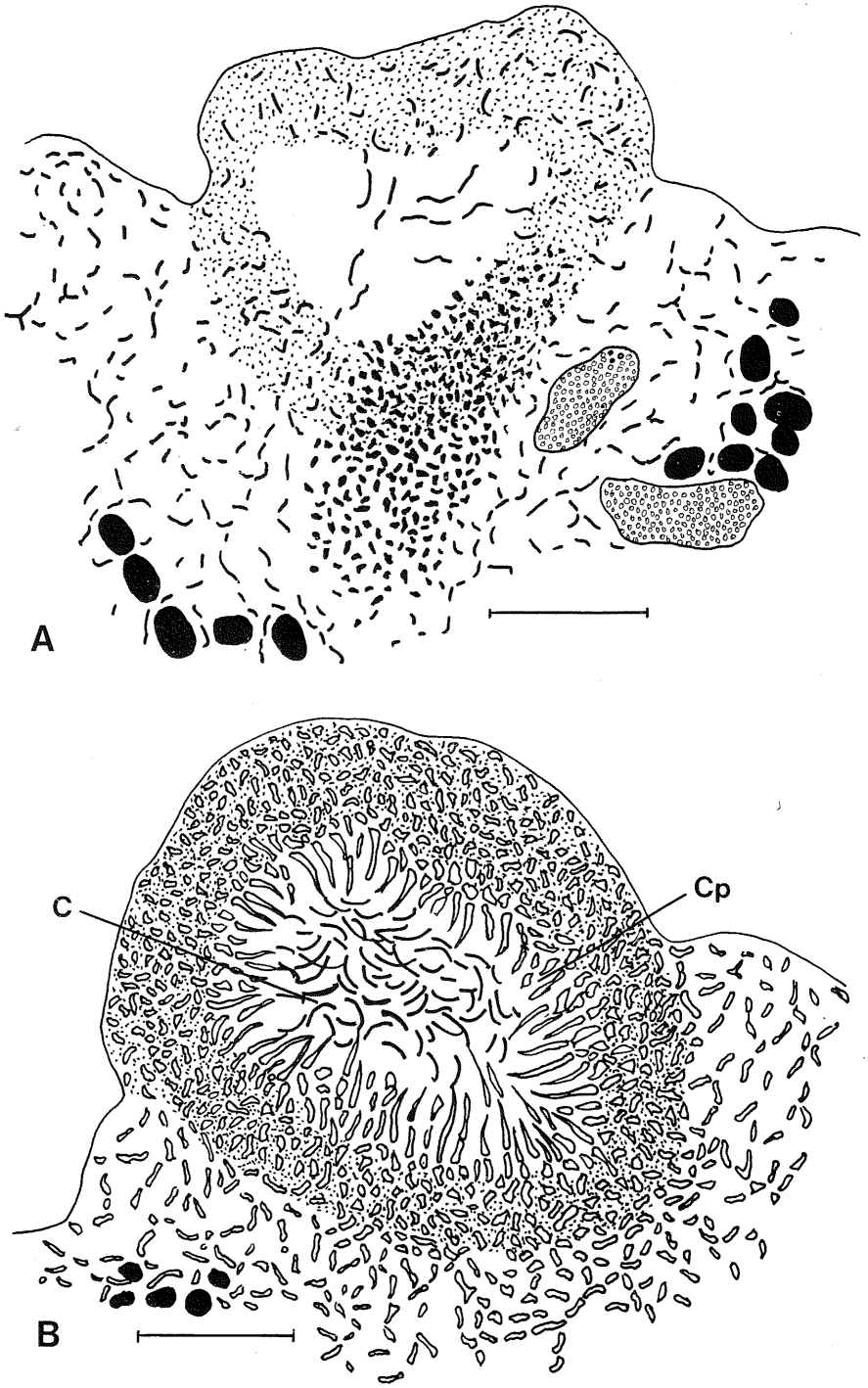


FIG. 9. *Muhria urceolata*. Pycnidium: A, early stages; B, fully developed with conidiophores (=Cp) and conidia (=c). Scales=25μm.

exactly the opposite situation to that found in *Psoroma durietzii* (James & Henssen, 1975, p. 146) where the *Nostoc*-containing cephalodia produce soralia, and apothecia are found in the green part. In joined phototypes apothecia (and pycnidia) have previously only been recorded to occur in the green part. P. W. James (*pers. comm.*) has, however, informed us that there now are examples known (in Stictaceae) where both phototypes are fertile—although this is very rare, and the types are not joined. In the case of *Muhria,* soredia carrying the green photobiont and the lichen mycobiont are evidently captured in the cyanobacterial cover and start to develop there. The earliest stages of this development are easily observed in some specimens (Fig. 10) and seems to be the commonest way of establishing this species, as well as in other photosymbiodemes. Alternatively, and surely quite infrequently (not observed in this study), *Muhria* ascospores may land on the cyanobacterial cover. If so, they most likely primarily associate with *Microcystis* and later capture the green photobiont as well as other blue-green ones.

The relative importance of the partners—the green and the blue-greens—is in good accord with the concept developed by James & Henssen (1976), although it may be explained differently here since the blue-green part does not develop any fruticose structures. In specimens from damp and shaded habitats the blue-green part is well developed and more dominant than in specimens from more exposed sites. The latter mainly consist of areoles with green photobiont and are conspicuously sorediate. This may be a result of the availability of nitrogen in the different habitats. Most cyanobacteria are able to take nitrogen directly from the air, and this is certainly of importance in the nitrogen deficient communities in the damp ravines. The nitrogen supply on rocks near lakes and roads is much better, and the need of the extra surplus from the blue-green partners, which themselves are not favoured by the drier and lighter conditions, is not so great. Further support to this theory is found in the behaviour of another crustose lichen *Placopsis gelida* (L.) Lindsay in similar habitats. When growing in damp, nitrogen deficient habitats it develops large reddish cephalodia. However, it also grows in a special form (the so-called '*P. lambii*') on stonefences and roofing tiles and there no cephalodia are produced. Whatever the explanation may be, it is evident that the development of the different parts of *Muhria* varies according to the ecological conditions.

A notable feature of *Muhria* is the undifferentiated blue-green part containing several different photobiont species, without the production of recognizable, discrete cephalodia. This is a new aspect of the photosymbiodeme concept which needs further and more detailed study. It is also noteworthy that the mycobiont is able to associate with one green algal partner and no less than three different blue-green ones. In many ways these latter associations seem to be rather loose, but evidently occur regularly and definitely form a normal pattern. It seems to be a more primitive method than that expressed in other photosymbiodemes, and it raises some intriguingly interesting questions on the lichenization process. A closer study of *Muhria* under laboratory conditions is desirable in order to get a better understanding of these basic questions.



conidiophores

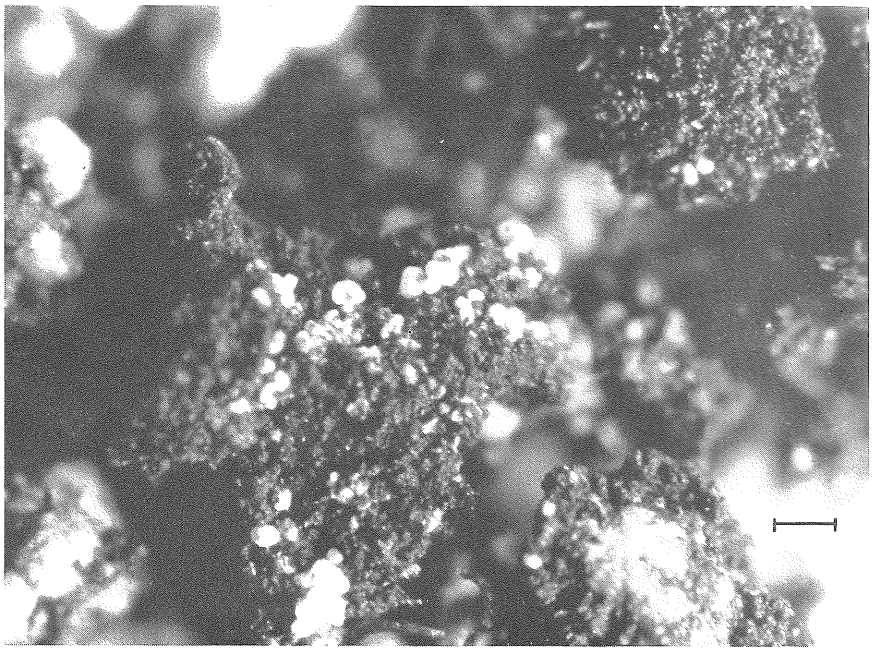


FIG. 10. *Muhria urceolata.* Soredia captured in the cyanobacterial cushions, early stages of juvenile areoles. Scale = 0·1mm.

Much to our surprise, whilst working with the taxonomic aspects of *Muhria,* we discovered two *Stereocaulon* species which behave in a similar way, *S. leucophaeopsis* and *S. tornensis.* Both have ± sorediate areoles containing a green photobiont which usually rest on a layer of mixed cyanobacteria within which the apothecia are formed (Fig. 11B) (a more detailed study will be published later). When thinking of how common cyanobacterial covers are over wet rocks, one cannot but wonder if this particular expression of photosymbiodemes is perhaps much more widespread and common. It is surely a phenomenon that should be sought for more carefully, especially among species growing on wet cyanobacteria-covered rocks in sheltered situations. *Muhria* and these two *Stereocaulon* species are, under any ciscumstances, new examples of the ecological and evolutionary potential lichens have in being able to associate with different photobiont partners.

TAXONOMIC AFFINITIES

The hemiangiocarpic ascocarp development suggests a relationship to the Gyalectales. However, members of that order differ in nearly all other important characters from *Muhria.* Most species have *Trentepohlia* as photobiont and cephalodia are very rarely present, nor does the thallus contain any lichen acids; the apothecia are waxy in appearance, often brightly coloured, with characteristic oil droplets in the excipulum (Jørgensen *et al.,* 1983, p. 47), the paraphyses are thin, unbranched, long and flexuose, and above all the asci are thin-walled, narrowly cylindrical

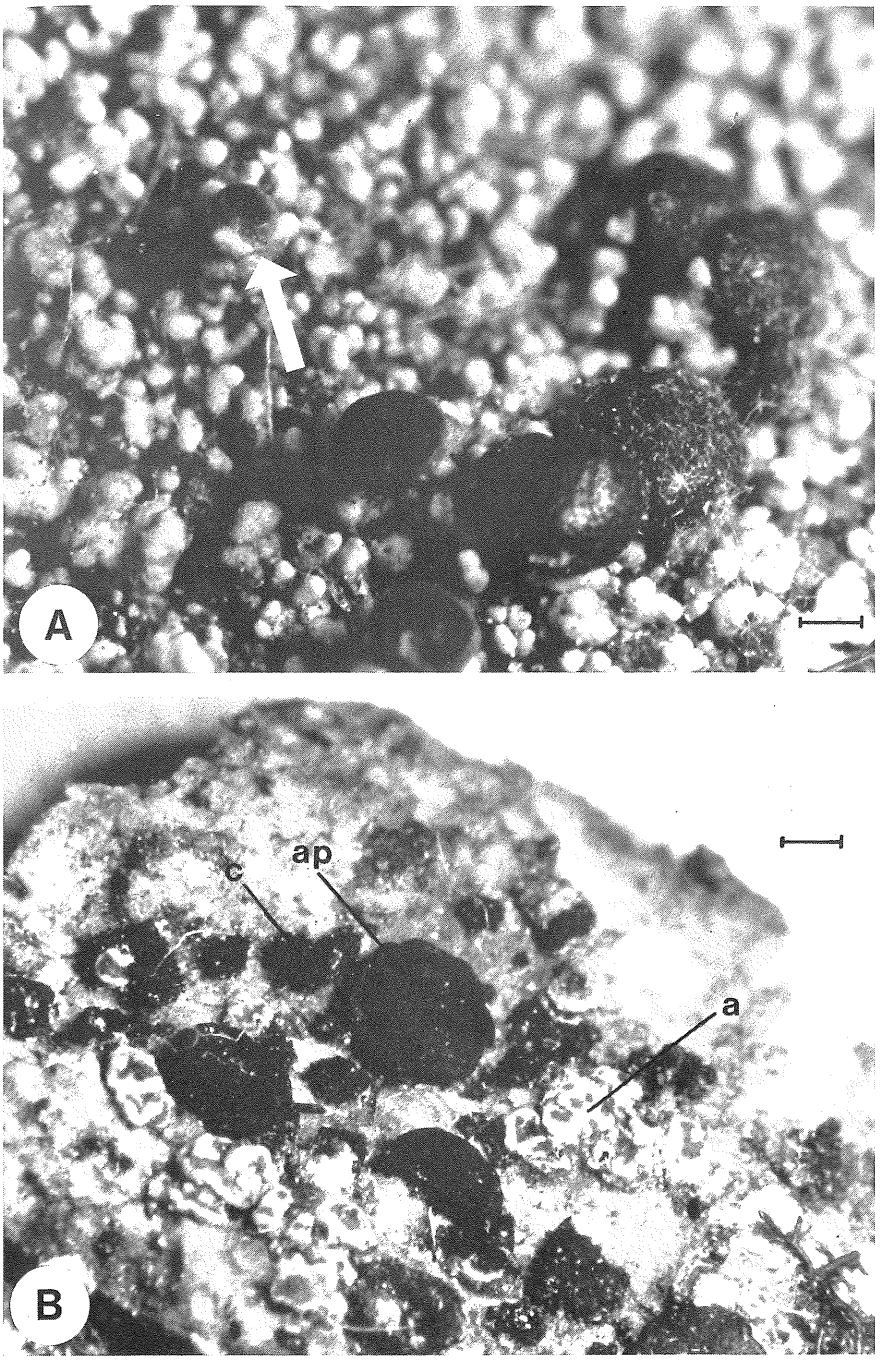


FIG. 11. A, *Stereocaulon dactylophyllum* f. *sessile*; note the apothecia formation on the squamules (best seen at arrow). B, *Stereocaulon leucophaeopsis*; note the presence of apothecia (=ap) between the areoles (=a) and the tufts of cyanobacteria (=c). Scales=0·1mm.

with no apical thickening or apical apparatus. The asci of *Muhria* are clearly of the lecanoralean type and, as most other characters support this relationship, *Muhria* must be placed in the Lecanorales.

Henssen & Jahns (1973, p. 366) include the family Trapeliaceae in the order Lecanorales. *Muhria* bears a striking superficial similarity to members of the genus *Trapelia,* in having an areolate thallus (with protococcoid algae) and small hemiangiocarpic ascomata which open in a similar stellate manner. However, *Muhria* differs in several important characters from that genus and family: species of the Trapeliaceae mainly contain gyrophoric acid and the internal structures of the apothecia, as described by Hertel (1970), are quite different from those found in *Muhria.* They have freely growing, thin, branched and anastomosing paraphyses which are not or scarcely thickened apically, and the asci are thin-walled, mostly non-amyloid and without any apical apparatus. These differences are so fundamental that it appears impossible to include *Muhria* in the Trapeliaceae.

Some similarities with two crustose members of the Stereocaulaceae, *S. leucophaeopsis* and *S. tornensis* (see Purvis & James, 1985) lead us to consider this family, and indeed except for the very notable difference in ascocarp development—which in the Stereocaulaceae is gymnocarpic—nearly all other characters are consistent with those of *Muhria.* Lobaric acid and atranorin is a common chemical combination in that family, as is the association with cyanobacteria and the negative amyloid reaction of the hymenial gelatine; the paraphyses, asci and spores are of the same kind as in *Muhria,* as well as the kind of pycnidia and conidia.

This relationship may appear surprising as one normally connects this family with species showing ± well-developed pseudopodetia. However, as pointed out by Lamb (1951, p. 530) there are neotenic forms in some of these species, which fruit on the primary squamulose thallus (Fig. 11A). Such forms give an indication of the course of evolution, and Lamb (op. cit., p. 563) has on this basis postulated crustose species as the ancestral form of this genus. *Stereocaulon leucophaeopsis* (Fig. 11B) and *S. tornensis* come close to Lamb's postulated ancestral form, but their cephalodia are more primitive than indicated by him (loc. cit.), their apothecia are produced in the blue-green part (exactly as in *Muhria*), and several cyanobacterial taxa are found together in a rather loosely organized structure. Maybe we here find the origin of the unusual situation that the cephalodia on the same *Stereocaulon* pseudopodetium may have different algae (*Gloeocapsa, Scytonema, Stigonema* or *Nostoc*), for example, in *S. ramulosum* (Lamb, op cit., 543).

Although *Muhria* has many characters in common with the Stereocaulaceae and its crustose growth form is not an obstacle for its inclusion in that family, the hemiangiocarpic apothecial development is so fundamentally different from the other members of the family that its inclusion would seem problematic. However, Jahns (1970, p. 30) reports that *Stereocaulon dactylophyllum* occasionally forms abnormal apothecia, the early stages of which are hemiangiocarpic (op. cit., fig. 78). This may, like the neotenic forms, indicate something about the phylogenetic origin. Therefore, the placing of *Muhria urceolata* as a primitive member of the Stereocaulaceae is entirely plausible.

Indeed, *Muhria* has so many characters in common with *Stereocaulon,* that an inclusion in that genus has been considered. However, the hemiangiocarpic ontogeny of the apothecia is so basically different from that normally found in *Stereocaulon,* that a new genus is needed to accommodate it.

PHYTOGEOGRAPHY

The discovery of such a primitive taxon in parts of Scandinavia that were totally glaciated during the Quaternary is unexpected. However, similar cases are known. Very relevant in this connection is *Erioderma pedicellatum* (Hue) P. M. Jørg. which had one of its few localities in Europe near the type of locality of *Muhria urceolata* (Ahlner, 1948, p. 42). *E. pedicellatum* seems to be a primitive member of the genus *Erioderma* (Jørgensen & Arvidsson, in prep.), closely related to species of the genus *Leioderma* (Galloway & Jørgensen, 1987). Most likely both these species invaded Scandinavia after the retreat of the glaciers. Their present restriction to Scandinavia may be explained ecologically. However, for *Muhria urceolata,* discovery outside the region can be expected. It is easily overlooked, often looking like an indistinct, poorly developed, sterile, sorediate crust, and it may prove to be quite widespread.

KEY TO THE CRUSTOSE STEREOCAULACEAE OF NW EUROPE

1. Thallus squamulose, forming a ± continuous crust, not associated with cyanobacteria, never sorediate; apothecia formed on the squamules, some on short pseudopodetia (Neotenic forms of normally pseudopodetiate species of *Stereocaulon*) 2
\+ Thallus areolate, areoles ± discrete, ± sorediate, associated with cyanobacteria; apothecia formed between the areoles, never on pseudopodetia 3
2. Squamules uniformly coloured, ± digitate; W Sweden
Stereocaulon dactylophyllum f. *sessile* Lamb
\+ Squamules with tumid whitish margins and dark centres, ± peltate; W Norway, W Sweden and Scotland
Stereocaulon vesuvianum f. *sessile* (H. Magn.) Lamb
3. Areoles uniformly grey-green, margins not tumid or raised, convex; apothecia small, less than 0·5mm diam., initially globose with star-like opening and later urceolate, pale chestnut brown; Norway and Sweden. . . . . *Muhria urceolata* P. M. Jørg.
\+ Areoles with tumid or raised whitish margins, darker centrally, concave to flat; apothecia larger, to 1·5mm diam., flat to convex, dark brown to blackish. 4
4. Thallus PD+, UV− (stictic acid); spores 20–25μm long; on acidic, often iron-rich rocks; Norway, Sweden, Scotland
Stereocaulon tornensis (H. Magn.) James & Purvis*
\+ Thallus PD−, UV+ (lobaric acid); spores 30–40μm long; on basic, heavy-metal rich rocks; Norway, Sweden, British Isles
Stereocaulon leucophaeopsis (Nyl.) James & Purvis*

*Dr B. J. Coppins has pointed out to us that Alstrup recently (1986) described two new crustose *Stereocaulon* taxa from Greenland. Alstrup most kindly on short notice put the

material at our disposal. *Stereocaulon crustatum* Alstrup is ecologically, chemically and morphologically identical with *S. leucophaeopsis*. The spores, which we find to be 5–7-septate and 35–45μm long, are slightly larger than that previously recorded for this species, a difference we regard as taxonomically insignificant. *Stereocaulon vesuvianum* var. *obscuresorediatum* Alstrup is sterile but is so similar to *S. tornensis* in the other characters that we do not hesitate to place it in synonomy with that name. Both species are here recorded for the first time outside Europe, and may prove to be widespread, for example in N America.

Acknowledgements

We are much obliged to Mr L.-E. Muhr (Karlskoga) who provided us with most of the specimens of this new taxon, and we have in gratitude named the genus after him. We are also indebted to Mr E. Timdal (O) and the directors and curators of the herbaria mentioned on p. 581 for sending us material. We also express our sincerest thanks to Dr B. J. Coppins (E), Mr P. W. James (BM), Prof. R. Santesson (Uppsala), and Mr E. Timdal for valuable discussions. We are also indebted to Mr J. Berge, Mrs S. Herland and Mr T. Tønsberg (Bergen) and Dr O. W. Purvis (Reading) for assistance and support in several ways during the preparation of this paper.

References

Ahlner, S. (1948). Utbredningstyper bland nordiska barrträdslavar. *Acta Phyt. Suec.* 22.

Alstrup, V. (1986). Contributions to the lichen flora of Greenland. *Int. J. Myc. Lichenol.* 3:1–16.

Galloway, D. J. & Jørgensen, P. M. (1987). Studies in the lichen family Pannariaceae II. The genus Leioderma. *Lichenologist* 19 (in press).

Henssen, A. & Jahns, H. M. (1973). Lichenes. *Eine Einführung in die Flechtenkunde*. Stuttgart ('1974').

Hertel, H. (1970). Trapeliaceae—eine neue Flechtenfamilie. *Deutsche Bot. Gesellsch.* N.F.4:171–185.

Jahns, H. M. (1970). Untersuchungen zur Entwicklungsgeschichte der Cladoniaceen unter besonderer Berücksichtigung des Podetien-Problems. *Nova Hedwigia* 20:1–177.

James, P. W. & Henssen, A. (1975). A new species of Psoroma with sorediate cephalodia. *Lichenologist* 7:143–147.

—— & —— (1976). The morphological and taxonomic significance of cephalodia. In Brown, D. H., Hawksworth, D. L. & Bailey, R. H. (eds), *Lichenology: Progress and Problems,* 27–77. London & New York.

Jørgensen, P. M. & Arvidsson, L. (in prep.) Studies in the lichen family Pannariaceae III. The genus Erioderma.

——, Vězda, A. & Botnen, A. (1983). Clathroporina calcarea, a misunderstood lichen species, and a note on the genus Clathroporina in Europe. *Lichenologist* 15:45–55.

Lamb, I. M. (1951). On the morphology, phylogeny and taxonomy of the lichen genus Stereocaulon. *Can. J. Bot.* 29:522–584.

MUHR, L.-E. (1987). Lavfloran i Gravbäcksravinen i Värmland. *Svensk Bot. Tidskr.* 81:17–36.

PURVIS, O. W. & JAMES, P. W. (1985). Lichens of the Coniston copper mines. *Lichenologist* 17:221–237.

WHITE, F. J. & JAMES, P. W. (1985). A new guide to microchemical techniques for the identification of lichen substances. *Bull. Brit. Lichen Soc.* 57 (Suppl.): 1–41.