STUDIES ON THE GENUS
COENOGONIUM EHRENBERG

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ABSTRACT

STUDIES ON THE GENUS COENOGONIUM EHRENBERG

by Flordeliz R. Uyenco

The present work is primarily a study of the morphology and taxonomy of the lichen genus Coenogonium Ehrenberg. This study was undertaken for the purposes of establishing the taxonomic bases on which this genus is placed and the characters by which the species of Coenogonium are separated. It was hoped that a detailed study of a homoiomerous lichen genus where the algal symbiont is more conspicuous than the mycobiont would contribute to the solution of the nomenclatural problems recently raised by taxonomists as to whether lichen names belong to the lichen thalli or to the fungal components.

Algal characters such as, the shape and sizes of the cells and the shape of the thallus, have been used in the past to identify the species of Coenogonium. This study was made to determine the value of these characters in the taxonomy of the genus. The specificity requirements of the fungus are established in the study; i.e., whether the different fungal species are obligately symbiotic with one algal species, or whether the lichen fungi may have different species of algal symbionts. The disposition of partially lichenized algae and of sterile thalli are also discussed and the role of the lichen fungi in determining the types of thalli is demonstrated.

This investigation is based upon a large number of herbarium specimens obtained from different herbaria in the United States, and on fresh material collected in Florida and Panama. The value of cultural work to supplement the classical taxonomic methods is considered in order to establish the role of the phycobionts in the taxonomy of the genus and to determine which species of Trentepohlia grow in symbiosis with the fungus. In this study of the genus Coenogonium, most of the emphasis has been placed on the lichen fungus morphology; i.e., the structure of the apothecia and of the spores.

A historical review of the taxonomical, morphological and physiological studies was made and information has been added to these from personal observations. The ecology and distribution of the genus Coenogonium are presented along with a distribution map of the species.

Keys to the species of the algal symbionts and of the lichen genus Coenogonium have been written, the latter based on some characters not previously considered by any author. Six species of *Trentepohlia* and one species of *Physolinum* are included in the key. Of the original forty-eight species referred to as *Coenogonium* by earlier authors, eighteen species have been recommended for transfer to the genus *Trentepohlia* as valid algal species or as synonyms; four species are considered as belonging to the Fungi Imperfecti and two species are treated as synonyms of *Coenogonium Linkii*. Eight species are considered doubtful; fifteen species are recognized and accepted as valid and a key has been made for these. One species is rejected as having been based on two discordant elements.

Eleven plates containing forty-five figures, five tables and eight maps supplement the written text.

STUDIES ON THE GENUS *COENOGONIUM* EHRENBERG

By

asalan
Flordeliz R. Uyenco

A THESIS

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INTRODUCTION

Purpose of the Study

This study was made for the purpose of establishing the characters by which Coenogonium species should be determined. In the past, workers have used the characters of both the alga and the thallus for the determination of the lichen-fungus. It was hoped that a detailed study of a lichen-fungus where the alga assumed a major role in lichen morphology would contribute to the solution of the nomenclatural problems recently raised by taxonomists as to whether lichen names should belong to the lichen thalli or continue to belong only to the fungal components.

Since the form of the thallus is mainly that of the alga itself, it was also the objective of this investigation to determine whether the different fungal species are symbiotic with only one definite algal species, or whether these lichen-fungi may form lichen thalli with various species.

The species of Coenogonium have been distinguished in large part on the shape and size of the algal cells.

It is possible, however, that the "species" named in such a manner may actually include different lichen-fungi, especially since many lichens were described in their sterile forms.

It was further necessary to demonstrate whether the fungus determines the shape of the thallus or if different species of algae form different thalli. The extent of the lichenization of the species of algae as well as environmental conditions were studied to determine their role in the different external forms of the lichen thallus. Only if the thallus characters were determined by the fungus could they be used in identification.

In addition to the basic questions concerning the nature of the species in *Coenogonium*, it was hoped that a workable key to the species of this genus could be prepared. Therefore, descriptions and illustrations of all the species examined were prepared.

Historical Review

The genus *Coenogonium* was founded by Ehrenberg in 1820 with the single species *C. Linkii* which was collected from the bark of trees at Santa-Catharina Island off the coast of Brazil. Ehrenberg observed in the apothecia of this genus the same structures found in the fructifications of Peziza and other fungi; that is, the surface of the apothecium is formed by elongated capsules that are stalked and containing spores which are not bare, contrary to what Acharius (1798) had supposed. Ehrenberg further observed in this genus the same organization found in the other lichens.

Coenogonium has been shifted in the Plant Kingdom from one group to another, and variously classified by systematists as alga, fungus or lichen. A study of the original descriptions of the forty-eight species belonging to this genus mention Chroolepus as the gonidial (algal) symbiont. Early authors described the thallus as consisting of confervoid or cylindrical cells with yellowish-green contents surrounded by colorless slender threads. Wainio (1890) mentioned Trentepohlia species as constituting part of the thallus of Coenogonium.

Much of the early investigations on the genus Coenogonium involved principally the system of classification, treating the algal and fungal symbionts as of equal taxonomic importance. The genus was placed in a confervoid algae by Agardh in 1824, a classification which was considered erroneous by Fée (1824) on account of the organization of the thallus, it being composed of cylindric fibers and attaching itself on the substratum by its side, in a manner of certain fungi. Fée, (*op. cit.*) after studying the asci, proposed that the Family Cornicularìae, previously used by Fries (1825), include the genus *Coenogonium*. Fries (*op. cit.*) assigned the genus *Coenogonium* to the Tribe Coenogoneae and the related genera *Collema*, *Leptogium* and *Lichina* to the Tribe Collemaceae and assembled the whole group under the Family Byssacées. His classification based on the fungus characters of these lichens greatly influenced nearly all subsequent lichen systematists, the first of whom was Endlicher (1836) who included the genus *Coenogonium* in the Tribe Collemaceae established by Fries, disregarding the Tribe Coenogoneae to which the genus originally belonged. Endlicher then grouped the other genera in his new Tribe Lecidineae.

Montagne (1846) considered *Coenogonium* as a degenerate lichen and therefore an anomalous genus and included it in the Family Byssacées designated by Fries to unite closely the lichens and the algae. Montagne, however, believed that the Family Byssacées emphasized the characters of the fungus too much and suggested that the Subfamily Collémacées be established to define the lichen properties of these plants more clearly. Montagne was the first to separate the plants whose ascocarps are open at maturity from those whose ascocarps remain closed and established the Orders Gymnocarpes and Angiocarpes to apply to these plants respectively. He extended his analysis of Fries' classification system by reorganizing the genera under the Family Byssacées into three tribes; namely, Collémacées, Cénogoniées and Lichinées. Montagne assigned the genera *Collema*, *Leptogium*, *Stephanophorus* and *Omphalaria* to the Tribe Collémacées; the genera *Coenogonium*, *Cilicia*, *Ephebe* and *Thermutis* to the Tribe Cénogoniées; and the genera *Lichina* and *Paulia* to the Tribe Lichinées. Payer (1850) adopted Fries' classification in part, and included the Tribes Collémacéae and Coenogonieae under the Family Lichens next to the Family Pezizes.

The lecidioid characteristic of the apothecium of the genus *Coenogonium* led Nylander (1858, 1862) to believe in the close relationship between this plant and the Lichineos and, following Payer's scheme, placed the genus in the Tribe Lecideinei under the Series Placodei of the Family Lichenacei. Nylander's classification system and the studies of Schwendener (1860) on the nature of lichens had important consequences on the taxonomy of the lichens.

De Bary (1866) considered Montagne's classification as a concentration of these plants in the fungi stressing the significance of the lichen characters that the genus *Coenogonium* possessed.

Thwaites published in 1849 a new genus of minute plants which he called Cystocoleus, to contain a form of Byssus nigra Huds., also called Chroolepus ebeneus. He described the thallus as growing by means of apical growth and consisting of rows of attenuate cylindrical cells with colorless cellulose walls and green-colored contents. These cells are surrounded by a dense covering of dark brown hyphae with rough walls and colorless contents. Hariot in 1890 recognized the composite nature of this plant and excluded Chroolepus ebeneus (=Cystocoleus ebeneus) from the genus Trentepohlia. He also noted that Persoon's Racodium rupestre was a synonym. De Bary, likewise, regarded the Cystocoleus of Thwaites as synonymous with Racodium rupestre Pers., and correctly described it as associated with Chroolepus. Glück later in 1896, treated Thwaites' material and called it Coenogonium germanicum, noting that the thallus consisted of Chroolepus filaments. It is thus evident that this species had been recognized primarily on the basis of the algal cells or on the color of the surrounding hyphae.

Karsten (1861), Schwendener (1862) and Nylander (1862) contributed much to the studies on the morphology of the genus and described several species, some of which were based on the algal constituents of sterile thalli.

Flotow (1869) in recognizing the systems of Fries and Nylander, divided the lichens into two series: Lichenes Heteromerici and Lichenes Homoeomerici, both of which, he believed, incorporated the principal characters on which the Family Lichens of Payer and Family Byssacées of Fries, as well as the Family Lichenacei of Nylander were based.

Tuckerman, in 1872 and later in 1882, organized the genus *Coenogonium* under the Series Gymnocarpi in which the apothecia are normally open and the spores are exposed. He established the Tribe Lecideacei under this Series to include those with free, round, open and disk-like apothecia bordered by a proper exciple. The Family Coenogoniei was placed under this Tribe to separate those with horizontal thallus and confervoid filaments. Wainio, in 1890, however, raised the Family into the Tribe Coenogonieae and established the Family Coenogoniaceae to include the single genus, *Coenogonium*.

Müller (1881), in discussing *Coenogonium pannosum*, stated that the algal symbiont of this lichen belongs to the Graphideen and that the genus *Coenogonium* is closely related to the genus *Biatorinopsis* Müll. Arg. on the basis of their spore characters.

Shirley (1889) designated the Tribe Lecideinei in classifying the genus Coenogonium and emphasized the absence of the cortical tissue usually found in lichens.

Wainio (1890), Lindau (1895) and Clements (1897) incorporated the genus Coenogonium in the fungi as evidenced by the schemes of classification that they presented. Wainio, in organizing the Class Ascophyta, assembled the Discolichenes and the Discomycetes in one group called Gymnocarpeae and the Pyrenolichenes and the Pyrenomycetes in the Pyrenocarpeae. He followed Montagne's arrangement of the tribes, restoring the genus Coenogonium into the Tribe Coenogonieae. He justified his scheme of classification on the homoiomerous structure of the thallus. The two types of spores of the genus Coenogonium became the basis later in the establishment of two Sections of the genus under the Tribe Coenogonieae. Clements in 1909 classified the genus under Order Pezizales, separating those plants with Chroolepus constituting their thalli as belonging to the Family Chrysotrichaceae, and further dividing the genus into the Section Holocoenis to include those with one-celled spores and the Section Coenogonium to comprise those with one septate spores. Wainio later in 1921, extended his analysis of the Family Coenogoniaceae, still upon the system he established in 1890, and divided the genus into two sections: Section Coenobiatora, to include all the species having one-celled spores, and the Section Coenobiatorina, for those with two-celled or one-septate spores. Lindau (1895) followed the classification of Tuckerman but proposed the addition of the Series Gymnocarpaceae to include those whose hymenium do not open with a pore but remain closed and spread out only at maturity. He organized the sub-group Cyclocarpineae under the Gymnocarpaceae and re-established the Family Coenogoniaceae to include the single genus Coenogonium and excluded the Tribe Coenogonieae in his classification of the genus.

Clements (1897), in his study on the polyphyletic disposition of the lichens, recognized the importance of the spores and placed the genus Coenogonium in the Family Chrysotrichaceae. He and Wainio later divided the genus into the two Sections as described above. This scheme was adopted by all subsequent workers of this genus.

Reinke (1894) and Schneider (1905) had opposed the classification systems organized by the earlier workers arguing that these incorporated the lichens in question in the system of the fungi.

In the lichen taxonomy of Zahlbruckner (1905, 1926) which is now generally used, the Coenogoniaceae and related families are placed among the Cyclocarpineae (a position first used by Lindau) which, to a great extent, are arranged according to their algal hosts. Zahlbruckner placed the genera *Coenogonium* and *Racodium* together in the Family Coenogoniaceae on the bases of their confervoid algal symbionts and on the homoiomerous character of their thalli. These genera are very similar in their appearance and habitat but are distinguished by their algal symbionts. In *Racodium*, the investing fungus lies in straight unbranching lines along the *Cladophora* filaments, while in *Coenogonium*, the dark fungal hyphae branch repeatedly, and wind around the irregular bulging cells of the *Trentepohlia* filaments. Zahlbruckner classified the Family Coenogoniaceae under the Ascolichenes and included the Sections Holocoenis and Coenobiatorina in distinguishing the different species in the genus. According to Zahlbruckner, *Coenogonium*, *Cystocoleus* and *Racodium* form an autonomous family, the Coenogoniaceae. Santesson (1952) disagreed to this idea and suggested that *Racodium* and *Cystocoleus* must be transferred to the lichenized Fungi Imperfecti, while *Coenogonium* is very closely related to *Dimerella* and should therefore be included in the Gyalectaceae. Zahlbruckner constituted the Family Gyalectaceae mainly on the algal characters of the lichens and included in it genera characterized by the presence of Trentepohlia, Phycopeltis, and Scytonema as phycobionts. Santesson, however, believes that some genera referred to the Gyalectaceae by Zahlbruckner are probably more closely related to the genera of other families than to those forming the natural center of the Gyalectaceae; such as Gyalecta, Dimerella, Microphiale and Ramonia. Santesson grouped the genera Dimerella, Coenogonium, Gyalecta and Semigyalecta together in the Family Gyalectaceae. He maintains that the anatomy of the apothecia and the characteristic thin-walled asci of these genera prove the very close relationship that exist among them. The close relationship between Coenogonium and Dimerella was reported as early as 1881 by Müller who stated that Coenogonium is closely related with his genus Biatorinopsis (=Dimerella) on the basis of their spore characters. Malme (1937) concurred with the statement of Müller and used spore characters to delimit the species of this genus.

Smith (1906), in examining the British forms of Byssus, Racodium and Cystocoleus, believed that these genera were associated with Chroolepus and therefore included them in the genus Coenogonium.

The remaining studies on Coenogonium have been primarily systematic. Hooker (1867), Leighton (1869), Krempelhuber (1876) among others, have added new species, or listed and redescribed old ones from various tropical and temperate regions throughout the world. Very few fundamental studies on the structure and development of the Coenogonium have been added.

The first description of the development of the apothecium of Coenogonium was made by Karsten in 1861 who described the fertilization apparatus of this plant as being analogous to the archegonia of the higher cryptogams. His work was severely criticized by Schwendener and Nylander who considered Karsten's descriptions to be without foundation since he did not examine the plants microscopically.

Fink (1915) adhered to the Class Ascolichenes of Zahlbruckner and placed the Family Coenogoniaceae within his new large group Lecanorales which only included lichens. This arrangement, in reality, is the same as the group Cyclocarpineae in the pure lichen system of Zahlbruckner. Fink's classification is based largely on the algal hosts and considered Coenogonium and Racodium as related to those belonging to Gyalectaceae and Ephebaceae. Nannfeldt (1932) later used Fink's Order Lecanorales in a somewhat wider sense in his new system of the Ascomycetes where it is included as a special group among the Ascohymeniales.

Dodge (1933) placed Family Coenogoniaceae between Rocellaceae and Ephebaceae, both of which have *Scytonema* as the algal symbiont. He suggested, however, that the Family Coenogoniaceae would be better dropped and the species distributed among the fungi and algae. He considers this family very aberrant among the lichens in several respects and recognizes the relationship of *Coenogonium* to *Patinella* and *Orbilia*. Santesson (1952), on the other hand, disagreed with Dodge and finds, instead, that *Coenogonium* is very closely related to *Dimerella* and *Gyalecta*, and must be included in the Family Gyalectaceae. The diagnostic value of the apothecium in deciding the speciation in *Coenogonium* has been emphasized by Santesson and he proposed that sterile specimens be considered as lichenized *Trentopohlia*.

A more exact knowledge of the composition of the genus *Coenogonium* led to the various classifications in which it has been placed by subsequent investigators. On account of the presence of oil drops containing carotene in their cells, two algal symbionts, *Trentepohlia* spp. Mart. and *Physolinum monile* Printz, were recognized. *Chroolepus* was later used as a section of the genus *Trentepohlia* under the Family Trentepohliaceae by Printz in 1939.

Collins (1928) in discussing the genus *Trentepohlia*, indicated that the terrestrial habit of the species of *Trentepohlia* makes them very accessible to lichen-forming fungi, and in many cases, it is rather an exception to find an alga that is completely free of fungi. Collins described *T. rigidula* (Müll. Arg.) Hariot as a species always epithallic on lichens and which may be attached either to rocks or to the bark of trees. De Toni (1889) mentioned *Trentepohlia villosa* as associated with *Coenogonium confervoides* Nyl. and *Trentepohlia monilia* de Wild. associated with *Coenogonium rigidulum* Müll. Arg.

After reviewing the literature on the genus *Coenogonium*, the writer believes that a critical evaluation of the morphological characteristics used in the classification of *Coenogonium* is necessary. It can be seen that in the Family Coenogoniaceae, the criteria in determining the species have emphasized thallus morphology and algal measurements, relegating the apothecium and the other fungal characters to a minor role without the proper understanding of their significance and value as a taxonomic feature.

THE LICHEN THALLUS

Morphology of the Thallus

The external form of the thallus of Coenogonium species is quite variable. Coenogonium Linkii, on which Ehrenberg constituted the genus, is characterized by a loose, spongy-byssoid thallus, its filiform and branched filaments forming a more or less determinate round or nearly reniform and flat tissue. The thallus is firmly attached to the substratum by one margin from which it grows erect or pendant. Occasionally, the Trentepohlia filaments composing the thallus become interwoven into a more or less parallel tissue, giving an appearance of a zonate, lamellate and radially-organized thallus. In C. Linkii, the algal filaments are evidently bound together so that at a later stage, the plant becomes composed of many imbricate thalli that are thinner towards the periphery.

In addition to the common and typical shelf-like forms of C. Linkii and C. Leprieurii, the thallus may be cushion-shaped and round, with the filaments comprising it firm, straight and closely aggregated; or it may be crust-like, as in *C. epiphyllum*; or densely-velvety, appearing like a dark felt of short hairs, as in *C. interplexum*. In several species of *Coenogonium*, the thallus may be partly or wholly adnate to the surface, occasionally expanded and effused and exhibiting a horizontal growth. Other species may be prostrate, adhering to the substratum as very thin, delicate and widely spreading filaments.

More rarely, the thallus of *Coenogonium* species forms small, erect and soft turf-like, homoiomerous growths on the surface of the substratum. In *C. moniliforme*, in which the algal symbiont is *Physolinum monile* (de Wildem.) Printz, the effused thallus is made up of short, moniliform filaments. In still other *Coenogonium* species, the branching threads of *Trentepohlia* are loosely woven together to form an adnate, irregularly tomentose and diffused thallus.

The upper surface of the thallus of *Coenogonium* is generally smooth, but it may also appear as if it were trimmed and wrinkled, as has been observed in *C. pannosum*.

The color of the thallus varies from yellow to golden-yellow, or green to yellow-green. It has been found that the color of the thallus is of no significance since the plant loses much of its color upon drying, as does

Trentepohlia. The filaments of the thallus of *Coenogonium* do not imbibe water easily, and it is particularly this characteristic that differentiates this genus from all the other lichens and provides its habitat restrictions.

Since the thallus is homoiomerous, there are no cortical, medullary or algal layers. The filaments of the algae are merely surrounded by fungal hyphae.

Lichen Substances

Attempts by the writer to identify lichen substances in the thallus and apothecia of the different species in the genus *Coenogonium* by the use of the standard chemical reactions were unsuccessful. Early investigators reported color reactions of the hymenium of certain species to dilute iodine solution, but the results are inconclusive.

Sato (1933) noted that the hymenium of *C. boninense* turned wine red in iodine. The same color reactions were observed by Nylander (1862) in the hymenium of *C. implexum* and by Wainio (1896) in *C. Leprieurii* and *C. subvirescens*. Zahlbruckner (1909) and Malme (1937) reported dark red color reactions of *C. interpositum* and *C. velutinum* with dilute iodine, while the hymenium of *C. Leprieurii* turned sordid red upon treatment with the same chemical. Tuckerman

(1862) reported that *Coenogonium moniliforme* gave a deep green color reaction with iodine but did not react with potassium hydroxide. Zahlbruckner (1909) further reported the hymenium of *C. curvulum* turning at first blue but later to yellow with iodine. Wainio (1921) indicated a dark blue color in the hymenium of *C. epiphyllum* when treated with iodine and a wine red color reaction in *C. subvirescens*. *Coenogonium disjunctum* and *C. Linkii* showed no color reactions with iodine, according to Nylander, and he added that *C. interplexum* changed to dark violet when treated with the same solution.

The absence of color reactions with paraphenylenediamine and potassium hydroxide when applied to the thallus and apothecia of the different *Coenogonium* species indicate that these plants do not possess the depsides and depsidones of more advanced lichens. It is believed that the different color reactions of the hymenium with iodine solution cannot serve as a taxonomic method in distinguishing the species. Dughi (1942) stated that there are in reality no negative reactions with iodine on lichen tissues provided that the concentration of the iodine is sufficient in every case. A positive and negative reaction to iodine refer to the special concentration of the chemical and the degree of reaction is the same in all specimens of the same "species" or "variety" and is independent of their age; or from thallus to thallus and even in different parts of the same thallus. In the present study, the different color reactions of the apothecia to iodine can be ascribed to the concentration of the iodine solution used. It can be inferred, however, that <u>Coenogonium</u>, being a homoiomerous lichen, does not possess an advanced type of thallus which might explain the absence of lichen substances commonly found in the more advanced forms.

Degelius (1954) found in his studies of the lichen genus <u>Collema</u> that the constancy of the reaction of the <u>Nostoc</u> alga to iodine varies from one species to the other. He remarked that the positive reaction depends on the presence of glycogen and has nothing to do with the fungus.

It is the opinion of the writer that the use of chemical reactions in separating the species in many other lichen genera cannot be used with the genus <u>Coenogonium</u>.

A polyhydroxy alcohol or sugar alcohol has been reported in certain species of <u>Trentepohlia</u>. This 4-carbon compound, known as erythritol, is usually present up to a concentration of 1.4% in the cells (Lewin, 1962). This compound contains a greater amount of photosynthetic energy ("reducing power") than do the corresponding sugars.

Several species of Trentopohlia have been reported positive for cellulose I, an important constituent of the cell walls. No sterols have so far been detected in any species, a condition that is considered anomalous since this plant reproduces sexually.

Ecology

The lack of complete ecological data on the collectors' labels presented some difficulties in the explanation of the ecological problems relative to the distribution of this lichen genus. In many instances, the exact location and substratum were not specifically defined. For example, C. Leprieurii bore only such information on the herbarium label as "On trees" or "On forest slope," and very often, only the country from which the material was collected was given, the specific locality having been omitted. These data would have been useful in interpreting the ecological distribution of the species of Coenogonium.

All altitudes and elevations have been converted to meters and insofar as possible, the scientific names of the tree substrates were obtained.

An analysis of all the habitats reported for the genus Coenogonium reveals that this is mainly a tropical genus belonging almost exclusively to warm, humid regions. It is widely distributed and occurs principally on the bark of trees, often associated with mosses and hepatics. Generally, damp localities which receive continuous precipitation are suitable places for the growth of this lichen. Fée (1824) mentioned Coenogonium as growing on the leaves of cinchona and angostura trees in Brazil. Santesson (1952) listed seven foliicolous species, two of which he considered as probably more or less obligately foliicolous lichens and the others as only facultatively foliicolous.

Since climatological data for the habitats reported for Coenogonium are not available for all the collections, it is not possible to make a detailed discussion on the habitat requirements of this genus, but generally speaking, it can be noted that the species of Coenogonium range in ecological distribution from high altitudes to sea level. These plants do not exhibit great tolerance to intense sunlight as evidenced by the fact that they occur abundantly in shaded areas, on the lower portions of the trunks of old trees and on the under side of branches and leaves of living trees. Species growing on leaves are characterized by their delicate, veil-like thin thalli which are so densely compressed on the under surface of the leaves that they are distinguished from one another with difficulty.

Coenogonium is rarely found on the surface of damp rocks. Two collections from Cuba and the Philippines were identified as *C. Leprieurii* and *C. disjunctum*, respectively.

The species of *Coenogonium* grow abundantly in tropical rain forests. In the drier parts of the tropical regions, they are commonly found in the montane mist forests where the increased elevations not only compensate for a drier climate but also provide moisture in the form of mist. Regions where dense forests prevail and where the trees are sheltered from wind and sunlight yield a variety of species of *Coenogonium*. Many forms of this lichen inhabit trunks, branches and twigs of living trees. *C. interplexum* has been collected from a dense wet limestone forest in Guatemala at an altitude of 900-1500 meters. The forest slopes of Cuba, with an altitude of 600-700 meters, yielded a rich collection of *C. Linkii* and *C. Leprieurii* which were found growing among mosses. An apparently similar slope in China also yielded *C. Leprieurii* at an elevation of 480 meters. It is interesting to note that *C. Leprieurii* seems to be the most cosmopolitan species in the group in that it occurred in all levels of altitude, ranging from

10 meters, in Costa Rica, to 2000 meters, in the Philippines. It grew on the banks of rivers in Brazil and the flood plains of Rio Sandalo in Costa Rica. *Coenogonium Leprieurii* was collected from exposed roots of a forest tree in a deep ravine in Jamaica at altitudes of from 840 to 1524 meters. It was likewise found on the bark of a palm tree and on evergreen trees in British Honduras and Mexico, respectively. A Spruce collection from the Amazon basin in Brazil showed a good growth of this species on leaves.

The bases of trees in the swampy woods of Louisiana provided good growth of *C. interplexum*, while *C. Linkii* dominated the growth on the bark of oak and other deciduous trees in Florida. *Coenogonium disjunctum* occurred in the summit forest of Panama and Costa Rica (about 1300 meters elevation) and was also collected from the twigs and bark of large trees in the wet forests of Mexico and Honduras.

Coenogonium curvulum, a species reported by Santesson (1952) to be probably more or less obligately foliicolous, was growing on bark in a collection from Puerto Rico. The wooded ravine of Trinidad, Puerto Rico, the Dominican Republic and Haiti yielded the greatest variety in species of *Coenogonium*.

A noteworthy comparison of the growths of *C. Leprieurii* and C. Linkii can be made on the collections from a dense forest in Peru. Coenogonium Leprieurii occurred at 625-1100 meters altitude but at higher elevations, 1067-1900 meters, C. Linkii dominated the collections. This latter species also exhibited an interesting growth response in that it occurred at lower elevations (750-1000 meters) in open woods, but required higher altitude for its growth in dense forests. A similar situation in the occurrence of both C. Linkii and C. Leprieurii was observed in the Dominican Republic where the latter species occurred at 200-500 meters elevation while C. Linkii grew at 900-1220 meters altitude. This was likewise observed in collections from Haiti and Puerto Rico where C. Leprieurii tended to grow in lower elevations while C. Linkii was found in the higher altitudes. Both species, however, grew in the same range of altitudes in Cuba (600-700 meters) and in Colombia (1760-2300 meters).

Coenogonium was found frequently in the hammocks of Florida. This habitat consists primarily of a community of broad-leaved evergreens and large deciduous trees with occasional pines. Such habitats are raised somewhat above surrounding, usually wetter, areas made up of swamp forests and marshes. These mesic habitats provide subtropical conditions of high moisture throughout the year and little variation in temperature.

Four different species of *Coenogonium* were collected from habitats in Florida ranging from solution sinks to dense and low hammocks. Many collections came from the bark of trees, including *Quercus virginiana*, magnolias, hollies and some tropical species such as *Ficus aurea*, *Lyssoloma*, *Bursera* and the prominent palm (*Sabal*). *Coenogonium* was found primarily on the lower portions of the trunks of these trees, associated with mosses and hepatics. They would also be found on the smaller branches if there was enough shade and moisture.

Coenogonium moniliforme, also reported by Santesson (1952) as a facultatively foliicolous species, was collected from the bark of *Lyonea* and other deciduous trees in the hammocks of Florida. A collection of the same species was made from a dead branch (of a living tree?) in Guatemala. An ecological distribution of this species cannot be accurately made due to the inadequacy of the collection. This species has an almost crustose thallus and hence is easily overlooked in the field.

Coenogonium species are not commonly found associated with other lichens. The spreading, horizontal, and sometimes prostrate growth of this plant on the substratum probably provides an unfavorable shade to other lichen thalli and so hamper their development. Coenogonium grows in shadier and wetter habitats than tolerated by most other lichens.

Few works have dealt on the ecology of the lichen genus Coenogonium and much less is known about the correlation between the ecological factors and the fruiting stages of this plant. The correlation between such ecological factors and the distribution of the species would provide an interesting study by future investigators of this group of plants.

Distribution

The only Coenogonium hitherto recorded from continental Europe was found by Hugo Glück in Saxony and the Harz in 1896. Glück named it C. germanicum. This plant grew abundantly on a siliceous substratum and attained a considerable size, in one instance, up to 1.5 meters. Santesson (1952) pointed out that this plant is a lichenized Hyphomycete with dark brown hyphae and is probably a synonym of Cystocoleus niger (Huds.) Hariot or Racodium rupestre Pers.

A similar situation exists in the case of C. ebeneum Smith, originally described to occur on rocks in Great Britain and which Santesson (1952) considers to be synonymous with *C*. *nigrum* (Huds.) A. Zahlbr. It is also a Hyphomycete and, therefore, cannot be referred to the genus *Coenogonium*.

Hale and Culberson (1960) reported four species of *Coenogonium* from the United States and Canada: *C*. *disjunctum*, *C*. *interpositum*, *C*. *Linkii* and *C*. *moniliforme*.

The present study covers North America, Central America, West Indies, South America, Australia, New Zealand, Eastern Asia and West Africa. The material examined was drawn from the collections available in the herbaria of Michigan State University, University of Michigan, University of Washington, University of Florida, Missouri Botanical Garden, the United States National Herbarium and the New York Botanical Garden. Some specimens were collected specifically for this study by the writer in Florida. Living collections were also provided for this work by Dr. G. W. Prescott from Panama, Dr. D. B. Ward from Florida and Dr. A. J. Sharp from Mexico; the cooperation of these botanists is gratefully acknowledged. Specimens were placed in polyethylene bags and mailed in regular envelopes. It was found that specimens of *Coenogonium* remained viable for at least a week or ten days after they were collected.

Since the identification of the species of *Coenogonium* was based only on fertile specimens, the distribution of the species cannot be entirely accurate. The relative abundance of each species could not be determined due to the lack of collections in some of the regions, the unequal intensity of the collecting and the sterile condition of much of the material. It may be noted that some areas were thoroughly collected but the materials were unidentifiable and could not be represented on the distribution map. As illustrated in the map, the West Indies have been more thoroughly covered than any other area included in this study. Coenogonium Leprieurii appears to be the most abundant species in this region and it occurs in almost all the islands, commonly on the bases of trees in dense thickets. Coenogonium Linkii, however, is the most widely distributed species, occurring in all the tropical countries covered in the study.

The indicated distribution of the genus in North America shows clearly that it is entirely southern in range, with the exception of one collection of C. interplexum from southern Michigan. A sterile specimen was seen from Black River, Jefferson County in New York State. These two localities are certainly unusual for this lichen genus. Other species of Coenogonium are found along the southern Atlantic Coastal Plain and along the Gulf Coastal Plain to Texas.

Coenogonium Leprieurii has been mentioned as capable of maintaining itself at all altitudes and thus has a wider range of distribution than all the other species. Although it has not been reported as occurring in the United States, it cannot be safely said that it is absent in this region as it may have never been encountered in a fertile condition. According to the herbarium data, this species, however, was the most abundant in any of the regions where it has been reported. *Coenogonium Linkii* ranks second in relative abundance and was particularly common in the West Indies.

Coenogonium velutinum was identified from Jamaica and the Juan Fernandez Islands in the Pacific Ocean off the southern coast of South America, indicating a wide geographical range for this species. *Coenogonium interpositum* is as widely distributed as *C. Leprieurii* and *C. Linkii* but did not show the same relative abundance in the collections. This may be partly due to the unequal intensity of the field work or the absence of fruiting bodies in some of the material. Although *C. botryosum* is reported only from Mexico, it is possible that it occurs also in the other geographical areas for the same reasons stated above. If some species of *Coenogonium* have seasonal production of apothecia, the collectors might not have collected the thalli at the appropriate time and this might explain the paucity of fertile material of certain species.

Coenogonium acrocephalum, *C. tomentosum*, *C. curvulum* and *C. pannosum* were identified only in collections from Puerto Rico, Bahamas and Guadeloupe, all of which are in the West Indies. *C. acrocephalum* and *C. pannosum* were first collected from Brazil while *C. tomentosum* was first reported from New Zealand. *C. curvulum* was found growing on leaves in Java by Schiffner.

The tropical areas in Eastern Asia show a discontinuous distribution of the genus *Coenogonium*, perhaps due to the lack of collections. *Coenogonium Leprieurii* is common to all the collections from Borneo, Ceylon, China and the Philippines. The range of distribution of this species can be gleaned from the fact that it also occurred in collections from Australia and West Africa.

The presence of pycnidia was noted in some of the collections but since this reproductive structure cannot be used to determine the species, the collections could not be included in the distribution map. The infrequent occurrence of thalli with asexual fruiting stages may be related to the environmental conditions. It is believed that *Coenogonium* species do not display great versatility in their methods of reproduction, a feature, perhaps, of a homoiomerous lichen. Long distance dispersal of Coenogonium is believed to be achieved principally by the sexual spores which are hardly complemented by conidia.

An analysis of the table of distribution of the genus Coenogonium (Table 1) show no evidence of endemism.

Although the tables given for each country may be incomplete, it presents the relative extent of field work done in these areas. More material is needed from Asia, Africa, Australia and New Zealand.

Table 1. Distribution of Coenogonium species in the different geographical areas. X signs refer to material seen, circles refer to literature records of original collection.

COENOGONIUM Species	NORTH AMERICA					CENTRAL AMERICA					SOUTH AMERICA						
	Alabama	Florida	Louisiana	Michigan	Texas	Costa Rica	Guatemala	Honduras	Mexico	Panama	Bolivia	Brazil	Colombia	Ecuador	Juan Fernandez Is.	French Guiana	Paraguay
acrocephalum												0					
botryosum									X								
complexum						X			X	X	0		X				
curvulum																	
disjunctum	X					X		X	X	X							
implexum		X	X		X							X	X				
interplexum		X	X	X		X	X			X			0				X
interpositum		X	0						X				X				
Leprieurii						X	X	X	X	X		X	X			0	
Linkii		X	X			X			X	X		X	X	X			X
moniliforme		X					X										X
ornatum									X								X
pannosum												0					
tomentosum																	
velutinum															X		
Total No. of Species examined	1	5	3	1	1	5	3	2	8	4		3	5	1	1		4
	11					22					21						

	2						X	X									Peru
	2					X		X									Surinam
	3				X		X	X									Venezuela
	4		X					X	X	X							Bahamas
	4					X	X	X				0				X	Cuba
	4		X				X	X	X								Dominican Republic
	1							X									Grenada
	1			X													Guadeloupe
38	5					X	X	X	X					X			Haiti
	8	X		X		X		X	X	X	X						Jamaica
	9			X	X		X	X	X	X		X	X			X	Puerto Rico
	2				X		X							X			Trinidad
	1							X									Borneo
	1							X									China
7	1							X									Ceylon
													0				Java
	4						X	X	X			X					Philippines
	2		0		0		X				X				0		Australia & New Zealand
	1							X									West Africa

THE ALGAE

Trentepohlia occurs in all the species of Coenogonium so far reported except in C. moniliforme where the algal symbiont is Physolinum monilia (de Wildem.) Printz.

The Lichenized Algae

The following descriptions refer to the lichenized algae found in the lichen thallus.

Trentepohlia: The filaments are generally 14-36 µ in diameter with the main axis usually larger than the branches. They are septate and sometimes constricted at the septa. The cells are uniformly cylindrical or barrel-shaped and 1-3 times as long as wide. In some species of Coenogonium, the algal filaments are fasciculate-conglutinate in arrangement and the threads are held together by very short funiculi. Branching is less common with lichenized filaments as compared to free-living plants whose branches may be dichotomous, one-sided or more commonly, at right angles to the main filaments. The apical cells of Trentopohlia appear to be somewhat longer than the other vegetative cells of the filaments and are free from the fungal hyphae.

Physolinum: The filaments are branched and consist of torulose or chain-like cells which are globose or elliptic. The globose cells measure about 18 μ in diameter while the elliptic cells are 10-15 x 22-32 μ in size.

The Algae in Culture

Since it is not possible to identify the species of Trentopohlia from the lichenized filaments, it was necessary to study the algae in culture. The culture studies were also designed to:

(a) provide a solution to the problem of whether each fungal species is symbiotic with only one algal species;

(b) understand the range of morphological variation; and,

(c) demonstrate indirectly the influence, if any, of the fungus component on the alga in the symbiotic relationship.

Although it was not possible to obtain in culture the algal symbionts of all the reported species of Coenogonium, the knowledge and experience gained from the limited culture study were useful in evaluating the importance of the algae for the identification of the species of Coenogonium, particularly in the case of sterile material that was named by earlier authors solely on the basis of the vegetative morphology of the algal symbiont and the lichen thallus.

It is obvious that plants grow differently in culture media, but it is necessary that one should determine the characteristics which are least variable in relation to the environmental conditions and how these characters behave under laboratory conditions. *Trentepohlia* has been reported by Collins (1928) to be a very variable genus. Hansgirg (1888) described the extreme variability of this alga in culture and claimed that polymorphism is common in *Trentepohlia*. It is possible that the external environment is partly responsible for the variations in the morphology of the alga in nature. Moreover, one cannot overlook the fact that an alga may exhibit more variable characters once it becomes overgrown with the fungus hyphae.

Bornet (1873) gave an excellent description of the algal symbiont of *C. confervoides* and illustrated its relation to the fungus constituent in detail.

Glück (1896) in his report on *C. germanicum*, stated that the algal symbiont of this lichen is the green alga, *Trentepohlia germanicum*. Skuja (1933), however, believed that Glück's description of the alga tallied very closely with that of *Trentepohlia aurea*.

Another attempt at isolating and growing the algal symbiont in Coenogonium has been that of Skuja on C. nigrum (1933). This plant, which was found growing on bark of trees in Lettland, appeared as a black mass of felted filaments. Skuja cultured the filaments of the thallus in four types of media; namely, distilled water, tap water, Benecke nutrient solution and Benecke agar media. Parts of the bark of Picea, Betula and Corylus were introduced into the nutrient solution and Benecke agar medium before these were sterilized. Skuja observed the development of the alga and identified it as Trentepohlia umbrina. He found in his culture studies of the algal symbiont that differences exist in the vegetative growth of the algae in the four types of culture media. He noted that branches developed rapidly in the filaments of the plants grown in distilled water. Those cultured in tap water measured from 4 to 6 or 8 microns in width and from 14 to 37 microns in length. The end cells were 50 microns long. In the nutrient solution, the cells were 10 microns wide and were relatively shorter than the cells of the filaments grown in the previous two cultures. The filaments were greener, and the cells were longer in the agar culture, while the articulate cells (?) were thinner. The vegetative cells tended to become barrel-shaped in appearance in agar medium. The haematochrome pigmentation was more distinct in the middle portions of the cells, while the light-green chromatophores concentrated at the peripheral part of the cells. The cells grown in agar medium were wider (up to 12 microns), rounder and had thicker cell walls which were layered. Skuja observed akinetes in the filaments, which led him to believe that the algal synbiont he had cultured was Trentepohlia umbrina.

Karling (1934) made a similar study on the morphology of C. Linkii collected from Honduras. He cultured the filaments in Detmer's agar and observed the vegetative growth and reproduction of the Trentepohlia. Karling presented very good descriptions and illustrations of the structure and development of the globular zoosporangium (the only type he saw in his cultures), and the behavior of the zoospores. The structure and morphology of the alga under the cultural conditions were, however, abnormal and Karling was unable to identify the particular species.

Materials and Methods

Specimens of Coenogonium which have been recently collected from Panama by Dr. G. W. Prescott, Department of Botany, Michigan State University, and from Florida by the writer and by Dr. D. B. Ward, Department of Botany, University of Florida, were used for culture studies in the present investigation.

Pringsheim's soil-water biphasic system (1950) and Bristol's inorganic medium (modified) (Starr, 1960) were used for the purpose. Peat and loam soil were employed separately to determine which soil type would best support the normal growth of the alga.

For the soil-water experiments, three sets of culture flasks were prepared: for the first set 72 grams of sandy loam soil were placed in the bottom of each of 250 ml. Erlenmeyer flasks, and then 100 ml. of Pyrex distilled water was added. The pH of the mixture was adjusted to 6.2, using $NaHCO_3$ buffer solution. In another set, a small amount of $CaCO_3$ (about one-sixteenth of a teaspoon) was placed in the bottom of the flasks before the soil and water were added. The pH was set at 7.5. In the third set of culture flasks, 72 grams of peat-soil were used, adding 100 ml. of the distilled water afterwards, setting the pH at 5.0. The flasks were then plugged with cotton and steamed for one hour on two consecutive days. The purpose of steaming the culture flasks was to kill the micro-organisms in the soil, such as protozoa, fungi and bacteria which might interfere with the growth of the algae.

Another type of culture medium, Bristol's inorganic medium with the following modified formula, was also tried.

$NaNO_3$	10.0 g.
$CaCl_2$	1.0 g.
$MgSO_4 \cdot 7\ H_2O$	3.0 g.
K_2HPO_4	3.0 g.
KH_2PO_4	7.0 g.
NaCl	1.0 g.
Distilled water	940 ml.
Soil-Water (steamed)	10 ml.
pH	7.5

To this solution was added 12 grams of agar and subsequently autoclaved for twenty minutes at 15 pounds pressure. The medium was then poured on sterile petri dishes and allowed to solidify.

Individual filaments from the thallus were picked by means of fine forceps and were washed carefully in distilled water, using capillary pipettes for the purpose. Equal amounts of the washed fragments were then introduced into the flasks containing the three types of culture solutions, while the same amounts were plated by means of a sterile inoculating needle on Bristol's inorganic medium. The flasks and plates containing the isolates were then placed under continuous fluorescent light (approximately 350 foot candles). The cultures were kept in a lighted refrigerator maintained at a constant temperature of 22°C. The flasks were placed at a distance of about five inches below the source of light.

Observations

Two days after the start of the experiments, the cultures were examined for vegetative growth and reproductive structures, if any. Cultures using peat-soil-water medium were filled with profuse growths of fungi, with very little growth of the algae. Therefore, this set of the cultures was subsequently discarded. The set of flasks containing a small amount of $CaCO_3$ exhibited a good growth of the algae while no appreciable change was noted in the third set of flasks which contained plain loam soil. It seemed evident, from these observations, that a slightly alkaline medium supported a good algal growth and, hence, this type of culture medium was utilized for the rest of the study.

The algae were then washed and transferred into new culture flasks containing the small amount of $CaCO_3$ and sandy loam soil and were kept at the same temperature and exposed to constant illumination. The pH was maintained at 7.5-8.

The algae were examined periodically to detect the presence of reproductive structures which were needed for the identification of the algae. It was noted that the basic medium inhibited the growth of the fungus while the vegetative growth of the algae progressed. Four days after the transfer of the algae to the fresh culture solutions, the fungus constituent appeared to loosen from the algal threads and disintegrate, leaving the alga to grow independently. The cell walls of the alga thus appeared clear and almost devoid of the surrounding hyphae when seen under the high-power objective of the compound microscope. At the same time, branching tended to become more free. This greater tendency to branch in all directions appears to be associated to a certain extent with the absence of the fungus hyphae around the cells. In the lichenized alga in nature, it has been shown that the fungus develops strongly around new branches that are just beginning to form. Karling (1934) believed that the fungus mycelia inhibit the development of branches to a certain degree and thus produce the characteristic appearance of the algal filament in the lichen thallus.

After a period of one week, round or ellipsoid reproductive structures were found attached either laterally or terminally, to the cells of the filaments. These were either sessile on the vegetative cells or attached to special hooked stalk cells, singly or in a whorl. These structures were later determined to be either sporangia or gametangia. The algal filaments continued to produce new branches and the apical cells were much elongated. The cells assumed a brighter green color and the yellow and golden-red globules of haematochrome decreased perceptibly.

Growth on the agar medium was not evident until seven days after inoculation, at which time the algal filaments started to show vegetative growth by spreading out on the agar plate. The difference in the rate of growth of the algae in the two culture media may be partly due to the thickness of the agar which presumably hampered the rapid growth of the algal filaments. It was further observed that the characteristic greenish-brown color of the Trentepohlia filaments remained longer in the plants grown on agar medium than on those in the soil-water medium.

By subjecting the cultures to alternate 16-hour light and 8-hour dark periods, the liberation of zoospores could be induced. Biflagellated zoospores and isogametes (in various stages of fusion) were observed in most of the cultures, both in the soil-water medium and in the solid inorganic medium (Pl. 5, Figs. 3 and 4), although vegetative growth in the latter medium seemed to be slower. Reproductive structures and motile cells were observed almost simultaneously in both types of media four to seven days after the transfer of the algae from one culture medium to a fresh one. The cells producing the motile zoospores or gametes, as the case may be, were seen to be much larger and longer than the other cells in the filament. Drawings were made by means of a Zeiss Drawing Apparatus to show the reproductive structures and cells of each of the <u>Coenogonium</u> species cultured. Measurements were taken of the cells of the filaments bearing reproductive structures and these were compared with those of the filaments supporting the apothecia in the lichen thallus. The ratios of the width to the length of these cells were also determined in order to show the variations in cell sizes between the algae grown in culture and the algal symbionts as they grow in nature. It is presumed that the cells bearing the reproductive structures in culture would have reached the "peak" of their normal growth and differentiation and thus would serve as a good index for comparison with the cells of the fertile threads of the lichen.

Results

In the present investigation, six species of *Trentepohlia* were isolated and successfully grown to maturity in Pringsheim's soil-water medium and in Bristol's solid inorganic medium.

Trentepohlia arborum was identified as the symbiont of three species of *Coenogonium*; namely, *C. Linkii*, *C. interplexum* and *C. interpositum*. *Trentepohlia aurea* was observed to be the algal symbiont of *Coenogonium Linkii* and *C. interplexum*. Two cultures of *Coenogoneum Leprieurii* presented two different algal symbionts; nemely, *Trentepohlia umbrina* and *T. odorata*. *Trentepohlia elongata* is symbiotic with *C. Linkii* and *C. interplexum* while *T. abietina* was identified as the algal symbiont of *Coenogonium interplexum*.

Discussion

Table 2 lists the species of lichen fungi and their corresponding algal symbionts. It can be seen from this table that there is no specificity of algal host in the lichen genus *Coenogonium*. Six different species of *Trentepohlia* exist in symbiosis with the four species of lichen fungi (*Coenogonium*) studied for their algal components. Therefore, a fungus can maintain a symbiotic relationship with

Table 2. Summary of phycobiont-mycobiont associations.

		Mycobionts			
		C. interplexum	C. interpositum	C. Linkii	C. Leprieurii
Phycobionts	T. abietina	X			
	T. arborum	X	X	X	
	T. aurea	X		X	
	T. elongata	X		X	
	T. odorata				X
	T. umbrina				X

any one of two or three different algal species. This fact strengthens the previous assumption that one should not rely solely on the algal component of the lichen in the determination of the species of Coenogonium. The variable size ratios obtained in the culture studies justify further the opinion that algal cell measurements cannot be a primary characteristic in the identification of the species of Coenogonium, especially when dealing with sterile material.

The figures shown on Tables 3 and 4 to describe the sizes of the algal cells represent the average measurements of ten cells taken from each culture flask. The range in size for length and width is also shown. As has been previously stated, only those cells bearing reproductive structures as well as those filaments supporting the apothecia in the lichen thallus were measured for comparison of their cell sizes.

Table 3 presents a comparison of cell measurement data from lichenized algae and algae grown in culture. An analysis of this table shows the following differences between species:

Trentepohlia arborum, as the symbiont of C. Linkii, C. interpositum and C. interplexum showed three patterns of growth:

Table 3. Comparison of cell sizes in lichenized and non-lichenized phycobionts arranged according to algal species.

Collection Number	Trentepohlia Species	Coenogonium Species	LICHENIZED
			Average Length x Width (μ)
18	T. abietina	C. interplexum	50 x 15
17	T. arborum	C. Linkii	38 x 17
65	T. arborum	C. interplexum	38 x 16
66	T. arborum	C. Linkii	38 x 14
67	T. arborum	C. interpositum	38 x 16
78	T. arborum	C. interpositum	49 x 15
109	T. arborum	C. interplexum	41 x 16
64	T. aurea	C. Linkii	52 x 15
114	T. aurea	C. interplexum	36 x 16
116	T. aurea	C. Linkii	35 x 14
117	T. aurea	C. Linkii	36 x 17
76	T. elongata	C. interplexum	35 x 16
77	T. elongata	C. Linkii	35 x 15
107	T. elongata	C. Linkii	34 x 13
4	T. odorata	C. Leprieurii	19 x 5
2	T. umbrina	C. Leprieurii	32 x 14

ALGA	SOIL-WATER MEDIUM		AGAR MEDIUM	
RATIOS Ave. L / Ave. W	Min. Max. Length x W (μ) Average Length x Width (μ)	RATIOS Ave. L / Ave. W	Min. Max. Length x W Ave. Length x Ave. Width (μ)	RATIOS Ave. L / Ave. W
3.3 : 1	32.6 - 47.6 x 14.4 x 18.6 39 x 16	2.4 : 1	26.2 - 44.2 x 9.3 - 13.8 37 x 12	3.1 : 1
2.2 : 1	32.6 x 46.5 x 12.9 - 20.9 40 x 14	2.4 : 1	22.6 - 42.3 x 14.5 - 17.6 38 x 16	2.4 : 1
2.4 : 1	34.6 - 47.4 x 12.7 - 18.6 41 x 16	2.6 : 1	32.5 - 44.8 x 13.8 - 16.7 39 x 15	2.6 : 1
2.7 : 1	24.6 - 42.6 x 9.3 - 17.5 34 x 14	2.4 : 1	30 - 42.6 x 13.5 - 17.1 38 x 15	2.5 : 1
2.4 : 1	52.3 - 65.1 x 13.7 - 17.4 58 x 15	3.9 : 1	26.6 - 40.6 x 11.6 - 20.3 30 x 14	2.1 : 1
3.3 : 1	40.5 - 69.2 x 10.9 - 18.6 50 x 14	3.6 : 1	53.8 - 65.1 x 11.9 - 16.7 58 x 14	4.1 : 1
2.6 : 1	35.2 - 58.5 x 13.2 - 17.2 44 x 15	2.9 : 1	32.3 - 44.9 x 14.5 - 16.6 39 x 16	2.4 : 1
3.5 : 1	31.6 - 55.8 x 14.2 - 16.1 41 x 15	2.7 : 1	31.3 - 52.6 x 14 - 17.6 41 x 16	2.6 : 1
2.2 : 1	20.8 - 48.8 x 9.3 - 20.9 34 x 15	2.3 : 1	20.3 - 32.7 x 9.2 - 13 26 x 11	2.4 : 1
2.5 : 1	19.7 - 46.5 x 6.6 - 16.9 34 x 13	2.6 : 1	29 - 37.2 x 12.1 - 18.5 33 x 14	2.4 : 1
2.1 : 1	30.6 - 46.5 x 13.3 - 16.7 38 x 16	2.4 : 1	29.1 - 35.5 x 12.9 - 16.4 34 x 14	2.4 : 1
3.1 : 1	27.9 - 63.3 x 13.1 - 15.4 47 x 15	3.1 : 1	38.6 - 55.8 x 16.9 - 23.3 47 x 20	2.4 : 1
2.3 : 1	30.2 - 46.5 x 10 - 18.6 37 x 15	2.5 : 1	25.7 - 33.9 x 9.3 - 17.1 29 x 13	2.2 : 1
2.6 : 1	37.2 - 65.1 x 14.5 - 23.5 53 x 19	2.8 : 1	37.2 - 42 x 14.7 - 16.4 40 x 16	2.5 : 1
4 : 1	14.4 - 23.4 x 3.1 - 5.6 20 x 5	4 : 1	13.3 - 16.1 x 3.8 - 7.7 14 x 6	2.3 : 1
2.3 : 1	23.9 - 48.8 x 11.3 - 18 34 x 15	2.3 : 1	No Growth	

Table 4. Comparison of cell sizes in lichenized and non-lichenized phycobionts arranged according to fungal species.

Collection Number	COENOGONIUM species	TRENTEPOHLIA species
18	C. interplexum	T. abietina
65	C. interplexum	T. arborum
76	C. interplexum	T. elongata
109	C. interplexum	T. arborum
114	C. interplexum	T. aurea
67	C. interpositum	T. arborum
78	C. interpositum	T. arborum
2	C. Leprieurii	T. umbrina
4	C. Leprieurii	T. odorata
17	C. Linkii	T. arborum
64	C. Linkii	T. aurea
66	C. Linkii	T. arborum
77	C. Linkii	T. elongata
107	C. Linkii	T. elongata
116	C. Linkii	T. aurea
117	C. Linkii	T. aurea

LICHENIZED ALGA		SOIL-WATER MEDIUM		AGAR MEDIUM	
Average Length x Width (µ)	Ratios L/W	Min.-Max. L. x Min.-Max W. Ave. Length x Width (µ)	Ratios	Minimum-Maximum Length x W Average Length x Width (µ)	Ratios
50 x 15	3.3 : 1	32.6 - 47.6 x 14.4 - 18.6 39 x 16	2.4 : 1	26.2 - 44.2 x 9.3 - 13.8 37 x 12	3.1 : 1
38 x 16	2.4 : 1	34.6 - 47.4 x 12.7 - 18.6 41 x 16	2.6 : 1	32.5 - 44.8 x 13.8 - 16.7 39 x 15	2.6 : 1
35 x 16	2.2 : 1	27.9 - 63.3 x 13.1 - 15.4 47 x 15	3.1 : 1	38.6 - 55.8 x 16.9 - 23.3 47 x 20	2.4 : 1
41 x 16	2.6 : 1	35.2 - 58.5 x 13.2 - 17.2 44 x 15	2.9 : 1	32.3 - 44.9 x 14.5 - 16.6 39 x 16	2.4 :1
36 x 16	2.2 : 1	20.8 - 48.8 x 9.3 - 20.9 34 x 15	2.3 : 1	20.3 - 32.7 x 9.2 - 13 26 x 11	2.4 : 1
38 x 16	2.4 : 1	52.3 - 65.1 x 13.7 - 14.7 58 x 15	3.9 : 1	26.6 - 40.6 x 11.6 - 20.3 30 x 14	2.1 : 1
49 x 15	3.3 : 1	40.5 - 69.2 x 10.9 - 18.6 50 x 14	3.6 : 1	53.8 - 65.1 x 11.9 - 16.7 58 x 14	4.1 : 1
32 x 14	2.3 : 1	23.9 - 48.8 x 11.3 - 18 34 x 15	2.3 : 1	No Growth	--------
19 x 5	4 : 1	14.4 - 23.4 x 3.1 - 5.6 20 x 5	4 : 1	13.3 - 16.1 x 3.8 - 7.7 14 x 6	2.3 : 1
38 x 17	2.2 : 1	32.6 - 46.5 x 12.9 - 20.9 40 x 17	2.4 : 1	22.6 - 42.3 x 14.5 x 17.6 38 x 16	2.4 : 1
52 x 15	3.5 : 1	31.6 - 55.8 x 14.2 - 16.1 41 x 15	2.7 : 1	31.3 - 52.6 x 14 - 17.6 41 x 16	2.6 : 1
38 x 14	2.7 : 1	24.6 - 42.6 x 9.3 - 17.5 34 x 14	2.4 : 1	30 - 42.6 x 13.5 - 17.1 38 x 15	2.5 : 1
35 x 15	2.3 : 1	30.2 - 46.5 x 10 - 18.6 37 x 15	2.5 : 1	25.7 - 33.9 x 9.3 - 17.1 29 x 13	2.2 : 1
34 x 13	2.6 : 1	37.2 - 65.1 x 14.5 - 23.5 53 x 19	2.8 : 1	37.2 - 42 x 14.7 - 16.4 40 x 16	2.5 : 1
35 x 14	2.5 : 1	19.7 - 46.5 x 6.6 - 16.9 34 x 13	2.6 : 1	29 - 37.2 x 12.1 - 18.5 33 x 14	2.4 : 1
36 x 17	2.1 : 1	30.6 - 46.5 x 13.3 - 16.7 38 x 16	2.4 : 1	29.1 - 35.5 x 12.9 - 16.4 34 x 14	2.4 : 1

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(a) increase in size of cells in both types of culture media, with the same cell length to width ratios:

(b) increase in size of cells in soil-water medium and a decrease in size of cells in agar medium; and,

(c) decrease in size of cells in soil-water medium and no appreciable change in size in agar medium.

Trentepohlia aurea, as the algal symbiont of *C. Linkii* showed variations of growth in several ways:

(a) decrease in size of cells in both soil-water and agar media, the cells in the former medium being smaller than those in the latter, although their size ratios are nearly the same;

(b) lichenized algal sizes are larger than those in culture but the size ratio of the cells in the soil-water medium is larger than those in the agar medium and the lichenized algae; and,

(c) cells in the soil-water medium are larger than the lichenized cells and those in the agar medium, the cells in the latter exhibiting higher size ratio than the lichenized cells, although the cells in the agar medium are smaller.

Trentepohlia aurea as a symbiont of *C. interplexum* showed a decrease in the size of its cells in soil-water medium and a further decrease in cell size and size ratio in the agar medium.

Trentepohlia elongata, as the symbiont of C. Linkii, showed two variations in growth:

(a) increase in cell size and ratio in soil-water medium and a decrease in size of cells in agar medium; and,

(b) increased size of cells in soil-water medium and in agar medium, the cells in the former being much larger than those in agar medium.

As a symbiont of C. interplexum, Trentepohlia elongata cells showed an increase in length and width in culture, the cells in the agar media displaying a lower size ratio than in the other two.

The cells of Trentepohlia abietina decreased in size in culture but have higher size ratio in agar medium.

Trentepohlia odorata gave a larger average length in soil-water medium but the average width of the cells in the agar medium were much increased, giving a size ratio lower than in both the lichenized alga and those in the soil-water medium.

Coenogonium interpositum is presented here with only one symbiotic algal species, Trentepohlia arborum. It is possible that more collections of this lichen would have yielded more significant results.

Collection numbers 18, 67, 77 and 78 (Table 5) present diverse growth patterns in comparison with one another. For instance, No. 18 shows a sharp decrease in average length and width measurements when grown in culture, while No. 67 shows a sharp increase in average cell size in soil-water medium. There is noted a large decline in average cell length in No. 77 when grown in agar medium; while a sharp increase is observed in No. 78 - a distinct contrast to No. 77. While both Nos. 67 and 78 are Trentepohlia arborum, their growth responses differ with respect to the culture media they are grown in. Here is an instance where two lichens with the same algal and fungal components and collected from two separate localities behave differently in culture. Obviously, there are some limiting factors that influence the growth of these four collection numbers in culture and it is possible that nutritional deficiencies in the medium play a role.

Collection No. 2 is not represented with any data on growth in agar medium in the Tables. The alga grew very poorly in this medium, being so much reduced in form that the attempt to culture it further in agar medium had

Table 5. Date *of collections from* **Florida** *and* **Panama**.

Collection No.	Species of Coenogonium	Species of Trentepohlia	Place of Collection	Date of Collection
2	C. Leprieurii	T. umbrina	Barro Colorado Island, Panama	Dec. 26, 1962
4	C. Leprieurii	T. odorata	" " " "	"
17	C. Linkii	T. arborum	Millhopper Hammock, Gainesville Alachua Co.	Feb. 6, 1963
18	C. interplexum	T. abietina	" " "	"
64	C. Linkii	T. aurea	Black Bottom Hammock, Sanford Seminole Co.	Feb. 9, 1963
65	C. interplexum	T. arborum	Low Hammock near Sanford, Seminole Co.	"
66	C. Linkii	T. arborum	" " " "	"
67	C. Interpositum	T. arborum	" " " "	"
76	C. Interplexum	T. elongata	Lieder Trail, Highlands Hammock State Park, Sebring, Highlands Co.	Feb. 11, 1963
77	C. Linkii	T. elongata	" " "	"
78	C. interpositum	T. arborum	" " "	"
107	C. Linkii	T. elongata	Rattlesnake Hammock, Everglades National Park, Dade Co.	Feb. 13, 1963
109	C. interplexum	T. arborum	" " "	"
114	C. interplexum	T. aurea	Redd Hammock, Everglades National Park, Dade Co.	Feb. 14, 1963
116	C. Linkii	T. aurea	" " " "	"
117	C. Linkii	T. aurea	" " " "	"

to be given up. The writer was unable to determine the limiting factors in this case. It showed significant increase in growth in the soil-water medium although the size ratios of the lichenized alga and the filaments grown in culture remained the same.

Collection numbers 67, 76, 78 and 107 grow better in culture and apparently, no limiting factor is present here.

The extent of the lichenization of the algae may be thought of as one of the factors that slows down or hastens the vegetative growth of the thallus. As has been described earlier, one of the first signs of growth of the algae in the culture media was the shedding off of the hyphal elements enveloping them. There appears to be an inverse relationship between the amount of hyphal threads around the alga and the rate of growth of the alga.

It might be well to mention at this point that the <u>Trentopohlia</u> species presented here have variable growth requirements and these do not necessarily correspond to the different taxonomic forms, nor do these have significant relation to size measurements.

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Conclusions

1. One species of the algal genus *Trentepohlia* can be associated with more than one fungus species of the genus *Coenogonium* in the development of a lichen thallus.

2. One species of the fungus genus *Coenogonium* can be associated with more than one species of the algal genus *Trentepohlia* in the formation of a lichen thallus.

3. The shelf-form of lichen thallus is a characteristic of the fungal component since both shelf-form (*C. Linkii*) and non-shelf-form of thalli (*C. interpositum*) have identical algal species.

4. Cell sizes of the alga cannot be used in the classification of the lichen nor in the identification of the species of *Coenogonium* as evidenced by the polymorphic tendencies shown by both the lichenized and the unlichenized algae.

Taxonomy

History

The species of *Trentepohlia* are largely polymorphic plants and many of them have been described on characters of little permanence. The genus was founded in 1817 by Martius and was based on *Byssus aurea* Linn. Agardh (1824), however, included *T. aurea* and the unrelated genus *Chantransia* in his new genus *Chroolepus*. More species were added to this list by subsequent workers who classified *Chroolepus* in various ways in the Class Chlorophyceae (green algae).

Kützing, in 1843, placed the genus *Chroolepus*, along with the genera *Cladophora* and *Stigeoclonium*, in the Family Confervinae based on the organization and shape of their cells. Rabenhorst (1864) added nine species and seven varieties to the list of Agardh, rejecting two of Kützing's previously described species. He classified *Chroolepus* under the Order Nematophyceae and Family Chroolepidae. Gobi published an interesting memoir on the genus *Chroolepus* in 1871 and a year later, Nordstedt described a new species from Brazil which he named *Trentepohlia pleiocarpa*. He was the first to recognize the priority of the name *Trentepohlia* over *Chroolepus* and this led to the subsequent transfer of the various species named by the earlier authors into the genus *Trentepohlia*.

Wolle (1887) described six species and two varieties which he classified in the Family Confervaceae under the Order Confervoideae. De Wildeman (1888) compiled all the species of *Trentepohlia* previously described into a new listing and included 16 new species and one variety. He organized these under the Order Confervineae and Family Confervinees, placing this after the Family Ulotrichiacees.

The remaining studies on Trentepohlia were mostly concerned with the description of new species or the redescription of old ones. The use of the vegetative habit of the thallus as the main character in the classification of the genus seemed to dominate the systems of the later authors.

Hariot (1889-90), brought together and analyzed the scattered descriptions of the Chroolepus and Trentepohlia species and presented a good listing of these under the name Trentepohlia. His work comprised enumerations and descriptions of the different species but were not fully illustrated and he failed to include keys to the species. Hariot based his classification on the cells of the thallus, their relative dimensions according to the two axes of the filaments, the shape of the cells, whether cylindrical or torulose; the type of extremity of the filaments and of the branches, and the differentiation of the filaments into the creeping and the erect threads, together with explanations on how these arise. He did not consider the structure of the sporangia as a good taxonomic character in view of what he thought was its great variability. Hariot further divided the genus Trentepohlia into two groups:

(1) species with cylindrical cells in long filaments; and,

(2) species with torulose or moniliform cells in a pulverulent growth layer.

Collins (1932) placed the genus Trentepohlia in the Family Trentepohliaceae under the Order Ulotrichales on account of the uninucleate cells and the presence of a single parietal laminate chloroplast in the cells. He listed ten species and five varieties of Trentepohlia from the United States of which one species and two varieties occur in Florida; namely, T. odorata (Wiggers) Wittrock, T. odorata var. umbrina (Kütz.) Hariot and T. odorata var. quercina Collins.

Printz (1927, 1939) considered the heterotrichous organization of the thallus of Trentepohlia as the main character in the classification of the genus and included it in the Order Chaetophorales. He placed the genus in the Family Trentepohliaceae mainly on the fact that the zoospores and gametes are formed in special cells differing more or less in shape and structure from the vegetative cells. He stated that these characters are important distinguishing features of the genus to justify its separation from the Order Ulotrichales. Printz (1939) has published what is considered to be the first comprehensive monograph of the Family Trentepohliaceae, complete with keys and illustrations. He placed the genera Trentepohlia and Physolinum in the same family and distinguished them by their reproductive structures and vegetative habit. Printz divided the genus into two sections and characterized each thus:

(1) Section Chroolepus - plants consisting mostly of free, more or less cylindric or torulose, irregularly branched, erect filaments, attached only at the base and not forming a distinct prostrate tissue; and,

(2) Section Heterothallus - plants consisting of distinct basal threads forming a pseudoparenchymatous tissue attached to the substratum on its underside; and, loose, unbranched or sparingly branched, upright threads.

The genera included in this study are placed in the Order Chaetophorales of Class Chlorophyceae (green algae) on the basis of the heterotrichous character of the filaments. The Family Trentepohliaceae, to which these plants belong, is characterized by the high degree of adaptability to a terrestrial existence, their sub-aerial habit, the presence of the haematochrome pigment in their cells and the absence of pyrenoids in the chloroplasts.

Some species of *Trentepohlia* and *Physolinum* occur as symbionts in certain genera of lichens, in addition to *Coenogonium*. Ahmadjian (1958) lists *Trentepohlia* as the algal symbiont of *Cystocoleus niger* (=*C. nigrum*), *Chaenotheca phaeocephala* var. *hispidula*, *Opegrapha atra*, *Graphis scripta* and *Arthonia radiata f. astroidea*. He also listed the genus as occurring in the following lichen families, among others: Cypheliaceae, Arthoniaceae, Chiodectonaceae, Dirinaceae, Rocellaceae, Lecanoactidaceae, Thelotremaceae and Gyalectaceae.

Physolinum monilia occurs as the algal symbiont of *C. moniforme*.

General Morphology of the Phycobionts

Trentepohlia and *Physolinum* are sub-aerial plants with decumbent filaments producing erect filaments which are simple or branched, parallel or irregularly arranged, and whose cells may be cylindrical or spherical. In the majority of the species, the *Trentepohlia* appear as orange-yellow tresses or cushions, although in a few species, like *T. umbrina* (Kütz.) Born., and *Physolinum monilia* (de Wildem.) Printz, they may occur merely as fine crusts. In many sepcies of *Trentepohlia*, the thallus shows differentiation into prostrate and erect threads but in *T. umbrina* the filamentous

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habit is poorly developed. Species belonging to the Section Heterothallus have upright filaments with few or no branches and are gradually attenuated. The basal threads form a pseudoparenchymatous tissue. In most cases, the plants of both Sections Chroolepus and Heterothallus have well-branched filaments, the branches being alternate and arising either from the top of the parent-cell or sub-terminally or rarely from the middle. The growth of the filament is apical.

The vegetative cells vary greatly in length and diameter, and it is very difficult to identify the species on this character alone. As has been shown in the culture studies, measurements of cells in different parts of the lichen thallus and under different cultural conditions showed a wide range of variation.

The cylindrical or barrel-shaped cells have thick cellulose walls which are sometimes plainly stratified, the successive layers being parallel or divergent. In forms showing divergent strata in their cell walls, the free ends of the apical cell are covered by characteristic caps of pectose (Pl. 3, Fig. 5), which represents a secretion and serve to restrict transpiration from the exposed tips. In T. aurea, the caps are commonly pushed aside during the growth of the apical cells and the remains of such displaced caps may be found attached to the lateral walls of the older segments; in such cases the apical cell forms new caps (Fritsch, 1956).

The characteristic yellowish to red color of the living plant is due to the presence in the cells of orange-red haematochrome globules of various sizes dissolved in fat (Geitler, 1923), especially around the discoid and band-shaped chloroplasts. In shaded habitats, the pigment may be masked by the chlorophyll so that the growths appear green. Haematochrome globules accumulate in large quantities in the cells of filaments exposed to well-lighted situations and during dry periods when growth is slowed down, greatly diminishing in size and numbers when the cells are shaded or when placed in nutritive mineral solutions.

The septa separating the cells are often provided with a single large pit which is occupied by a protoplasmic strand. A distinct characteristic of this genus is the absence of pyrenoids in the cells. Older cells are commonly multinucleated.

Trentepohlia and Physolinum are widely distributed and occur attached to or forming matted layers on rocks, tree-trunks, wood-work, and on leaves and bark of trees.

They range from arctic or high mountain regions to the damp tropical or sub-tropical climates where they grow profusely as epiphytes on leaves (Schmidle, 1897). In temperate climates, they are found wherever the necessary degree of moisture exists. They are thus most common in wet mountainous regions and are usually comparatively rare in the lowlands. It is possible that the original range of these plants was in tropical regions, and that from there, they either spread to the damp mountainous areas of the temperate regions or they survived in these regions after certain climatic changes.

Plants of Trentepohlia and Physolinum can withstand long periods of drying without appreciable change (Howland, 1929), making them suitably adapted to terrestrial existence. Oltmanns (1922) has reported that the highly refractive yellow and golden-red globules in the cells of Trentepohlia act as light filters which enable the plants to withstand the intense illumination of the tropics and thus compete successfully with other algae. A curious adaptation to the terrestrial habit of Trentepohlia is found in the fact that the mature sporangia are frequently shed entire from the filaments and the zoospores are released only when they fall into the water, or are wet with dew or rain.

Vegetative reproduction by fragmentation is probably of frequent occurrence. Howland (1929) reports that propagation by swarmers in T. aurea only takes place at certain times of the year. The zoospores are formed in special ellipsoid or ovoid sporangia and are of three kinds:

(1) sessile sporangia which may be terminal, lateral, intercalary, or rarely axillary (Pl. 3, Fig. 2). They are formed merely by the enlargement of a vegetative cell. The zoospores are liberated without the detachment of the sporangium from the main cell. Karsten (1861) reported that such sporangia were soon transformed into globular forms when thalli were grown in water, and that the globular forms occurred most abundantly in moist places.

(2) stalked sporangia which appear only as terminal or lateral appendages and are formed by the cutting off of a tubular outgrowth from a somewhat enlarged supporting cell which may give rise to several such sporangia (Pl. 3, Fig. 1). The apical part of the outgrowth swells up to form the sporangium which is often bent in a characteristic sickle-shaped manner. The stalked sporangia become detached and dispersed by wind, the liberation of the biciliate zoospores taking place on subsequent wetting.

(3) funnel-sporangia which are produced terminally from

the apex of a cylindrical cell and become detached at maturity. Oltmanns (1922) believes that this type of sporangia is but a modification of the stalked sporangia. It is not presently known what kinds of reproductive cells are formed by the funnel-sporangia.

The sessile sporangia produce biflagellated zoospores which have been observed in certain cases to behave as isogametes (Wille, 1889). However, they can also germinate without fusion or may give rise to aplanospores (Meyer, 1911). This type of sporangium is often regarded as a gametangium (Pl. 5, Fig. 1). These structures are commonly produced on the basal parts of the plant, in which case, sexual fusion readily takes place.

The stalked sporangia produce a considerable number of bi- or quadriflagellated zoospores liberated through a terminal or lateral opening. The zoospores appear to germinate directly (Karsten, 1891). The usual production of the stalked sporangia on the erect threads facilitates wind dispersal.

The zoospores vary in size and shape but are generally flattened and ovoid. The characteristic light green color is more or less diffused in the cells. The two flagella are borne posteriorly and appear to be of equal length and approximately twice the length of the zoospore. They range from 6 x 12 μ in size to slightly larger after their release from the sporangia. Gametes are smaller, measuring about 4 x 8 μ in size (Pl. 5, Fig. 2). Sexual fusion has been observed in culture, the process taking place especially after the cultures have been placed briefly in the dark (Figs. 3 and 4).

In many cases, stalked and sessile sporangia occur on the same plant, the sessile sporangia being produced from the cells of the prostrate filaments while the stalked sporangia are developed on the upright threads. This has been reported in *T. umbrina* (Fritsch, 1935), a fact which the writer considers as questionable since *Trentepohlia umbrina* has a thallus where there is no distinction between the prostrate and erect systems.

Physolinum monilia (de Wildem.) Printz grows and develops branches by a process similar to budding and the sporangia produce only aplanospores (Pl. 4, Fig. 5). The vegetative cells are chain-like and moniliform and these bear the sporangia directly. The chromatophore in the vegetative cell is long, narrow and ribbon-shaped, one or several in each cell. Intercalary cell division is not known to occur in this plant and hence, growth is apical. This species is the algal symbiont of *Coenogonium moniliforme* Tuck.

Key to Species

The six species of Trentepohlia found symbiotic with Coenogonium in this study belong to the Section Chroolepus. In the preparation of the key below, the system of classification by Printz (1939) was adopted because of his use of more reliable characters, such as the type of sporangia and the shape of the cells. This key is for the identification of the species of Trentepohlia and Physolinum which are known to be found as phycobionts in Coenogonium based on culture studies.

1. Cells globose to elliptic, 10-18 x 22-32 μ; filaments chain-like, branched; reproduce by means of aplanospores; algal symbiont of C. moniliforme . . . . Physolinum monile

1. Cells cylindrical or barrel-shaped, 14-36 μ in diameter, 1-3 times as long as wide; filaments variously branched; zoosporangia and gametangia produced, sessile or on stalk cells; algal symbiont of C. interplexum, C. interpositum, C. Linkii and C. Leprieurii 2

    2. Cells cylindric 3

    2. Cells elliptic 6

3. Cells mostly between 5-10 μ wide, occasionally slightly

thicker or thinner; sporangia ovoid, lateral or terminal . . . . <u>Trentepohlia</u> <u>abietina</u>

3 - Cells more than 10 μ wide 4

4. Cells 11-17 μ wide, 1-3 times longer than wide; cell walls stratified, smooth or rugose; sporangia sickle-shaped 5

4. Cells up to 20 μ wide, 3-4 times longer than wide; branches often one-sided; sporangia single, ovoid or elliptic attached directly on vegetative cells . . . . <u>T</u>. <u>elongata</u>

5. Cells 14-17 μ wide; sporangia in groups of 2-8, attached to swollen end cells of a branch . . . . <u>T</u>. <u>arborum</u>

5. Cells thinner, 11-17 μ wide; sporangia single, attached on one-celled sub-sporangial cells arising eccentrically from a not swollen base . . . . <u>T</u>. <u>aurea</u>

6. Cells ± swollen, elliptic, often single or in short, easily breaking threads; cells 14-15 μ wide . . . . <u>T</u>. <u>umbrina</u>

6. Cells ovoid-elliptic or nearly cylindrical, united into long threads, loose and richly branched; cell wall slightly thickened; cells 5-6 μ wide . . . . <u>T</u>. <u>odorata</u>

Systematic List

Trentepohlia abietina (Flot.) Hansg.

Prodomus Alg. 1886. 86. *Chroolepus abietinum* Flotow in Kütz. Phyc. germ. 228. 1845.

Synonyms: *Trentepohlia velutina* (Kütz.) Hansgirg. Prodr. der Alg. von Bohmen. I. 2. 1888.

T. abietina var. *cupressicola Hansgirg*. *Ibid*.

Exsicatti: Wittrock and Nordstedt, Alg. 917 and 1418. 1882.

Thallus reddish or nearly golden-yellow, thin, caespitose, becoming ashy when dry; cells of prostrate threads more or less torulose; cells of erect filaments cylindrical, 12-16 μ wide, 1-3 times longer than wide; terminal cells sometimes considerably longer; cell walls consisting of divergent layers, difficult to recognize in living specimens; cell wall at end of tip cell fairly wide; calyptra poorly developed; gametangia terminal or lateral; zoosporangia globose or ovoid, 12-25 μ in diameter (Pl. 4, Fig. 2).

This species resembles very closely the fragile forms of *T. aurea* except for the more delicate and flexuous filaments of the former; the gametangia are smaller and are found anywhere on either the basal or erect filaments.

Trentepohlia abietina is generally found in places with high humidity, particularly in shady forests, on the bark of coniferous trees and occasionally on deciduous trees (Printz, 1939). Symbiotic with C. interplexum. It is here reported for the first time from Florida.

Phycobiont studied: **FLORIDA:** On bark of Pinus glabra, Solution sink, Millhopper's Hammock, 8 miles east of Gainesville, Alachua County, Uyenco 18, 6 February 1963 (MSC).

Trentepohlia arborum (Ag.) Hariot

Jour. Bot. France. 20:345. Figs. 8 & 9. 1890.

Conferva arborum Ag. Systema Algarum 21. 1824. - Orig. coll.: Marianas Isl., Gaudichaud (no date).

Synonyms: Tretepohlia pleiocarpa Nordst. Bot. Not. 131. 1882.

Trentepohlia bisporangiata Karsten. Ann. Jard. Bot. Buitenzorh. 10:1-66. 1891.

Trentepohlia Wainioi Hariot, Journ. Bot. France. 3:381. 1889.

Trentepohlia Kurzii (Zeller) de Toni, Sylloge Algarum. I. 261. 1889.

Trentepohlia polycarpa de Wildem. p.p. Bull. Soc. Bot. Belg. 26:71-80. 1888.

Chroolepus flavum var. tahitense Grun. Abhandl. zool.-bot. Vereins. 1861.

Exsicatti: Wittr. and Nordst., Alg. Exsicc. 409 and 516. 1882.

Filaments long and branching at right angles, branches somewhat thinner than the main filament; end cells of the sterile branches often attenuated and more or less cuspidate; cells 14-17 μ wide, 1-3 times longer than wide; wall colorless or slightly yellowish, more or less firm, convergent stratified, smooth or rugose; gametangia sessile, usually terminal, sometimes 3 or more attached laterally by a short branch; zoosporangia ovoid or globose, rarely single, 2-7 arranged in a characteristic manner around the large swollen apical cells by means of their bent stalk cells; zoosporangia 11-24 μ wide, opening through a pore which lies opposite their point of attachment to the stalk cells; gametangia lateral, sessile, globose to elliptic, 19 x 22 μ in size. (Pl. 3, Fig. 1).

The vegetative filaments of this species resemble very closely T. aurea and is difficult to distinguish from the latter, except for the characteristic arrangement of the zoosporangia in T. arborum.

This species is common in the tropics growing on rocks and tree trunks (Printz, 1939). Symbiotic with C. Linkii, C. interplexum, and C. interpositum. It is reported here for the first time from Florida.

Phycobionts studied: FLORIDA: On bark of Carya tomentosa, in limestone sink, Millhopper's Hammock, 8 miles northwest of Gainesville, Alachua Co., Uyenco 17, 6 February 1963 (MSC); on bark of citrus, Low Hammock near Sanford, Seminole Co., Uyenco 65, 9 February 1963 (MSC); on bark of Quercus virginiana, growing among liverworts, Low Hammock near Sanford, Seminole Co., Uyenco 66, 9 February 1963 (MSC); on bark of sweet gum, Low Hammock near Sanford, Seminole Co., Uyenco 67, 9 February 1963 (MSC); on bark of sweet gum, Lieder Trail, Highlands Hammock State Park, Sebring, Highlands Co., Uyenco 78, 11 February 1963 (MSC); on bark of Lyssoloma, Rattlesnake Hammock, Everglades National Park, Dade Co., Uyenco 109, 13 February 1963 (MSC).

Trentepohlia aurea (Linn.) Mart.

Flora Crypt. Erlang. 351. 1817. Byssus aurea Linn. Spec. Pl. 2:1347. 1759. Lichen aureus (Linn.) Ach. Lich. Suec. Prodr. 11. 1798. Conferva aurea (Linn.) Dillw. Brit. Conf. London. pl. 35. 1809. Ectocarpus aureus (Linn.) Lyngb. Hydrophyt. Dan. 164. pl. 44. 1819. Chroolepus aureum (Linn.) Wolle. Freshw. Alg. U.S. 121. pl. 115. f. 1-21. 1887.

Synonyms: Amphiconium petraeum Nees. Syst. Pilze 69. 1817. in adnot.

Trentepohlia velutina Kutz. Phyc. gen. 1843.

Trentepohlia Tuckermanniana Mont. Sylloge gener. spec. pl. crypt. 1856.

Trentepohlia villosa de Toni. Sylloge Algarum 235. 1889.

Trentepohlia polymorpha Deck. Script. Bot. Hort. Petropolit. IV. 1893.

Trentepohlia germanica Gluck. Flora 82:268. 1896.

Trentepohlia Gobii Meyer Bull. Soc. Nat. Moscou, S. Biol. 45. 1963.

Exsicatti: Wittr. and Nordst., Alg. Exsic. 40, 918, 1228, 1419. 1882.

Thallus golden-yellow to orange-red, yellowish to greenish-gray when dry forming thick, extensive felt-like growths on the shady sides of tree trunks; cells of basal filaments cylindrical or somewhat swollen, erect filaments cylindrical,

parallel or irregular, richly branched; branches obtuse, sometimes tapering; cells 11-17 μ wide, 1.5 - 3 times longer than wide; cell walls smooth or somewhat scaly or divergent stratified; pectic calyptra of the tip cell not developed in a capitate form, appearing like a cylindrical stump, often pushed to the side during the growth of the cell; gametangia round or elliptic, terminal or lateral, borne directly on the vegetative cells of either the prostrate or the erect threads; zoosporangia oval, 11-17.5 μ in diameter, mostly single, rarely in two's, each attached to a subsporangial cell by means of special curved stalk cells; base not swollen (Pl. 3 Figs. 3 and 5).

This is an extremely variable species and distinguished by the cylindrical, obtuse filaments of moderate diameter and by the solitary or seriate gametangia.

Trentepohlia _aurea_ is widespread in cold, temperate climates and in tropical regions, growing mostly on old wood, stems, rocks and limestone, often associated with mosses and hepatics (Printz, 1939). Symbiotic with _C_. _Linkii_ and _C_. _interplexum_. This species is reported here for the first time from Florida.

Phycobionts studied: FLORIDA: On bark of sweet gum, Black Bottom Hammock, 8 miles west of Sanford, Seminole County, *Uyenco* 64, 9 February 1963 (MSC); on bark of *Lyssoloma*, Redd Hammock, Everglades National Park, Dade Co., *Uyenco 114*, 14 February 1963 (MSC); on bark of *Ficus*, Redd Hammock, Everglades National Park, Dade Co., *Uyenco 116*, 14 February 1963 (MSC); on bark of *Dipholis salicifolia*, Fire Road near Gate 3, Redd Hammock, Long Pine Key, Everglades National Park, Dade Co., *Uyenco 117*, 14 February 1963 (MSC).

Trentepohlia elongata (Zeller) De Toni

Sylloge Algarum I. 5:243. 1889. *Chroolepus elongatum* Zeller. Hedwigia 12:190. 1873.

Exsicatti: Wittr. and Nordstedt, Alg. Exs. 1421. 1882.

Filaments extended, attenuated, branched, obtuse; branches often one-sided, short or long, frequently spreading, distant or close to one another; threads nearly tufted-verticillate, branches of approximately the same width as the main filaments; cells 13-20 μ wide, 29-53 μ long; sporangia 12-36 μ in diameter, sessile or stalked, single (Pl. 3, Fig 2; Pl. 4, Figs. 1, 3 and 4).

Common on tree trunks and native to East Asia (Printz, 1939). Symbiotic with C. interplexum and C. Linkii. This species is being reported for the first time from Florida.

Phycobionts studied: FLORIDA: On bark of oak tree, Lieder Trail, Highlands Hammock State Park, Sebring, Highlands Co., Uyenco 76, 11 February 1963 (MSC); on twigs of sweet gum, Lieder Trail, Highlands Hammock State Park, Sebring, Highlands Co., Uyenco 77, 11 February 1963 (MSC); on twigs and bark of Lyssoloma, Rattlesnake Hammock, Everglades National Park, Dade Co., Uyenco 107, 13 February 1963 (MSC).

Trentepohlia odorata (Wiggers) Wittrock

Scand. Vaext. 4:16. 1880. Chroolepus odoratum Wiggers Primitiae Florae Holsatiae. 122. 1780.

Synonyms: Chroolepus irregulare Kütz. Spec. Alg. 427. 1849.

Chroolepus betulinum Rabenh. Krypt. Flor. v Sachs. 225. 1863.

Chroolepus quercinum Rabenh. Fl. Eur. Algar. III. 372. 1868.

Trentepohlia lichenicola De Toni, Sylloge Algarum. I. 235-249. 1889.

Trentepohlia sinense De Toni Ibid.

Thallus felt-like, reddish-yellow to orange-red, yellowish to gray-green when dry, forming a more or less dense, pulverulent or tomentose growth on the substratum; threads not distinguished into prostrate or erect filaments; branched; cells more or less rounded, ovoid-elliptic to nearly cylindrical, 10 μ in diameter, 1-1.5 times longer than wide; cell wall either thin or thick and stratified, layers oblique or concentric; calyptra narrow; gametangia nearly spherical to elliptic, lateral, terminal or intercalary; zoosporangia similar in shape, 13 μ in diameter (Pl. 5, Fig. 5).

This species occurs mostly on the bark of deciduous trees, vary rarely on coniferous trees. Cosmopolitan but never abundant (Printz, 1939). Symbiotic with *C. Leprieurii*.

Phycobiont studied: PANAMA: On bark of palm tree, Barro Colorado Island, Canal Zone, *Prescott 4*, 26 December 1962 (MSC).

Trentepohlia umbrina (Kütz.) Born.

in Wille, Algol. Mittheil 26. 1878. *Chroolepus umbrinum* Kütz. Phyc. gener. 283. 1843. *Protococcus umbrinus* Kütz. Phyc. gener. 169. pl. 7, f. 2. 1843. *Trentepohlia odorata* var. *umbrina* (Kütz.) Hariot Jour. Bot. France. 36:317. 1890.

Synonyms: *Protococcus salicis* Ag. Systema Algarum 88. 1824.

Chroolepus irregulare Kütz. Species Algarum. 427. 1849.

Protococcus crustaceus Kütz. Sp. Alg. 203, n. 19. 1849.

Lepraria Jolithus Engl. Bot. pl. 2471. (sec. Kütz., 1849).

Pleurococcus seriatus Wood Fresh. Alg. U.S. 78. pl. 10, f. 2. (sec. Wolle, 123. 1887).

Trentepohlia Bleischii var. piceae Wille Bot. Not. 6. 1878.

Trentepohlia polymorpha Deck. Script. Bot. Hort. Petropolit. IV. 1893.

Exsicatti: Wittr. and Nordst. Alg. 42, 221, 915, 916 and 1423. 1882.

Thallus thin, appearing as a fine crust on the substratum; reddish-brown in color, fading when dried; filaments generally poorly developed and very indistinct, no distinction between prostrate and erect portions; cells of filaments elliptic, irregularly connected, easily separating from one another into groups of cells or breaking at the thick septa into single cells; 14-15 μ wide, 2-2.5 times longer than wide; wall thick, concentric stratified; gametangia similar to the vegetative cells, but with a short neck; zoosporangia globose, single, 15 μ in diameter, zoospores quadriflagellated. (Pl. 3, Fig. 6).

This species is very variable especially as to the size of the cells. Printz reported the range as 7-35 μ thick and 1-2 times longer. The specimen studied here has the characteristic elliptic cells which break easily into small fragments.

Very common in temperate regions, occurring on the bark of deciduous trees, rarely on conifers and on rocks (Printz, 1939). Symbiotic with C. Leprieurii.

Phycobiont studied: PANAMA: On bark of palm and Ficus, Barro Colorado Island, Canal Zone, Prescott 2, 26 December 1962 (MSC).

THE FUNGUS

Morphology

Thallus

The fungal elements which surround the algal filaments consist of a network of thin, delicate, hyaline or colorless threads which are septate. These branching hyphae range in size from 1.5 to 2.5 μ in diameter, although in some species of *Coenogonium*, particularly in *C. Linkii*, the hyphae may reach up to 3.5 μ in width. These threads grow around the *Trentepohlia* and *Physolinum* filaments in a longitudinal direction, anastomosing and spreading moderately or irregularly. The hyphae may partially cover the algal filaments or they may completely envelop the algae, especially when the former are pressed together. In this case, they appear like a dense, compact, cylindrical coat around the algae.

Fungal filaments appear to be denser and more articulated near the base of the thallus, and do not become intracellular at all. Obviously, the fungus hyphae do not have any injurious effect on the algal cells. The apical cells of the algal symbionts are usually free of hyphal elements, especially during a period of rapid growth when the fungal hyphae appear to lag behind. However, if the growth of the alga is very slow, the hyphae may extend up to and around the tip of the algal cells and the young branches. The number of hyphae around each algal filament varies. They are particularly abundant around the branches and may often be several cells in thickness.

Apothecia

The apothecia are found attached to the filaments of the thallus, scattered here and there, singly or in groups. In the shelf-like forms of the genus, they can be found on either the upper or the lower surfaces of the thallus.

The apothecia vary in size from 0.2 mm. (*C. curvulum*) to 1.5 mm. in diameter as in *C. implexum*.

The external features of the apothecium are quite variable. The fructification is generally round in shape and may be biatorine or lecidioid in structure. It may be sessile or provided with a short stalk and has been described variously as substipitate, sub-pedicillate or subsessile (Pl. 1, Fig. 2). In many species of *Coenogonium*, the young apothecium is at first stalked appearing like a top or goblet-shaped, gradually becoming subsessile or sessile, as the case may be, while the disk widens at maturity.

The disk of the apothecium may be flat to slightly concave or concave, and is oftentimes convex (Pl. 1, Figs. 1-6). Generally, the disk of the young apothecium starts as concave in shape, later becoming convex as development proceeds. In _C_. _velutinum_, the disk may appear pruinose, a characteristic that distinguishes this species from the other members of the genus.

The color of the apothecium has been variously described as carneous-yellow or carneous-orange to yellowish-orange or saffron yellow. It has been found that the color of the apothecium may change upon drying and the original color is not fully retained. However, the orange-carneous color seems to be the general appearance of the mature fructification in the living state. The apothecium is always, however, whitish in color during the early stages of its development, turning into the specific color upon reaching maturity. In _C_. _Linkii_, the apothecia of the living lichen is pale-yellow and changes to red when dried. The apothecia of _C_. _pannosum_ is whitish-orange when young and become flesh-colored when fully developed (Müller, 1881). Dodge (1933) separated _C_. _Leprieurii_ from the other species of _Coenogonium_ on the color of the disk. The use of this differentiating character, however, was refuted by Santesson (1937), who stated that the apothecia of probably all species of *Coenogonium* get the same color and appearance if they are repeatedly moistened and dried.

In many species of *Coenogonium*, the margin of the apothecium may be present, but rarely, it is absent. The young apothecium of *C. acrocephalum* has a thin, unrolled margin which thickens as the apothecium develops, later becoming thinner again and finally disappearing at the maturity of the apothecium. The margin is oftentimes entire or smooth, rarely crenulate or subdenticulate. In *C. moniliforme*, the margin of the apothecium becomes fringed after it is fully developed, while in *C. curvulum*, the margin is uneven; or it may even be seen wearing away, as in *C. ornatum*. This margin is not always concolorous with the apothecial disk as observed in many species of *Coenogonium*. Generally, the margin is paler in color than that of the disk, or it may be fleshy to whitish-carneous and sometimes white. It was observed to turn paler very frequently when the dried material is wet with water.

The apothecium has a well-developed proper exciple. It is largely euparaplectenchymatous and is easily distinguished from the other tissues of the apothecium (Pl. 1, Fig. 6).

The hypothecium is pallid or colorless and is formed from thin, delicate hyphae that are woven closely and irregularly, sometimes becoming conglutinate. In C. velutinum, the hypothecium is yellow in color and paraplectenchymatous, a characteristic that has been observed likewise in C. curvulum, where the cells are globose to angular in shape. The hypothecium in C. interpositum and C. Leprieurii is composed of paraplectenchymatous tissue, the cells of which are angular and thin-walled. In C. Linkii, the hypothecium is very thin, often becoming evanescent as the apothecium matures.

There are neither algal nor medullary layers in the apothecium of Coenogonium.

The hymenium consists of the asci bearing the spores and the paraphyses. The hymenium ranges from 40-75 μ in thickness and is generally colorless. In C. velutinum the hymenium is light yellow in color and reaches from 100-110 μ in thickness. In fresh specimens, the hymenium has a gelatinous texture. The asci are thin-walled and 8-spored. They are generally clavate but can occur in various other shapes; such as, sub-elongate, sub-cylindric or cylindric-clavate to fusiform-cylindric with round apices, and sometimes as sub-clavate in shape. Asci vary in size from 4-8 μ in width but may attain a width of 20 μ as in C. Leprieurii.

The anatomy of the apothecium, the characteristic thin-walled asci and the structure of the spores of the genus Coenogonium are very similar to those among the members of the family Gyalectaceae.

The paraphyses occur as filiform slender threads between the asci. They are free and loosely arranged and not at all conglutinate. These sterile structures are either septate or aseptate and are never observed to form branches. Their apices are variable and may be clavate or capitulate (capitate), round or globose to sub-globose-clavate, occasionally appearing as obovoid or truncate. The filament is commonly from 1-1.5 μ in width although it may become as wide as 3.5-4.5 μ, as in C. Linkii. The apex is generally about 3 times wider than the main filament, or it may not be wider at all, as in C. velutinum (Pl. 2, Figs. 1-5).

The ascospores are either simple or septate (two-celled) and are always observed to be hyaline and thin-walled. They vary in shape from ovate to fusiform and such intermediate forms as oblong, ob-ovate, elliptic and fusiform-elliptic (Figs. 1-5). A distinct characteristic of C. curvulum which easily separates it from the other species of Coenogonium is the arcuate shape of its spores (Pl. 2, Fig. 6).

The terms used to describe the shape of the spores here are taken from the Systematics Association: Descriptive Terminology of Taxon, 1962. Although this publication is meant for plane surfaces and not for tri-dimensional forms like the spores, for instance, it has been found useful and proper, however, when used to describe optical sections. The descriptive term, *fusiform*, has been added to the terminology to correspond to the forms which are linear in shape but are broader in the middle and have rounded ends.

The spores may be arranged in various ways in the ascus. In many species, they are linear and uniseriate; in others, they are obliquely uniseriate. Biseriate spores are found in *C. Linkii*, *C. curvulum*, *C. moniliforme* and *C. acrocephalum*. Occasionally the spores are irregularly biseriate, as has been observed in *C. interpositum* and in *C. disjunctum*. *C. velutinum* has been described as having its spores arranged in a sub-uniseriate manner in the ascus.

The size of the spores vary from 5-15 μ in length and from 2-4.5 μ in width. *C. disjunctum* has been reported and observed by the author to have the largest measurement in length; 11-15 μ; while *C. implexum* and *C. Linkii* have been observed to measure up to 4.5 μ in width.

Development of the Apothecium

Karsten (1861) described the development of the apothecium as consisting of a branch cell of the alga that becomes a free central cell surrounded by hyphal elements which develop gradually into a globose ball. He considered the central cell as a sporangium that starts the development of the apothecial initial. Karsten compared these structures to the archegonia of higher cryptogams, adding that some cortical layers below these round apothecial initials "lift themselves up" and empty their contents into so-formed openings or holes on the wall of this globose ball, a process which he interpreted as fertilization.

Schwendener (1862) disagreed with the views of Karsten and considered the "holes" referred to by Karsten as the lamina of the fungal threads that surround the young algal branch. Schwendener further disproved the idea of fertilization since he did not observe any formation of supposedly male organs.

Nylander (1862) criticized the descriptions made by Karsten of the tissues comprising the hypothecium and his discussion of the development of the paraphyses and asci. Regarding the "cellulose layer" or the "cortical envelope of the apothecia" and the "cuticle" mentioned by Karsten in discussing the fructification of Coenogonium, Nylander believed that these structures have nothing to do with fertilization nor with the production of the hymenium. The "central cells" believed by Karsten to be the primordial cells of the apothecium are nothing else but the cavities of the young branches which are in the form of small tubercles, according to Nylander. The "free endogenous cells" observed by Karsten in the cuticle of the young apothecium are not true spermatia.

Karling (1934) presented an interesting contribution to the studies on the structure and development of C. Linkii. He described the earliest stages in the development of the apothecium as consisting of a whorl of short mycelial branches which, with subsequent growth, become more and more numerous and entangled. This apothecial initials grow to considerable size and become definitely spherical. Karling did not describe the origin and development of the ascogenous layer beyond his observations on the formation of a compact pseudoparenchymatous mass which later becomes the apothecium.

The development of the apothecium in Coenogonium does not differ markedly from that of the other related genera of lichens. In most lichens, an apothecium is

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initiated in the medulla or algal layer of the thallus and first appears as a closely woven hyphal ball, the lower side of which may reach the substrate but does not merge with it. The upper portion grows out of the thallus and at maturity the apothecium appears to rest on the surface of the thallus.

In the genus Coenogonium, on the other hand, the apothecial initials are distinguished easily at the early stages of their development as small nodules on the young branches of the algal filaments. They do not possess any interior or central cavity at the beginning. These young branches are globular outgrowths, white and heteromorphous, that arise from the side of the algal filaments. They are entirely composed of a fairly obscure tissue of hyphal cells which are distinctly formed, and which never contain any algal elements (Pl. 4, Fig. 6). When the young globose apothecium attains a diameter of about 0.2 mm., there is observed in its center the first signs of a hymenial layer of about 35-40 μ thick. Parallel, short-celled hyphae perpendicular to the surface project from the middle portion of this round structure to its edge and form a layer of about 12-20 μ thick. These are the rudiments of paraphyses which later become frequently branched and resemble the irregular sterigmata of a fungus fructification. The internal structure of this young apothecium consists of a dense, interwoven, entangled fibrous mass of tissue which later differentiates into the hypothecium.

The surrounding hyphae which appear to support the apothecia become embedded deeply in the basal part of the developing hypothecium which, at this stage of development, is appressed against the loose reticulum of algal cells beneath it. Commonly the adjacent hypahe around the apothecial initials become entangled and as the apothecium develops, become included in the tissues of the fructification.

As development of the apothecium proceeds, the differentiation of the tissues takes place in the excipulum. Certain filaments near the surface consisting of large cells grow at right-angles to the surface and remain distinct from the deeply-situated hyphae. These hyphae continue to grow in this course until a thicker growth occurs in the outer part of the excipulum. The peripheral ends of the threads thus form a fine paraplectenchymatous covering, which in effect, always differentiates sharply, while the other cells beneath these expand themselves considerably to form the paraplectenchymatous tissue of the hypothecium (Pl. 1, Fig. 7). As the apothecium reaches a diameter of 0.4 to

0.5 mm., the hymenium forms a clearly defined layer of about 40 to 50 μ thick and paraphyses, asci and spores are developed.

This angiocarpic pattern of development of the apothecium is characteristic for most lichens which have a proper exciple.

Whether some cells in the apothecial initials function as spermatia, or whether the process of fertilization takes place in the young apothecium of Coenogonium remains to be proven. Meanwhile, the assumption that fertilization of a young ascogonium does take place is highly probable and it is hoped that future investigators of this lichen genus will turn their interest towards this phase of the fungus morphology.

Pycnidia

The asexual fruiting body of the Coenogonium is the pycnidium. Two forms were observed among the collections studied in the present work. One is spherical and the other is pear-shaped. These structures occur attached to the filaments of the thallus on either the upper or lower surfaces of the thallus. The white color of the pycnidium persists as such even after it has reached maturity or even in the dried condition of the plants.

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The wall of the pycnidium is made up of an interwoven mat of hyphal threads which are thin-walled and septate throughout. It does not appear to have any markedly differentiated layers, since the outer portions of the wall gradually merge into the fertile layer beneath.

Conidia are formed within the pycnidia in an exobasidial manner. These conidia are fusiform in shape, straight, and are two-celled. They vary in size from 9-11 x 2-3 µ. The conidiophores which bear the conidia are very slender threads, septate, long and flexuous and have been observed to branch very rarely except near the base (Pl. 2, Fig. 7).

Sterile filaments, called "anaphyses" and "sterigmata" by various authors, occur between the conidiophores. These slender filaments are elongated and generally simple, but may oftentimes be seen to branch.

The pycnidia were found in most forms of the lichens thalli, from the shelf-like forms to the expanded or horizontal types of growths. It is obvious that asexual reproduction of this type in <u>Coenogonium</u> is not restricted to the type of thallus nor probably to the species of algal symbiont present.

In the course of the study of herbarium material, a number of collections were found with well-developed pycnidia but no apothecia. These collections, therefore, could not be identified but are recorded here.

Material seen: MEXICO: Cosolapa. 1200 m., Veracruz, Turpus, 3, 1921-22 (US).

COSTA RICA: On bark of trees, 1100 m., La Palma de San Ramon, Province of Alajuela, Brenes 53, 1925? (NY); San Ramon, Province of Alajuela, Brenes 14484, February 1931 (NY); Colinas de San Ramon de San Pedro, Province of Alajuela, Brenes 18998, 18 January 1934.

CUBA: Woods, 900 m. alt., Cobre Range of Sierra Maestra, Loma del Gato & vicinity, Fre. Leon, Fre. Clement & Fre. Roca 10117, 11 July-14 August 1921 (NY).

DOMINICAN REPUBLIC: In primitive cloud and rain forest on top of Loma Campana, Province of La Vega; alt. about 1036 m., Allard 18709, 1 January 1948 (US); cloud forest, ridge above Los Amaceyes, 300-3200 ft., Cordillera Septentrional, Imshaug 23305, 2 August 1958 (MSC).

PUERTO RICO: Luquillo Mountain, Wilson 125, July 1902 (NY); on Acrista monticola, Monte Torrecilla, 900-100 m. alt., Britton, Cowell & Brown 5666, 20 March 1915 (NY).

BOLIVIA: Yungas, 6000 ft., Rusby 280, 1885 (NY).

BRAZIL: Bahia, Wilson, (No date) (US).

AUSTRALIA: Tarwin, Leighton, (No date) (NY).

Taxonomy

General

For the taxonomy of the genus Coenogonium, the writer is inclined to share the views of Santesson (1952) that the spores and apothecial characters, rather than the different morphology of the symbiotic algae, should be used as bases for the distinction of the different families and for the establishment of the relationships of Coenogonium with the other genera. It is my opinion, however, that this genus should remain in the Family Coenogoniaceae and that Racodium be excluded from this family until the apothecial characteristics of the latter are definitely established. It is believed that the effect of the fungus on the algal symbionts to produce the different types of thalli merits the separation of this family from the Gyalectaceae.

The following characteristics are being considered in the present study as of importance in the taxonomy of the genus Coenogonium: the type of spores, external features of the apothecia (whether sessile, stalked, flat, convex, immarginate, etc.), and the special types of thalli formed with the fungus. As to the spores, it is especially their septation, shape and size as well as their arrangement in the ascus that are of taxonomic importance. The septation of the paraphyses and the shape of their apices can constitute some of the diagnostically important species characters. Other morphological characteristics, such as, the color of the apothecial disk, the size of the margin, as well as the size of the apothecia are usually not constant to the same degree and are, therefore, being considered here as "supporting" characters in the delimitation of the different species of Coenogonium.

Before identifications of the material were made, all the original descriptions of the species were collected and a literature key of the whole genus was made. It was hoped that the descriptions might provide an over-all understanding of the nature and range of variations of the species so that they could be separated on a comparative basis; and also that such a method might serve as a guide in determining the delimitation of the different species. For this purpose, it was necessary that large numbers of specimens had to be examined and studied.

The apothecia of the dry specimens were examined by soaking them in distilled water and teasing the material to separate the asci and the paraphyses from the rest of the fungal tissues. Sections of the apothecia were also prepared for the study of the different anatomical structures.

Below is a list of the herbaria from where the dried specimens were obtained. (Abbreviations according to Lanjouw and Stafleu, Index Herbariorum, Part II, 1954):

MO - Missouri Botanical Garden, St. Louis, Missouri
NY - New York Botanical Garden, New York, N. Y.
US - National Museum, Smithsonian Institution, Washington, D. C.
MSC - Michigan State University, East Lansing, Michigan
MICH - University Herbarium, University of Michigan, Ann Arbor, Michigan
FLAS - Herbarium, Agricultural Experiment Station, Gainesville, Florida
TENN - Herbarium of the University of Tennessee, Knoxville, Tennessee

Earlier authors in searching for knowledge and experience concerning the disposition of the lichenized *Trentepohlia* (=Chroolepus) or the sterile forms of *Coenogonium*, established a large number of species of this genus. Of the original forty-eight species described as and referred to *Coenogonium*, about half of this number were found to have been based on specimens with a sterile lichen-fungus or a lichen-fungus with immature apothecia. Four species were

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determined as belonging to the Fungi Imperfecti (Santesson, 1952) and six species have been transferred to the genus *Trentepohlia*, three as valid algal species and three as synonyms of *Trentepohlia* (Hariot, 1890, 1891). Fifteen species are accepted as valid in the present study and a key to these species has been made. Two species are treated as synonyms of *C. Linkii* and eight species are considered as doubtful or insufficiently known. Twelve species are being rejected as *nomina dubia* and one species is considered as a *nomen confusum*.

Lichenized Hyphomycetes

The species belonging to this group have been observed to be lichenized Hyphomycetes with dark brown hyphae and the fungi probably belong to *Racodium* or *Cystocoleus* in the Fungi Imperfecti.

1. *Coenogonium ebeneum* (Dillw.) Smith, Handbook of British Lichens. 75. 1921. *Conferva ebenea* Dillw. British Confervae, t. 101; Introd. no. 79. 60. 1809.

2. *Coenogonium germanicum* Glück, Flora 82:268-285. 1896.

3. *Coenogonium nigrum* (Huds.) A. Zahlbr. Ann. Naturhist. Mus. Wien. 25:241. 1911. *Byssus nigra* Huds. Flora Anglica. 487. 1762.

4. *Coenogonium Schmidlei* Simmer Allgem. Botan. Zeitschrift. 5:190. 1899.

Non-Lichenized Trentepohlia

The following species attributed in the past to the lichen-genus *Coenogonium* have already been transferred to *Trentepohlia* as valid algal species or synonyms, presumably on the fact that no trace of fungal hyphae were present on the thallus:

1. *Coenogonium deplanatum* Krempelh. Flora 59:250. 1876. Treated by Hariot in 1891 as a synonym of *Trentepohlia setifera* Farlow.

2. *Coenogonium depressum* Müll. Agr. Flora 64:525. 1881. Transferred to *Trentopohlia* by Hariot (1890) as a valid algal species.

3. *Coenogonium dialeptum* Nyl. Ann. Sci. Nat. Bot. IV. 16:90. 1862. Transferred to *Trentepohlia* by Hariot (1889) as a valid algal species.

4. *Coenogonium diffractum* Krempelh. Flora 59:250. 1876. Transferred to *Trentepohlia* by Hariot (1891) as a valid algal species.

5. *Coenogonium effusum* Krempelh. Flora 59:250. 1876. Treated by Hariot (1891) as a synonym of *Trentepohlia setifera* Farlow.

6. Coenogonium simplex Müll. Arg. Flora 73:16. 1890. Treated by Hariot (1891) as a synonym of Trentepohlia dialepta (Nyl.) Hariot.

Partially-Lichenized Trentepohlia

The following species (or varieties) were described and established by various authors from thalli without apothecia or with only immature apothecia. In the absence of spores, it is impossible to identify these in Coenogonium and although fungal hyphae were present, it is best to treat these species in the algal genus Trentepohlia.

1. Coenogonium afrum Mass. Memor. I. R. Instit. Veneto. 10:43. 1861. Chroolepus afrum Mass. Memor. I. R. Instit. Veneto. 10:43. 1861. - Orig. coll.: Africa australis, Wawra.

2. Coenogonium cancellatum Leight. Trans. Linn. Soc. London 27:172. 1869. - Orig. coll.: New Eliya, Central Province, Ceylon, Leighton.

3. Coenogonium confervoides var. arborum Nyl. Ann. Sci. Nat. IV. 16:92. 1862. Conferva arborum Ag. Syst. Algar. 88. 1824. - Orig. coll.: Marianas Is. and Brazil, Gaudichaud.

4. Coenogonium dialeptizum Stirt. Proc. Phil. Soc. Glasgow 11:103. (1878) 1879. - Orig. coll.: Upper Amazon, Brazil, Trail.

5. Coenogonium Echinus K. Müll. Bot. Zeit. 15:387. 1857. Orig. coll.: Brazil, Karl Müller.

6. Coenogonium heterotrichum Müll. Agr. Bull. Soc. Bot. Belg. 32:162. 1893. - Orig. coll.: San Marcos de Dota, Costa Rica, Tonduz 6115.

7. Coenogonium patagonicum Müll. Arg. Flora 71:47. 1888. - Orig. coll.: Patagonia and Australia, Caracciolo 1882.

8. Coenogonium pulvinatum Krempelh. Verh. Zool. - Bot. Gesellsch. 26:445. 1876. - Orig. coll.: Lima, Peru, Barranca.

9. Coenogonium rigidulum Müll. Arg. Flora 65:490. 1882. - Orig. coll.: Queensland, Australia, Wilcox.

10. Coenogonium subtorulosum Müll. Arg. Jour. Linn. Soc. Lond. Bot. 32:207. 1896. - Orig. coll.: New Zealand, Colenso 1656.

11. Coenogonium subvirescens (Nyl.) Nyl. Flora 57:72. 1874. Coenogonium Leprieurii var. subvirescens Nyl. Ann. Sci. Nat. Iv. 16:89. 1862. - Orig. coll.: Rio Negro, Amazon, Brazil, Spruce 28.

This species was distinguished from *C. Leprieurii* on the basis of its thinner algal threads. As Nylander's specimens were sterile, it cannot be proved that this species is not identical to *C. Leprieurii*.

12. *Coenogonium tenuissimum* Krempelh. Nuov. Giorn. Bot. Ital. 7:26. 1875. - Orig. coll.: Borneo, (collector unknown), 1886.

This species was described by Krempelhuber as a young form of *Coenogonium*. According to Müller (1890), the species resembles *C. depressum* which was, however, transferred in 1891 to *Trentepohlia* as an algal species by Hariot.

Lichenized Coenogonium

The following eight taxa were described from specimens with ascocarps. No material of these taxa, however, were available for study and they are not included in the key.

1. *Coenogonium boninense* Sato, Jour. Jap. Bot. 8:390. 1933. - Orig. coll.: On bark of tree, Bonin: Mt. Sekimon, Hahazima Island, Japan, *Sato 106*.

Thallus lamellate, spongiose-byssoid, spread in a flabellate form, 10-25 mm. wide and 5-15 mm. long, sometimes imbricate and overlapping, one margin attached to the bark of tree, ashy-green; alga Trentepohlia, cells 24-30 x 7-9 µ; hypha covering algal filaments about 15 µ wide. Apothecia about 10-20 on the thallus. Apothecia round, about 0.5 mm. wide, situated on both the lower and upper surfaces of thallus; disk flat to somewhat convex, carneous or pale yellow, margin thin, pale; hymenium wine red in iodine; paraphyses wide continuous, 60-65 x 1.5 µ, septate, not branching, apex capitate; asci cylindrical, 45-50 x 4-6 µ; 8-spored; spored colorless, ellipsoid, simple, 5-8 x 3.5 µ.

2. Coenogonium congensis Dodge, Ann. Miss. Bot. Gard. 40(4):350. 1953. - Orig. coll.: Belgian Congo, Yangola, 20 km. west of Yangambi, J. Louis 12070.

Thallus dimidiate; apothecia convex, sessile, orange-yellow, margin concolorous, slightly dentate; paraphyses unbranched, tips not thickened; spores uniseriate, fusiform, bilocular, 6 x 2.5 µ.

3. Coenogonium Deightoni Dodge, Ann. Miss. Bot. Gard. 40(4):349. 1953. - Orig. coll.: Sierra Leone, Njala (Kori), F. C. Deighton M4396 a.

Thallus very thin; apothecia sessile, flat, disk cinnamon-brown, margin paler; paraphyses unbranched, conglutinate, tips moniliform but not thickened; spores fusiform, simple, 6-8 x 2.5 - 3 μ.

4. Coenogonium epiphyllum Wain. Ann. Acad. Sci. Fenn. 15(6):156. 1921. - Orig. coll.: Luzon, Philippines, Robinson.

Thallus a thin crust, adnate, ashy-yellow; apothecia minute, concave, pale white, margin paler, thin, prominent; paraphyses wide, septate, apex capitate-clavate; spores uni- to biseriate; fusiform to fusiform-elliptic, septate, 6-8 x 2.5 - 3 μ.

Santesson believes that this represents a good autonomous species. Wainio reported the type as "parce lectum, duobus apotheciis," and growing on leaves of trees.

5. Coenogonium interplexum f. contextum Stirt. Proc. Phil. Soc. Glasgow 10:297. 1877. - Orig. coll.: Wellington, New Zealand, John Buchanan, s.n.

The description given for this species indicated that it is similar to C. interplexum except for the reaction of the apothecium to iodine solution (violet-red color). No further information was given on the characteristics of the lichen-fungus. Only a study of the spore characters can the exact relationship of this form of C. interplexum be determined.

6. *Coenogonium interponendum* Nyl. Jour. Bot. 15:225. 1877. - Orig. coll.: On trunks and leaves of trees in old forests, Costa Rica, *H. Polakowsky 496*.

Thallus adnate to effused; apothecia yellowish-carneous; spores 8 x 2.5 µ, septate, fusiform; algal filaments 17-20 µ wide.

Nylander reported that this species is similar to *C. interpositum* except in the size of the algal filaments of the latter which he described as from 14-28 µ wide. If the separation from *C. interpositum* is actually based only on the algal characters, this species should be a synonym of *C. interpositum*.

7. *Coenogonium retistriatum* Leight. Trans. Linn. Soc. Lond. 27:172. 1869. - Orig. coll.: Ceylon, *Leighton*, *s.n*.

No spore measurements were given in the description of this species and it is not possible to identify the fungus on the basis of its straited fungal elements alone.

8. *Coenogonium Tuckermani* Mont. Ann. Sci. Nat. IV. 7:143. 1857. - Orig. coll.: Venezuela, *Fendler*, *s.n*.

Based on an imperfect specimen, the description of this species given by Montagne is very inadequate.

Key to the Species of Coenogonium

1. Spores simple 2

1. Spores one-septate 6

    2. Thallus thin, circular or spongy-byssoid, imbricate, shelf-like; apothecia sessile, flat, or convex, margins thin, pale, uneven; spores uniseriate, oblique, ovoid-elliptic to slightly fusiform-elliptic, 6-10 x 2-4 μ; paraphyses apex clavate or capitate . . . . *C. Leprieurii*

    2. Thallus amorphous or adnate to effused, expanded or dense, caepitose-tomentose 3

3. Apothecia flat or convex, subsessile, margins thin; paraphyses not septate, apex not wide, subtruncate . . 4

3. Apothecia flat to concave, sessile, margins thick, entire; spore fusiform; paraphyses septate; thallus dimidiate or caespitose-tomentose 5

    4. Margin entire; spores irregularly biseriate, elliptic and acute on both ends, 6-10 x 2-3 μ; thallus adnate, expanded . . . . . . *C. interpositum*

    4. Margin wearing away, fringed; spores uniseriate, narrowly fusiform, 8-10 x 2-4 μ; thallus amorphous . . . . *C. ornatum*

5. Spores biseriate, fusiform, 7.5-9 x 2.5-3 μ; paraphyses apices abrupt and widely capitulate; thallus dimidiate . . . . *C. acrocephalum*

5. Spores uniseriate, 8-11 x 2-2.5 μ; paraphyses apices ob-ovoid; thallus filaments short, caespitose . . . . *C. tomentosum*

   6. Thallus prostrate and thin, or adnate, expanded or spongy-byssoid 7

   6. Thallus shelf-like or crust-like 13

7. Spores uniseriate, thallus adnate to effused, pannose, expanded or loosely tomentose 8

7. Spores sub-uniseriate to biseriate; apothecia sessile; paraphyses not septate 12

   8. Apothecia sessile, flat, margins thick, smooth, white; spores ovate or short-elliptic, 7-12 x 2-4.5 μ; paraphyses septate . . . . *C. implexum*

   8. Apothecia subsessile or stalked; paraphyses septate 9

9. Apothecia flat to concave, margins uneven, pale; spores fusiform-elliptic, 6-9.5 x 2-3.5 μ . *C. complexum*

9. Apothecia flat to convex, margins smooth, thin or slightly thickened, white or pale 10

10. Spores elliptic or fusiform-elliptic 11

10. Spores fusiform, 6-7 x 1.5-2 μ . . . . . *C. pannosum*

11. Spores 6.5-10 x 2-3.5 μ . . . . *C. interplexum*

11. Spores 10 x 3 μ . . . . *C. botryosum*

12. Spores sub-uniseriate, fusiform-elliptic, 9-11 x 3-3.5 μ; apothecia concave to barely convex, margins thin, smooth, pale; paraphyses apex not at all wider; thallus spongy-byssoid consisting of short, aggregated filaments . . . . . . *C. velutinum*

12. Spores biseriate, curved, 8-9 x 2-3 μ; apothecia flat to concave, margins thick, smooth, white; paraphyses apices sub-globose to clavate; thallus thin consisting of long, prostrate filaments . . . . *C. curvulum*

13. Apothecia flat, sessile or rarely sub-sessile, margins thin, smooth, white; spores uniseriate to biseriate, short-fusiform, 9-13 x 3-5 μ; paraphyses non-septate, apices, globose-clavate; thallus crust-like, filaments moniliform; phycobiont a *Physolinum* . . . *C. moniliforme*

13. Apothecia flat to convex, subsessile; paraphyses septate, apices sub-globose or globose to clavate; filaments not moniliform; phycobiont a *Trentepohlia* . 14

14. Margin thin, smooth or sometimes rugged, pale; spores biseriate, ovate or short-fusiform, 6.8-12.5 x 2-4 μ; thallus shelf-like, imbricate . . . . *C. Linkii*

14. Margin toothed or slightly toothed, white; spores irregularly biseriate, fusiform, 11-13 x 2-4 μ; thallus adnate to effused, pannose, expanded . . . . . *C. disjunctum*

Coenogonium acrocephalum Müll. Arg.

Flora 63:525. 1881. - Orig. coll.: Apiahy, Brazil, *Puiggari 156*.

Thallus dimidiate, yellow, becoming whitish beneath; algal symbiont *Trentepohlia*. Apothecia 7.5 mm. in diameter, round, sessile; disk flat to concave, orange-carneous to pale; margin of young apothecium thick, becoming thinner and then immarginate at maturity, entire; hymenium 55 μ high, epithecium distinct; paraphyses loose, 3-4 μ wide, septate, apices abrupt and widely capitulate; asci cylindrical, 8-spored; spores simple, biseriate, fusiform, 7.5-9 x 2-3 μ.

This species is related to *C. Leprieurii* but differs from it by its larger spores and wider apothecia with entire margin. The paraphyses of *C. acrocephalum* are wider, very loose and the apices abrupt. Müller described the spores of this species as 7-8.5 μ long. In my studies of the specimens from the West Indies, the Puerto Rico material measured 7.4 x 3.3 μ in size, while the collection from Cuba had much longer spores, up to 9.3 μ.

Material seen. CUBA: El Guama, Palmer & Riley 616, 24 March 1900 (US). PUERTO RICO: Luquillo Mts., Wilson 100, July 1902 (NY).

Coenogonium botryosum Knight

Synops. Queensland Flora. I. Suppl. 74. 1886. - Orig. coll.: On bark of trees, Mt. Perry, Knight.

Thallus dense, velvety, consisting of closely aggregated short threads together with a few very slender filaments, both cohering by very short funiculi; yellow-green; algal symbiont Trentepohlia, cells of filaments 1-2 times longer than wide. Apothecia sub-sessile, round; disk flat, yellow-orange; margin paler, uneven; hypothecium colorless; paraphyses septate, 1.4-1.7 μ wide, apices clavate to globose, capitate, 3.3 - 4 μ wide; asci clavate, 8-spored; spores one-septate, elliptic, uniseriate, ca. 10 x 3 μ.

Some algal cells in the thallus of this species appear like the elliptic cells in C. moniliforme. I found the algal filaments in the material slightly narrower than the size reported for the species by Knight but this character is not a reliable taxonomic difference.

Material seen: MEXICO: Veracruz, Turpus 223 (US).

Coenogonium complexum Nyl.

Ann. Sci. Nat. IV. 11:222. 1859. - Orig. coll.: On trees in Bolivia, Weddell.

Thallus adnate, pannose, expanded, golden-yellow; algal symbiont Trentepohlia, filaments fasciculate-conglutinate, scarcely branching, cells 2.5 - 5 times longer than wide. Apothecia round, subsessile; disk flat to concave, carneous-yellow to yellow-orange; margin paler, thin, uneven; paraphyses septate, 1.5 - 2 μ wide, apices sub-globose, capitate, 3.3 - 4 μ wide; asci cylindrical, 8-spored; spores one-septate, oblong to fusiform-elliptic, 6-10 x 2.3-3.2 μ.

Nylander described the spores as 6-10 x 3-4 μ. I found the spores of the material from Central America and the West Indies to have the same range in size (6-8.5 x 3 μ) and those from South America to be larger (10 x 3.2 μ).

Material seen: COSTA RICA: South bank of Rio Pejivalle, 650-800 m., Cartago Province, Dodge & Thomas 4408, 26 September 1929 (MO 70722); forest near farmhouse in Finca

Castilla, 30 m., Limon Province, Dodge & Groeger 9207, 23 July 1936 (MO 154712). MEXICO: On bark, Cuernavaca, 6500 ft., Pringle, 31 October 1908 (US, MICH). PANAMA: On twig, drowned forest in valley of R. Puente between the Tunnel and Natural Bridge, 70 m., Canal Zone, Dodge & Allen 8863, 6 January 1935 (MO 154705).

COLOMBIA: Rio Magdalena, Weir, (no date) (NY).

HAITI: On twigs, elfin woodland forest, north of Foret des Pins (Shada station), near Dominican border, 5800 ft. (Dept. de l'Ouest), Wetmore 2931, 14 July 1957 (MSC). TRINIDAD: On Theobroma cacao, St. Pat's Ravine, Arima Valley, Fleming (MSC).

Coenogonium curvulum A. Zahlbr.

Ann. Crypt. Exot. 1:164. 1928. - Orig. coll.: On leaves, Java, Schiffner 3056.

Thallus prostrate, adhering to substrate, green; algal symbiont Trentepohlia, filaments more or less dichotomously branched, cells short-cylindric, 2.5 - 3 times longer than wide. Apothecia 0.1 - 0.3 mm. in diameter, biatorine, round, sessile, slightly constricted at the small base; disk slightly concave, pale yellow-carneous; margin white, prominent, entire; excipulum paraplectenchymatous; hypothecium colorless; hymenium 40 - 55 μ high; paraphyses filiform, simple, 1.5 μ wide, apices distinctly sub-globose to clavate, 3.8 μ wide, conglutinate; asci sub-elongate to cylindrical, 8-spored; spores one-septate, biseriate, oblong to elliptic, round on both sides, curved or arcuate, 8-9 x 2-3 μ.

Zahlbruckner described the size of the cells in the algal filaments as 14-16 x 17-19 μ. In the single specimen examined, I found the algal cells to measure 6-8 μ wide and about 2.5 to 3 times as long. This difference in size is not, however, important in the taxonomy of the species. The characteristic curved spores are considered the significant diagnostic feature.

Santesson (1952) reports this species as probably more or less obligately foliicolous. The material examined in the present work, however, was found on a bark substrate.

Material seen: PUERTO RICO: Vicinity of Mayaguez, Britton & Marble, 4-10 March 1906 (MICH 13423).

Coenogonium disjunctum Nyl.

Bot. Zeit. 20:178. 1862. - Orig. coll.: On trunks and dead wood, Martinique and Cuba (collecter not known).

Thallus adnate, pannose, expanded, yellow-green; algal symbiont Trentepohlia, filaments cylindrical, 3-5 times longer than wide. Apothecia 0.6-0.7 mm. in diameter, round, stalked; disk flat, carneous-yellow, margin pale, thin, smooth sometimes rugged; paraphyses septate, 1.5 μ wide, apices sub-globose to clavate, 3.5 - 4.5 μ wide; asci cylindrical, 8-spored; spores one-septate, irregularly biseriate, fusiform, 7.5 - 13 x 2-4 μ.

This species is easily distinguished from _C_. _Linkii_ by the effused and adnate thallus and the larger size of the spores.

Specimens from the United States and Central America had the same spore sizes (11-13 x 2-4 μ), while those from the West Indies were smaller, only 7.5 μ long. The material examined from the Philippines had relatively the largest size of spores, 12-13.2 x 2.8 - 3 μ.

Material seen: **ALABAMA:** (locality and collector not known) (Willey Lichen Herbarium) (US).

COSTA RICA: Morpho Valley, alt. 4400 ft., _Danilson 51_ (Date not known) (MICH). **HONDURAS:** On twigs, Landetilla Valley, _Chickering_ _148 d_, June-July 1929 (MICH). **MEXICO:** On tree bark, Jolapa, _Pringle_, 25 June 1908 (MICH 15407). **PANAMA:** Summit forest, Cerro Campana, _Bartlett_ & _Lasser_, 1 September 1940 (MICH 16936).

PUERTO RICO: On twigs, Rio Icaco and adjacent hills altitude 465 to 720 m., Sierra de Naguabo, Shafer 3636, 30 July - 5 August 1914 (NY).

PHILIPPINES: On trees and rocks, 2300 ft. elev., Lamao River, Mt. Mariveles, Bataan, Central Luzon, Williams 805, 2 January 1904 (NY).

Coenogonium implexum Nyl.

Ann. Sci. Nat. IV. 16:92. 1862. - Orig. coll.: On barks among mosses, Tarwin, Victoria, Australia, Ferd. Müller.

Synonym: C. inflexum Hook. Handbook New Zealand Flora 581. 1867.

Thallus adnate, pannose, expanded, bright yellow; algal symbiont Trentepohlia, filament cells 2-4 times longer than wide. Apothecia 1 mm. in diameter, round, sessile; disk flat, carneous-yellow; margin white, thin, entire; paraphyses septate, 1.5 - 2 µ wide, apices clavate, 2 - 3.5 µ wide; asci cylindrical, 8-spored; spores one-septate, uniseriate, oblique, short-fusiform, 7-12 x 2.4 - 4 µ.

This species resembles C. interplexum except for the larger and wider paraphyses of the former. Nylander gives the measurements of the spores as 8-11 x 3.5 - 4.5 µ and the algal filaments as 10-14 µ wide. The spores in the material examined had a wider range and I found the algal filaments very variable in size. The size of the algal cells as a diagnostic character cannot be generalized in this case.

This species has been reported as foliicolous by Nylander and Santesson but I have not encountered any epiphyllous material.

The collections from South America and Australia were identical in their size of spores, and those from the United States and the West Indies had the same length of spores; the width of the spores in the West Indies collection was smaller (2.4 μ).

Exsicatti: Malme, Austr. Amer. n. 113.

Material seen: FLORIDA: On twig, southeast Florida, J. D. Smith 55, March 1877 (US); on bark, (no locality), Curtiss, 1879 (US). TEXAS: On bark, Hardin Co., 7 miles south of Silsbee near Bruce Reid's place; alluvial area, longleaf pine belt, Whitehouse 25968, 19 November 1951 (MO 184372). LOUISIANA: On bark of living tree, woods near Varnada, Washington Parish, McFarland 187, 24 January 1953 (MO 184371).

BRAZIL: Rio Grande do Sul, Porto Alegre (a), 9 September 1892 (Exp. Regn. I. Lich. n. 478), and Cruz Alta, 17 April 1893 (Exp. Regn. I. Lich. n. 1255), Malme 113

(MSC). COLOMBIA: (no locality), *Mutis*, 1760-1808 (US).

JAMAICA: On bark, Kinloss to Barbecue Bottom, 1300 ft., Trelawny Parish, *Imshaug 16060 c*, 10 May 1953 (MSC).

AUSTRALIA: Tarwin, Tasmania, (Collector not known), *no. 49*, 1855 (US); on tree, Mt. Arthur, Tasmania, *Wilson* 23 February 1891 (MSC 3237); Warburton, Victoria, *Bastow*, March 1902 (MSC).

Coenogonium interplexum Nyl.

Ann. Sci. Nat. IV. 16:92. 1862. - Orig. coll.: On trunks of trees, Colombia, *Lindig 2561*.

Thallus adnate, pannose, expanded, loosely tomentose, light yellow; algal symbionts *Trentepohlia abietina*, *T. arborum*, *T. elongata*, or *T. aurea*, cell shape and filament size variable. Apothecia 0.5 - 1 mm. in diameter, round, subsessile; disk flat to slightly concave, carneous-yellow or orange, margin whitish-carneous or white, thin, entire; hymenium 70-75 μ high; paraphyses slender, about 1 μ wide, septate, apices clavate to obtuse, 3.3 μ wide; asci cylindrical, 8-spored; spores one-septate, uniseriate, linear, short-fusiform or fusiform-elliptic, 6.5 - 10 x 2.5 - 3 μ.

This species is similar to *C. implexum* except for its consistent smaller spores, thinner paraphyses and somewhat longer algal cells. Nylander (1862) described the spores as 8-10 μ long but I found spores that were shorter and slightly wider. Malme (1937) has described the range in length to be 8-11 μ. I found the species not to be variable as to spore sizes. Specimens from the West Indies, South America and the United States had the same range, while those from Central America were slightly longer.

Müller (1893) and Santesson (1952) reported foliicolous specimens from Boruca, Costa Rica, (Pittier no. 6114), but are sterile and unidentifiable. A collection from Ann Arbor, Washtenaw Co., Michigan, reported by Fink (1935) as _C_. _interpositum_, has characters that closely agree with this species.

Exsicatti: Malme, Austr. Amer. n. 329.

Material seen: FLORIDA: On bark, among mosses at bases of trees, (no locality), _Calkins_ _170_, 1889 (MSC 120023); (no locality), _Calkins_, _1890_ (US); bases of trees on moss, Jacksonville, Duval Co., _Calkins_ _963_, (no date) (MSC); at base of oak trees, Jacksonville, Duval Co., (collector not known) (Willey Lichen Herbarium) (US); on pine tree near base of stem, Solution Sink, Millhopper's Hammock, 8 miles east of Gainesville, Alachua Co., _Uyenco_ _18_, 6 February 1963 (MSC); on bark of citrus, Low Hammock near Sanford, Seminole Co., Uyenco 65, 9 February 1963 (MSC); on bark of oak tree (Quercus virginiana), Lieder Trail, Highlands Hammock State Park, Sebring, Highlands Co., Uyenco 76, 11 February 1963 (MSC); on bark of Lyssoloma, Rattlesnake Hammock, Everglades National Park, Dade Co., Uyenco 109, 13 February 1963 (MSC); on bark of Lyssoloma, Redd Hammock, Everglades National Park, Dade Co., Uyenco 114, 14 February 1963 (MSC). LOUISIANA: Foot of trees in swampy woods around Covington, St. Tammany Parish, Langlois 799, 1894 (US). MICHIGAN: On old trees, Ann Arbor, Washtenaw Co., Smith, July 1932 (MICH).

COSTA RICA: On tree, Cerro de la Carpintera, Province of Cartago; altitude 1500-1850 meters, Standley 35565, February 1924 (US). GUATEMALA: On twig, Dept. Alta Verapaz; wet forest near Tactic, above the bridge across Rio Frio, altitude about 1400-1500 m., Standley 90425, 30 March 1941 (MO 166103); on twig, Dept. Alta Verapaz: dense wet limestone forest near Chirriacte, on the Peton highway, altitude about 900 m., Standley 19142, 9 April 1941 (MO 166101). MEXICO: Veracruz, Turpus 125, February 1921-22 (US).

PARAGUAY: On trees, Grand Chaco: ad Rio Negro. 15 September 1893. (Exp. Regnell. I.), Malme 330 (MSC).

BAHAMAS: On bark, Coppice, Stoppes Hill, Crooked

Island, *Brace 4823*, 9-23 January 1960 (NY). JAMAICA: On bark, Dolphin Head, 1750 ft., Hanover Parish, *Imshaug 15627 a*, 23 April 1953 (MSC). PUERTO RICO: Ravine on estate of H. Guggenbühl, vicinity of Mayaguez, *Britton* & *Marble 651*, 4-10 March 1906 (NY); Quebradillas, *Bro*. *Hioram*, January 1913 (NY).

Coenogonium interpositum Nyl.

Ann. Sci. Nat. IV. 16:91. 1862. - Orig. col.: Reunion (Bourbon) Island, *Lepervanche*-*Mezieres* & Louisiana (ex. herb. Tuckerm.).

Thallus adnate, pannose, expanded, yellow-green; algal symbiont *Trentepohlia arborum*, filaments sparingly branched, cells cylindrical, about 3 times as long as wide. Apothecia 0.7 - 0.8 mm. in diameter, round, sub-sessile; disk at first concave, becoming convex, carneous-yellow to pale orange; margin pale, thin, entire, rarely sub-denticulate; excipulum paraplectenchymatous, cells angular; hypothecium yellowish; hymenium 70-75 µ high, colorless; paraphyses simple, conglutinate, 1-1.5 µ wide, apices clavate, 2-4 µ wide; asci cylindric-clavate, 8-spored; spores simple, irregularly biseriate, elliptic to fusiform-elliptic, 6-10 x 2-3 µ.

Zahlbruckner (1909) and Malme (1937) used this name for a species with one-septate spores and it was also cited by Fink (1935) in the same manner. Nylander distinguished this species from C. disjunctum by its smaller spores and thinner algal filaments. The latter species has distinctly one-septate spores. The size of the algal cells, however, is not believed to be a useful taxonomic character, especially in the case of dried specimens where the filaments do not imbibe water easily, thus rendering the measurements of algal cells extremely difficult and inaccurate for comparative purposes. A comparison of spore sizes among the geographical areas present interesting information. Specimens from the United States and the West Indies were exactly the same in spore measurements; those from the Philippines were 6 x 2.5 µ; the collections from Central America were 6.3-8 x 2.8-3 µ in size. The spores in the single fertile collection from Colombia measured 7.5 - 8.5 x 2.2 µ.

Exsicatti: Malme, Amer. n. 330.

Material seen: FLORIDA: On trees (no locality), Sprague, (no date) (MSC 10877); on twig, in hammocks near the Homestead road, between Cutler and Longview Camps, Dade Co., Small & Carter 1347 & 1348, 9-12 November 1903 (NY); on twig, Royal Palm Hammocks, Dade Co., Lowe, 29 January

1916 (Tenn.); on bark of trees, Sanford, Seminole Co., Rapp, May 1928 (FLAS 29040); on trunk of live oak, in low hammock, Lake Marion, Osceola Co., McFarlin 8, 21 January 1931 (MSC); on sweet gum tree, Low Hammock near Sanford, Seminole Co., Uyenco 67, 9 February 1963 (MSC); on bark of sweet gum tree, Lieder Trail, Highlands Hammock State Park, Sebring, Highlands Co., Uyenco 78, 11 February 1963 (MSC).

MEXICO: On living tree, Chichen Itza, Yucatan Peninzula, Steere, 13 June 1932 (MICH 1253); on tree in forest, San Miguel, Cozumel Island, Quintana Rio, Steere, 6-8 August 1932 (MICH 2726).

COLOMBIA: On tree trunk, Dept. El Valle: Cordoba; altitude 50-100 meters; dense forest, Killip & Garcia 33447, 17 February 1939 (US).

BAHAMAS: (no locality), Eggers 4463, (no date) (NY).

DOMINICAN REPUBLIC: On bark, Santo Domingo, Rose, March 1913 (MICH 8238); in wooded ravines along trail to Goodrich rubber grove, vicinity of Piedra Blanca, Prov. of La Vega; altitude 200-500 meters, Allard 17142, 21 November 1947 (US). **HAITI:** Mossy tree in deep shade, ravine on east slope above road NW of Foret des Pins, Dept. l'Ouest, Imshaug 22909, 16 July 1958 (MSC). **JAMAICA:** Fern gully, near Ocho Rios, 700 ft., St. Ann Parish, Imshaug 15797 a, 6 May 1953 (MSC). PUERTO RICO: On twigs, La Romana, Rio Dulce, Johnston, 7 April 1913 (MICH 8269); El Yunque, Chamberlain, February 1941 (MO 158071).

PHILIPPINES: On bark, Lake Manguao, Palawan, Merrill 9014, April 1913 (US).

Coenogonium Leprieurii Nyl.

Ann. Sci. Nat. IV. 16:89. 1862. Holocoenis Leprieurii Clements, Gen. Fung. 174. 1909. C. Linkii var. Leprieurii Mont. Ann. Sci. Nat. III. 16:47. 1851. Orig. coll.: French Guiana, Leprieur.

Synonyms: Dictyonema sericeum var. camerunense Henn., Mitteil. von Forschungsreisend. ind Gelehrten aus dem Deutsch. Schutzgebeit. II:144. 1889.

C. Leprieurii var. lamellifera Wain. Ann. Acad. Sci. Fenn. 15(Ser. A). 6:157. 1921.

C. Leprieurii var. panniforme Wain. Jour. Bot. 34:204. 1896.

Thallus spongy-byssoid, thin, circular, extending out horizontally in a prostrate growth, becoming imbricate with one margin affixed to substrate, shelf-like, yellow-green; algal symbionts Trentepohlia umbrina or T. odorata. Apothecia situated on both upper and lower surfaces of thallus, 1—5 mm. in diameter, round, sessile or rarely sub-sessile; disk flat or somewhat convex, carneous or pale yellow; margin white, thin, uneven; excipulum euparaplectenchymatous; hypothecium colorless, partly paraplectenchymatous; hymenium about 60 μ high; paraphyses slender, 0.7 - 2.5 μ wide, simple, rarely septate, apices capitate, clavate to subglobose, 1.7 - 5 μ wide; asci cylindrical or cylindric-clavate, 4.7 - 6.5 μ wide, 8-spored; spores simple, uniseriate, linear, oblong-elliptic or fusiform-elliptic, 5.5 - 10 x (1) 2-4 μ.

Montagne established C. Linkii var. Leprieurii on the basis of the apothecium being plane from the beginning, provided with a rudiment of a stalk, remaining as such or deviating to convex shape, and maintaining hardly a trace of a margin. He also distinguished this variety from C. Linkii on the color of the apothecium. Montagne, however, made no mention about the septation of the spores. Santesson (1952) considers the color characteristics as not reliable since the apothecia of probably all species of Coenogonium get the same color and appearance if they are repeatedly moistened and dried. Tuckerman (1882) also believed that this variety cannot be kept apart by the given color differences.

Nylander distinguished C. Leprieurii from C. Linkii on the simple spores, the more slender filaments of the thallus and of the paraphyses.

C. Leprieurii var. lamellifera was established by Wainio on the basis of the wide, lamellate thallus. This character is not considered taxonomically significant.

Wainio established C. Leprieurii var. panniforme on the size of the spores, being 1.2-1.4 μ wide. This may be a growth form of C. Leprieurii and probably belongs to this species.

I found this species quite constant in the size of its spores since specimens from Asia, South America, Central America, West Indies and the single fertile collection from West Africa all had the same spore sizes.

Exsicatti: Malme, Austr. Amer. n. 114.

Material seen: COSTA RICA: On tree, Cerro de la Carpintera, Prov. of Cartago; altitude 1500-1850 meters, Standley 35596, February 1924 (US); on tree, El Silencio, Prov. de Guanacaste, near Tilaran, altitude about 750 meters, Standley & Valerio 44619, 13 January 1926 (US); west bank of Rio Siquirres, 70-200 meters, Limon Prov., Dodge, Catt & Thomas 5574, 7 December 1929 (MO 70721); flood-plain of Rio Sandalo, peninsula of Osa, 1-10 m., Puntarenas Prov., Dodge & Groeger 9925, 21 August 1936 (MO 154706); flood-plain of Rio Sandalo, peninsula of Osa, 1-10 meters, Puntarenas Prov., Dodge & Groeger 10051, 23 August 1936 (MO 154707); on twig, flood-plain of Rio Sandalo, Peninsula of Osa, 1-10 meters, Puntarenas Prov., Dodge & Groeger 10163, 25 August 1936 (MO 154708); on bark of trees, Canas Gordas, altitude 1100 m., Quiros 1338, 17 November 1945 (MO 160735); on bark of trees, Penshurst (Limon), M. Q. C. 1490, 13 October 1948 (MO 166111). **GUATEMALA:** Near the Finca Sepacuite, Alta Vera Paz, Cook & Griggs, 8 April 1902 (US); on twigs, common on jungle, Vaxactum, Bartlett, 20 March 1931 (MICH 15153); on twigs, Monte Santa Teresa, Lundell, 12 April 1933 (MICH 2721); on twigs, wet forest, Escoba, across the bay (west) from Puerto Barrios, Dept. Izabal, near sea level, Standley 72905, 3 May 1939 (MO 166110).

HONDURAS: On trunk of palm, Valentin, El Cayo District, Mains, 23 June 1936 (MICH 3556). **MEXICO:** Belleville, Oaxaca, Orcutt 2934, 23 February 1910 (US); on evergreen trees in deep jungle, virgin upland evergreen jungle, elev. 920 m., El Suspiro, 10 km. north of Berriozabal, State of Chiapas, Hale & Sodertrom 20208, 22 March 1960 (US).

PANAMA: On tree, common, Hills north of Frijoles, Canal Zone, Standley 27531, 19 December 1923 (US); on twig Barro Colorado Island, Canal Zone, Shattuck, 1931 (MO 68651); abandoned cocoa plantation, Las Cascadas near summit, Canal Zone, Dodge & Hunter 8841, 23 December 1934 (US); forest along telephone trail between the Rio Indio Hydrographic Station and the Natural Bridge of R. Puente, Canal Zone, Dodge & Allen 8910, 13 January 1935 (MO 154704); Prov. Coclé: El Valle de Anton, altitude 600 m., Martin 2937, 24 July 1935 (MO 73207); Las Cruces, Canal Zone, Martin 3073, 31 July 1935 (MO 73209); Barro Colorado Island, Canal Zone, Martin 3115, 31 July 1935 (MO 73210); Barro Colorado Island, altitude 20-75 m., Martin 4135, 11 August 1937 (MO 73969); on bark, Barro Colorado Island, Weston, (no date) (MICH); on tree bark, Barro Colorado Island, Prescott (4), 25 December 1962 (MSC).

BRAZIL: On bark of tree, Rio de Janeiro: Corcovado, Malme 331 a, 15 August 1892 (MSC 152231); on bark of trees, Rio Grande do Sul, pr. Sao Leopoldo, Malme 114, 18-26 October 1892 (MSC 151832); on tree trunk, Amazon Basin, altitude 2510 ft., Rusby 752, 28 September 1921 (NY); on twig, Rio Grande do Sul, Pareci Novo, Lima 19 (155), 3 December 1948 (MO 166104); S. Gabriel, Amazon & Andini, Spruce 228, (no date) (NY). COLOMBIA: On dry twigs, La Sierra, Dept. Antioquia: Medellin; altitude about 200 m., Archer 1335, 3 January 1931 (US); on tree, El Choco: La Concepcion, Archer 2009 a, 30 April 1931 (US). PERU:

On tree trunk, East of Quimiri Bridge, dense forest, Dept. Junin: La Merced; altitude about 700 meters, Killip & Smith 24039, May 29-June 4, 1929 (US); on bark, in jungle east of Tingo Maria, Dept. San Martin: altitude 625-1100 m., Allard 20797 b, 30 October 1949-19 February 1950 (US). SURINAM: (no locality), Weigelt, 1827 (MO 25591); Tafelberg (Table Mountain), Maguire 24598 a (B), 1 September 1944 (NY). VENEZUELA: (No locality), Fendler, May 1856 (NY); on tree trunks in humid forest, Colonia Tovar & vicinity, in meadows & forest; altitude 1700-2300 meters, State of Aragua, Pittier 10033, 28 December 1921 (US); Colonia Tovar, altitude 1800-2000 m., Allart 349, December 1924 (NY).

BAHAMAS: On alga, Rifle Range Coppice, New Providence, Britton 564, 6 September 1904 (NY); on wood, Cherokee, Abaco, Brace 1936 & 1967, 30 December 1904 (NY); CUBA: On rocks, Valley of the Rio Bayamita, south slope of the Sierra Maestra; altitude 900-1050 meters, Maxon 3975, 5-7 April 1907 (US); on tree trunk, forest slope, Santa Ana, about 6 miles north of Jaguey, Yateras, Oriente; altitude 600-625 m., Maxon 4194, 25 April 1907 (US); on rock, Loma del Gato, around summit of San Juan in mossy cloud forest with huge boulders and cliffs, Sierra Maestra, Oriente, Imshaug 24695, 12 August 1959 (MSC). DOMINICAN REPUBLIC: On bark, in ravine near Goodrich rubber groves, vicinity of Piedra Blanca, Province of La Vega; altitude 200-500 meters, Allard 16915, 16922 & 16962 a, 12 November 1947 (US). GRENADA: Montane thicket, Summit of Mt. Sinai, 2100 ft., St. David Parish, Imshaug 16180, 13 July 1953 (MSC); on bark, secondary forest, Mt. Sinai Waterworks, 1300 ft., St. David Parish, Imshaug 16261, 21 July 1953 (MSC). HAITI: On base of shrub in thicket, vicinity of Dondon, Dept. du Nord, altitude about 400 meters, Leonard 8736 a, 8 January 1926 (US); base of tree in dense thicket, Pailborean Pass, vicinity of Ennery, Dept. de l'Artibonite, altitude 325-900 meters, Leonard 9552, 5 February 1926 (NY); on twig, elfin woodland forest, ridge north of Foret des Pins (Shada Station), 5800 ft., near Dominican border, Dept. de l'Ouest, Imshaug 22752 & 22720, 14 July 1953 (MSC); on twig, elfin woodland, ridge about Foret des Pins, 5800-5900 ft., Dept. de l'Ouest, Wetmore 3178, 18 July 1958 (MSC). JAMAICA: On slopes above Tweedside, altitude 2000-3000 ft., Maxon 969 a, 11 April 1903 (US); on tree, along the trail from Morce's Gap, 5000 ft., to Vinegar Hill (3950 ft.) Maxon 1517, 23 April 1903 (US); on log, vicinity of Hollymount, Mount Diablo, Maxon 1903, 8-9 May 1903 (US); exposed roots of forest tree, deep ravine in mountain forest above House Hill, St. Thomas; altitude 500-700 meters, Maxon 9117, 6—12 June 1926 (NY & US); Lumsden, St. Ann's, Orcutt 6088, 1928 (US); on twig, Hollymount, Mt. Diablo, 2754 ft., St. Catherine Parish, Imshaug 14227, 28 January 1953 (MSC). PUERTO RICO: Quebrado de Limones, Mesa Mt., vicinity of Mayaguez, Britton & Marble, 4-10 March 1906 (NY); vicinity of Utuado, Britton & Cowell G, 15-20 March 1906 (NY); ravine near Utuado, Wheeler 991, 15-20 March 1906 (NY & MICH 13295); Finca Alvarez, Quebradillas, Bro. Hioram E, January 1913 (NY); on tree, mountain forest, 905 m. altitude, Barrio des Maizales, Sierra de Naguabo, Britton & Hess 2299, 9 March 1914 (NY); Rio Icaco & adjacent hills, altitude 465-720 m., Sierra de Naguabo, Shafer 3759, 30 July - 5 August 1914 (NY); on twig, Rio de Maricao, 600-720 m. altitude, Britton & Cowell 4234, 14 February 1915 (NY & MICH 14433); on wood & trees, Yunque, Fink 781, 11 December 1915 (MICH 8558); on trees in forest, Chamberlain, April 1941 (MICH).

BORNEO: On twig, Gat, Upper Rejang River, Sarawak, J. & M. S. Clemens 5901, 15 July 1929 (NY). CEYLON: (no locality), Thwaites C 34, (no date) (NY). CHINA: On mossy slope, 480 m. altitude, Ta Chai Shan (Yung Hsien), Kwangshi, Cheo 2622, 26 August 1933 (NY). PHILIPPINES: On twigs of living shrubs, Lamao, Province of Bataan, Merrill 3568, October 1903 (US); Apo, 6500 ft., (collector not known), 2676, 1 April 1905 (NY). WEST AFRICA: Prince's Island, Marm, 1861 (NY).

Coenogonium *Linkii* Ehrenb.

in Nees ab Esenb. Horae Phys. Berol. 120, Pl. 27. 8120. - Orig. coll.: Santa Catharina, Brazil, Chamisso.

Synonyms: *C. andinum* Karst. in Nyl. Bot. Zeit. 20:178. 1862.

C. confervoides Nyl. Flora 41:380. 1858. - Orig. coll.: Mexico, Fr. Müller (Schimper Herb.).

Rejected name: *C. controversum* Pers. in Gaudich. Voyage Uranie, Bot. 7:214. 1826. Nomen novum for *C. Linkii* and *Conferva arborum* Ag. - Orig. coll. of *C. arborum*: Marianas Island, Gaudichaud.

Thallus shelf-like, pendant, lamellate, spongio-byssoid, orbicular, occasionally dimidiate, attached at one side to the substratum in the manner of some polypores; reniform or round, sometimes zonate, yellow-green; algal symbionts *Trentepohlia arborum*, *T. aurea* or *T. elongata*, covered by hyphae 2-3 μ wide. Apothecia on different levels on the thallus, either on the upper or lower surface, 0.6 -

1.2 mm. in diameter, round; young apothecia white, nearly pedicellate, top or cup-shaped, gradually widening and becoming subsessile; disk flat or convex, carneous or pale-yellow becoming red; margin pale, thin, entire; excipulum euparaplectenchymatous; hypothecium white or colorless, thin; hymenium gelatinous, about 40-60 μ high; paraphyses septate, 1-3 μ wide, apices capitate, sub-globose to clavate, 2.3 - 5 μ wide; asci cylindrical to fusiform-cylindric, about 4-7 μ wide, 8-spored; spores one-septate, biseriate, straight to oblique or slightly curved, ovate to short-fusiform, 6.8 - 12.5 x 2-4 μ.

Ehrenberg illustrated the spores of this species as simple; Santesson believes that this might be incorrect on account of the poor optical equipment used by Ehrenberg. Nylander (1862) described this species as similar to C. Leprieurii except for the septate spores and the wider filaments and paraphyses of the former. He also mentioned simple spores with only poorly developed septa apparent. I found this character occurring in some of the materials examined and unless the very thin septa were carefully stained, the two-celled nature of the spores was likely to be overlooked.

Coenogonium andinum was separated from C. Linkii on the basis of its wider algal filaments and paraphyses. As this character does not seem sufficient to establish another species, the writer believes that C. andinum should be a synonym of C. Linkii.

Nylander distinguished C. confervoides from C. Linkii solely on the wider algal filaments and more distinct confervoid cells of the former. Since algal characters cannot be used in maintaining a separate species, C. confervoides is treated here as a synonym of C. Linkii.

The spore sizes of this species were observed to be quite variable in the collections studied and a comparison can be made of these variations among the geographical areas represented. Below is a summary of the range in length and width of the spores:

United States - 7-9.3 x 2-3 µ

South America - 6.8-10.4 x 2-3.5 µ

Central America - 7.5-12 x 2-3.5 µ

West Indies - 12.5 x 2.5-4 µ

Philippines - 8.7-9.3 x 2.3-3.4 µ

Australia - 11.9 x 4 µ

Exsicatti: Malme, Austr. Amer. no. 113.

Material seen: FLORIDA: On bark of *Carpinus* and Magnolia, on moss, 6 mile Cr., *Calkins* *82*, *90* & *116*, (no dates) (MO 33775 & MICH 962 & US); on bark of *Carya tomentosa*, Millhopper Hammock, in limestone sink, 8 miles northwest of Gainesville, Alachua Co., *Uyenco* *17*, 6 February 1963 (MSC); on bark of sweet gum tree, Black Bottom Hammock, 8 mi. west of Sanford, Seminole Co., *Uyenco* *64*, 9 February 1963 (MSC); on bark of oak among liverworts, Low Hammock near Sanford, Seminole Co., *Uyenco* *66*, 9 February 1963 (MSC); on twigs of sweet gum tree, Lieder Trail, Highlands Hammock State Park, Highlands Co., *Uyenco* *77*, 11 Feb. 1963 (MSC); on twigs and bark of *Lyssoloma*, Rattlesnake Hammock, Everglades National Park, Dade Co., *Uyenco* *107*, 13 February 1963 (MSC); on bark of *Ficus* tree, Redd Hammock, Everglades National Park, Dade Co., *Uyenco* *116*, 14 February 1963; on bark of *Dipholis* *salicifolia*, Fire Road near Gate 3, Redd Hammock, Long Pine Key, Everglades National Park, Dade Co., *Uyenco* *117*, 14 February 1963 (MSC). LOUISIANA: Caris Creek, near St. Francesville, West Feliciana Parish, *Flint*, 15 July 1938 (Prescott).

COSTA RICA: On twigs and tree, El Muneco, on the Rio Navarro, Prov. Cartago, altitude 1400-1500 meters, *Standley* & *Valerio* *51055*, 6-7 March 1926 (US). MEXICO:

Veracruz, *Turpus 222*, 1921-22 (US). PANAMA: Marraganti, *Williams 1092*, 8 April 1908 (NY); on trees, Achajuela, *Cornman 3003*, 3 November 1917 (MO 158769).

BRAZIL: On barks of trees, Rio Grande do Sul: Cascada de Herminegilda pr. Pelotas, *Malme 329*, 11 December 1892 (MSC); on *Piptadenia durissima*, Porto Alegre, Rio Grande do Sul, *Rambo 94*, 1931 (MO 71064). COLOMBIA: Vicinity of Medellin, *Rev. Charetier 208*, 1911 (US); on twig, Bosques de Yanaconas, altitude 1760, *Azael*, 5 February 1938 (US); Cordillera Oriental, Dept. Norte de Santander; region del Sarare: Alto de Sta. Ines, bosques 2150-2250 meters, *Cuatrecasas*, *Schultes* & *Smith 12440*, 19 October 1941. ECUADOR: Camino de los Colorados, *Prescott T-48*, 10 February 1958. PARAGUAY: (no locality), *Morong 1441*, 1888-1890 (NY). PERU: On Pajnail trail 3500-5000 ft., *Bassler*, October 1922 (NY & MO 166292); on tree trunk, Dept. Ayacucho: Aina, between Huanta and Rio Apurimac, altitude 750-1000 meters, open woods, *Killip* & *Smith 23146*, 7-17 May 1929 (MO 70247 & US); on twigs, Dept. Junin, Pichis Trail, Enenas, altitude 1600-1900 meters, dense forest, *Killip* & *Smith 25658*, 30 June-2 July 1929 (US). VENEZUELA: On tree trunks in humid forest, Colonia Tovar & vicinity, in meadows & forests; altitude 1700-2300 meters, Aragua

State, Pittier 10034, 28 December 1921 (US).

CUBA: (No locality), Wright, (no date) (US); on twig, south of lumber camp, crest of Sierra Nipe, altitude 600-700 meters, Oriente, Morton & Acuna 3240, 16-17 October 1941 (US); on bark, near Topes de Collantes, Trinidad Mts., Las Villas, Imshaug 24628, 2 August 1959 (MSC). **DOMINICAN REPUBLIC:** On twig, cloud forest, ridge above Los Amaceyes, 300-3200 ft., Cordillera Septentrional, Imshaug 23276, 2 August 1958 (MSC); on twig, wet montane mist forest, Casabito, 4000 ft., between El Rio and Jayaco, La Vega, Wetmore 3433, 4 August 1958 (MSC). **HAITI:** On bark, elfin woodland forest, ridge north of Foret des Pins (Shada Station), 5800 ft., near Dominican border, Dept. de l'Ouest, Imshaug 22753, 14 July 1953 (MSC); on tree branch, shrub thicket at summit of Montagne Noire, 5500 ft., Kenscoff, Dept. de L'Ouest, Wetmore 2774, 7 July 1958 (MSC). **PUERTO RICO:** Mt. Morales, near Utuado, upper slopes of tree, Howe 1153, 19 March 1906 (NY & MICH 13296); (no locality), F. L. S. 2864, 15 July 1913 (MICH 7042); on twigs, Rio Icaco & adjacent hills, 465-720 meters, Shafer 3736, 30 July - 5 August 1914 (NY & MICH 13422); near La Juanita, Britton 905, 7 February 1915 (NY); on tree in mountain forest, Monte Cerrote, near Adjuntas, 900-1050 meters altitude, Britton & Brown 5466, 15 March 1915 (NY & MICH 14434); on Acrista, Monte Torrecilla, 900-1100 meters altitude, Britton, Cowell & Brown 5666, 19-20 March 1915 (MICH 14435). TRINIDAD: On a small tree, forest, Broadway, February 1928 (MO 943076).

PHILIPPINES: Bontoc Subprovince, Luzon, Fr. Vanoverbergh 874, October 1910 (US); on trees, Baguio, (no collector's name), 1618, 20 September 1904 (US).

AUSTRALIA: Tasmania, Lindley, (no date) (NY).

Coenogonium moniliforme Tuck.

Proc. Am. Acad. Sci. 5:416. 1862. - Orig. coll.: Cuba, (unknown locality), corticolous, Wright n. 172.

Synonym: Biatorinopsis torulosa Müll. Arg. Rev. Myc. 10:114. 1888. - Orig. coll.: Guarapi, Paraguay, corticolous, Balansa 4165.

Thallus effused, crust-like, margin widely pallid, glaucous-green to deep yellow; algal symbiont Physolinum monilia (De Wildem.) Printz, filaments branched, cells subglobose to elliptic, about 18 μ in diameter, elliptic cells 10-15 x 22-31.5 μ. Apothecia appressed on the thallus, round, 0.2 - 0.4 mm. in diameter; disk flat, carneous-red, turning paler when wet with water; margin white, thin, entire; excipulum and hypothecium colorless; hymenium 50-60 μ high; paraphyses simple, 1.2-2 μ wide, apices slightly capitate, sub-globose to clavate, 2-4.5 μ wide; asci sub-cylindric to clavate, 8-spored; spores one-septate, uni- to biseriate, oblong- elliptic to fusiform-elliptic, 9-13 x 3.2 - 5 μ.

Santesson (1952) reports this species as facultatively foliicolous. Most of the materials I examined had larger spore sizes than those mentioned by Nylander in his re-description of this species (1862). No variation in the range of spore sizes was observed in collections from Central America, United States and the West Indies. The original descriptions made by Müller and Tuckerman did not mention the size of the spores except to state that they were 3-4 times longer than wide. Malme (1937) gave the measurements of the spores in the specimens he examined from Paraguay as 9-11 x 3-3.5 μ. Knight (1886) and Shirley (1889) mentioned this species as closely allied to _C_. _botryosum_ on account of the elliptic cells found in their short filaments. The algal filaments are _Trentepohlia_ unlike those of _C_. _moniliforme_ which are _Physolinum_ _monile_. The spores of _C_. _botryosum_ are uniseriate and 10.4 x 3 μ in size, while those of _C_. _moniliforme_ are irregularly biseriate and relatively larger, 9-13 x 3.2 - 5 μ.

Exsicatti: Malme, Austr. Amer. 111 & 112.

Material seen: FLORIDA: On trees, (no locality), Austin, (no date) (MSC 13140); Pine Island, Charlotte Harbor, Charlotte Co., J. D. S. & C. F., March 1878 (NY); on bark, Caloosa River, Polk Co., Austin, 1878 (US); southwest Florida, Austin 42, March 1878 (US); on bark of Ficus, Fuch's Hammock, Homestead, Dade Co., Uyenco 100, 12 February 1963 (MSC).

GUATEMALA: On dead branch, Dept. Chimaltenango, along Rio Guacalate, southeast of Chimaltenango, altitude about 1700 m., Standley 80054, 14-23 December 1940 (MO 166105).

PARAGUAY: On bark, Aregua pr. Asuncion, (Exp. Regn. I. Lich. n. 1626), 21 August 1893, Malme, (no date) (MSU 151829). SURINAM: On bark, (no locality, collector not known, no date), (Willey Lichen Herbarium) (US).

CUBA: (no locality), Wright, (no date) (US). HAITI: elfin woodland forest, north of Foret des Pins (Shada Station), near Dominican border, 5800 ft. (Dept. de l'Ouest), Wetmore 2878, 14 July 1958 (MSC). JAMAICA: On trees, (no locality), Harris, (no date) (MICH 12378); on stems of Pisonea aculeata, Hope Gardens, 680 ft. alt., Harris, 14 January 1915 (NY).

Coenogonium ornatum Müll. Arg.

Bull. Herb. Boissier. 4:96. 1896. - Orig. coll.: On bark, Queensland, Australia, Shirley n. 1787.

Thallus amorphous, filaments closely aggregated, not at all fasciculate, bright-green; algal symbiont Trentepohlia, cells of filaments 2-3 times longer then the width. Apothecia 0.4-0.6 mm. in diameter, round, sessile; disk flat to convex, carneous-purple; margin concolorous with disk, wearing away at maturity; paraphyses simple, 1.5 μ wide, apices clavate, sub-truncate, 1.5 - 2 μ wide; asci clavate, 8-spored; spores simple, uniseriate, fusiform, 8-10 x 2.3 - 4 μ.

Nylander (1862) stated that this species was closely related to C. interpositum. It is believed that the distinct immarginate structure of the apothecium, the arrangement of the spores in the asci and the texture of the thallus merit the separation of this species from the other members of the group.

I found the spores in the materials from the West Indies of the same length but slightly narrower than those from South America. Specimens examined from Central America had longer spores than those from either of the two but the widths were identical with the specimens from the West Indies, 2.5 μ.

Exsicatti seen: Malme, Austr. Amer. no. 113.

Material seen: **MEXICO:** Veracruz: Mirador, Baldwin Jr. 14406, 20 May 1950 (US).

PARAGUAY: On bark of Acacia, 9 August 1893, (Exp. Regn. I. Lich. n. 1552), Malme 112 (MSC 151830). **VENEZUELA:** On tree trunks, Colonia Tovar, 2000-2100 m., Pittier 10033, 28 December 1921 (NY).

JAMAICA: (no locality), Cummings 170, February and March, 1905 (NY). **PUERTO RICO:** (no locality), Britton, (no date) (MICH 11758 b).

Coenogonium pannosum Müll. Arg.

Flora 64:234. 1881. - Orig. coll.: On bark, near Apiahy, Central Brazil, Puiggari 1026.

Thallus adnate, slightly tomentose, upper surface appearing wrinkled, yellow-green; algal symbiont Trentepohila, cells barrel-shaped. Apothecia 0.3 - 0.5 mm. in diameter, round, sub-sessile; disk flat, rarely convex, pale to whitish-orange; margin paler, thin, entire; paraphyses slender, 1.5 μ wide, apices obovoid, 2.7 - 3.5 μ wide; asci cylindrical, 8-spored; spores one-septate, uniseriate, fusiform, 6-7 x 1.5 - 2 μ.

The immarginate structure of the apothecium and the very narrow spores distinguish this species easily from the others which have one-septate spores.

Material seen: GUADELOUPE: Souface, Ep. 400 m., Questel 3616, 20 January 1939 (MO 161488). JAMAICA: East slope of John Crow Mts. above Ecclesdown, 2300 ft., Portland Parish, Imshaug 14544 a, 11 February 1953 (MSC). PUERTO RICO: On tree, Sierra de Naguabo 600 m. altitude, Britton & Cowell 2194, 8 March 1914 (MICH 13294 & NY).

Coenogonium tomentosum Müll. Arg.

Jour. Linn. Soc. Lond. 32:206. 1896. - Orig. coll.: On bark, New Zealand, Colenso 1615.

Thallus tufted, tomentose, bright-yellow; algal symbiont Trentepohlia, filaments short, closely aggregated, not interwoven cells twice longer than wide. Apothecia 0.3 - 1 mm. in diameter, round, sub-sessile; disk flat to slightly concave, white when young, becoming carneous-orange as it matures; margin white, prominent, entire; parphyses slender, septate, capitate, globose; asci clavate, 8-spored; spores simple, uniseriate, fusiform, 8 - 10.5 x 2.5 µ.

The original description for this species described the size of the spores as 10-11 x 2.5 μ. The specimen from the Dominican Republic was observed to have shorter spores (7.6 μ) but the characteristic uniseriate arrangement of the spores in the ascus and the globose-capitate apex of the paraphyses place it in this species.

Material seen: **BAHAMAS:** Soldiers Road, New Providence, Britton 3180, 30 January 1905 (NY); Mt. Pleasant, New Providence, Britton 760, 13 September 1904 (NY).

DOMINICAN REPUBLIC: In heavy woods near Goodrich rubber grove, vicinity of Piedra Blanca, Province of La Vega, altitude 200-500 meters, Allard 18987, 19 January 1948 (US).

Coenogonium velutinum A. Zahlbr.

Nat. Hist. Juan Fernandez 2:332. 1924. - Orig. coll.: Masatierra, Juan Fernandez, Skottsberg, s.n.

Thallus adnate, cushion-shaped, round, bright-yellow; algal symbiont Trentepohlia, filaments short, closely aggregated, cells cylindrical. Apothecia 1-2 mm. in diameter, round, biatorine, sessile; disk concave to slightly convex, orange-yellow, pruinose; margin pale, whitish, thin, entire; excipulum and hypothecium paraplectenchymatous, the latter pale yellow; hymenium colorless to slightly yellow near the surface, about 100 µ high; paraphyses slender, 1.3 - 2 µ wide, simple, apices not at all wider; asci cylindrical to clavate, 8-spored; spores one-septate, irregularly uniseriate, elliptic to fusiform-elliptic, 9-11 x 2.6 - 3.5 µ.

This species is easily distinguished from the others by the pruinose apothecia and the almost truncate shape of the apices of the paraphyses. It is similar to *C. disjunctum* except for the uniseriate spores, the slightly smaller size of the spores and the aseptate paraphyses.

Material seen: JUAN FERNANDEZ: Yunque Mts., 500 m., Masatierra, *Skottsberg*, 24 April 1917 (NY).

JAMAICA: South slope of Mossmans Pk., 500 ft., Blue Mts., St. Thomas Parish, *Imshaug 14616*, 19 February 1953 (MSC).

DISCUSSION

It is often difficult to establish whether an organism is a lichen or not. Easily misinterpreted situations occur frequently in the genus Coenogonium where the algal symbiont is more conspicuous than the mycobiont. In the past, the algal characters, e.g., shape of cells, cell sizes of the filaments and the shape of the thallus, have been used to identify the species of Coenogonium. The problem of taxonomy has been further aggravated wherever slightly or partially lichenized algae (Trentepohlia or Physolinum) were encountered and names were given to the consortium based on the algal component alone.

Some authors have assigned equal importance to the alga and fungus in lichen taxonomy; others have given scientific names to the consortia as a whole. Thus, two consortia with the same fungus but with different algal symbionts may have different scientific names. The International Code of Botanical Nomenclature, Art. 76 (1950) states, in part: "For nomenclatural purposes names of lichens shall be taken as applying to the fungal component." Such provision should clarify the misinterpretations raised by taxonomists who maintain that lichens form a taxonomic unit. As is well known, a consortium is not a genetical unit and cannot therefore be considered taxomonically as such.

It has been shown that neither the lichen-fungi nor the lichen-algae form distinct taxonomic groups but that they show relationships with many groups of non-lichenized fungi and algae. The names of the lichen-fungi have usually been thought of as the names of the lichens. Lichens, however, are biological entities, not taxonomic units. The fundamental fact which must be observed in the taxonomy, therefore, is that the lichen-fungi, not the lichens, are being classified.

The name Coenogonium has been erroneously used to refer to the members of the Trentepohliaceae which are more or less surrounded by fungal hyphae. It is evident that this designation was given for the consortium in which the taxonomical position and the morphology of the algae have been the bases for the classification of the genus. Since, as has been discussed above, the lichen is considered as a biological group and not a taxonomic unit, the generic name Coenogonium must, from a strictly taxonomic point of view, belong to the fungal component.

The present investigation is the natural result of combined herbarium, laboratory and field studies. The importance of culture studies in this group of lichens cannot be overemphasized. Here is a situation where the experimental method has proven useful as a means of solving a taxonomical problem. It not only supplements the classical morphological methods in taxonomic studies (herbarium and field work) but also shows that the genus _Coenogonium_ can be treated in the same manner as the other members of lichen groups where the fungal characters are the primary bases for their classification. The results obtained in the laboratory reveal the role of the fungus in the symbiotic relationship, i.e., in determining the shape of the thallus, and therefore, permits its use as a taxonomic character. It was demonstrated that the alga does not control the shape and development of the lichen. It has been shown how a shelf-like _Coenogonium_, for instance, could be formed by a lichen-fungus producing apothecia that bear either simple spores (_C_. _Leprieurii_) or septate spores (_C_. _Linkii_). The expanded, loose growth on a piece of bark may be a _Coenogonium_ with simple spores (_C_. _interpositum_), or one-septate spores (_C_. _interplexum_). A cushion-shaped thallus with wrinkled or tomentose surface could be that with simple spores (C. tomentosum) or one-septate spores (C. botryosum). Thus, it is unwise to identify the species of Coenogonium in nature or to rely on measurements of algal cells. The size of the algal filaments do not have any taxonomic importance in so far as shape of the thallus is concerned. It was demonstrated that the lichenized Trentepohlia does not branch freely and its cells are generally smaller in size than those of the free-living algae. If the extent of the lichenization of the filaments has an evident influence on the size of the algal cells and the branching of the filaments, it is apparent, therefore, that the fungus has some inhibitory effect on its symbiont. This could account for the different types of thalli in the genus.

The results of the culture studies further show that the reproductive characteristics of the lichen-fungus are of real importance for the species taxonomy of Coenogonium, the algal characters not being reliable as such. The biological characteristics of the fungus, the special substrata and geographical distribution do not seem to be equally important in establishing the specificity requirements of the lichen-fungus as to its algal symbiont. The morphological characteristics are believed to be more important in taxonomy.

All the specific epithets given to sterile or undeveloped *Coenogonium* species have been rejected in the present study. It is believed that a partially lichenized *Trentepohlia* with only a sterile lichen-fungus, should not be named as a *Coenogonium* but rather, the species of *Trentepohlia* should be identified. It is suggested that material with sterile lichen-fungi can be conveniently disposed of by simply indicating them as "slightly or heavily lichenized *Trentepohlia*."

Zahlbruckner (1926) based his classification system of orders and suborders on the fungal characters, but in the case of families, the algal characters have been the primary basis. The genus *Coenogonium* provides a case where the lichenized fungi do not show distinct specialization for individual species of *Trentepohlia*.

The thalli of *Coenogonium* vary considerably in size according to their age and location. Specimens with mature apothecia have been found to vary from 10-25 mm. and this range was observed in several species. At what age of the thallus the apothecia first appear is uncertain. The thalli grow and persist for several years, and whether or not the fungus fruiting bodies appear annually or at certain seasons of the year, may provide an interesting study for future investigators. The collection data reveal that fertile specimens were encountered at all months of the year for Coenogonium Leprieurii and at scattered periods in other species. This information, of course, depends on the intensity of the collection and, therefore, cannot be generalized.

The algae have been demonstrated to be capable of growing apart from the fungus. Whether they can produce a concentric or any specific shape of thallus if maintained at the suitable conditions of growth required by them over a considerable length of time remains to be studied.

The nature of the relationship between the lichen-algae and the fungal hyphae and the penetration of the hyphae among the algal cells have yet to be established. Haustoria have not been observed in the material examined and apparently the fungus has no effect other than the partial inhibition of branching of the alga. Haustoria in lichens are usually not discernible except by electron microscopy.

It is hoped that this comparative study of the morphology, including the reporductive structures, of both the algal and fungal components of the lichen-genus loosely referred to as Coenogonium, may provide a basis for future work towards the completion of a monograph of this genus.

SUMMARY

1. One species of *Trentepohlia* can form lichen thalli with more than one fungus species.
2. One fungus (*Coenogonium*) can form lichen thalli with more than one species of *Trentepohlia*.
3. The shelf-like form of lichen thallus is a characteristic of the fungal component since both the shelf-form and the non-shelf form of thalli have identical algal species.
4. Characters of algal cells, such as, size measurements and shape, cannot be accepted as valid in the determination of the species of *Coenogonium*.
5. Six species of *Trentepohlia* are recognized for the first time as phycobionts in the lichen-genus *Coenogonium*.
6. Four species of *Trentepohlia*; namely, *T. abietina*, *T. arborum*, *T. aurea*, and *T. elongata* are being reported for the first time from Florida.
7. *Physolinum monilia* occurs as the phycobiont of *C. moniliforme*.

8. Of the original forty-eight species referred to as Coenogonium by earlier authors, eighteen species have been recommended for transfer to the genus Trentepohlia as valid algal species or as synonyms. Four species are considered as belonging to the Fungi Imperfecti and two species are treated as synonyms of Coenogonium Linkii. Eight species are considered doubtful and one species is rejected as having been based on two discordant elements.
9. Fifteen species are recongized and accepted as valid and a taxonomic key has been made for these.

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LIST OF DISTRIBUTION MAPS

Map

1. Distribution of known *Coenogonium* species
Black circles represent material seen and examined;
light circles, type localities, no material seen

2. *Coenogonium acrocephalum* Müll. Arg. (dark circles)
Coenogonium botryosum Knight (light circles)
Coenogonium complexum Nyl. (dark squares)
Coenogonium curvulum A. Zahlbr. (light triangle)
Coenogonium pannosum Müll. Arg. (light squares)
Coenogonium tomentosum Müll. Arg. (dark triangles)

3. *Coenogonium disjunctum* Nyl. (dark squares)
Coenogonium implexum Nyl. (dark triangles)
Coenogonium moniliforme Tuck. (dark circles)

4. *Coenogonium interplexum* Nyl. (dark circles)
Coenogonium ornatum Müll. Arg. (dark triangles)

5. *Coenogonium interpositum* Nyl. (dark triangles)

5. & 6. *Coenogonium Leprieurii* Nyl. (dark circles)

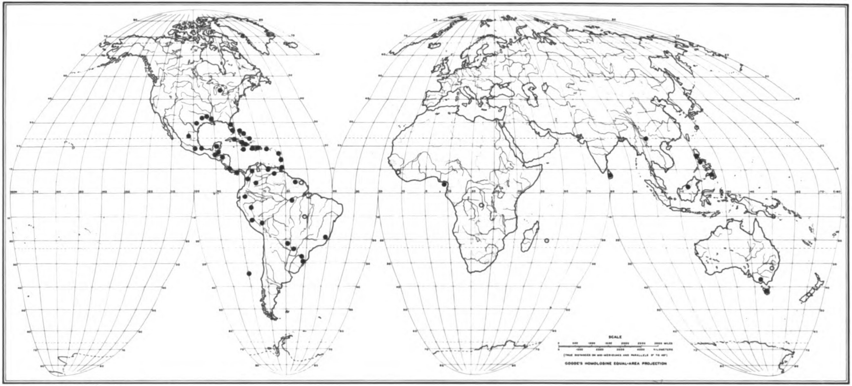
7. *Coenogonium velutinum* A. Zahlbr. (dark circles)

7. & 8. *Coenogonium Linkii* Ehrenb. (black squares)

Distribution map of known *Coenogonium* species. Black circles represent material seen and examined; light circles, type localities, no material seen.

WORLD, CONTINENTS

No. 201HC



GOODE'S SERIES OF BASE MAPS
HENRY M. LEPPARD, EDITOR

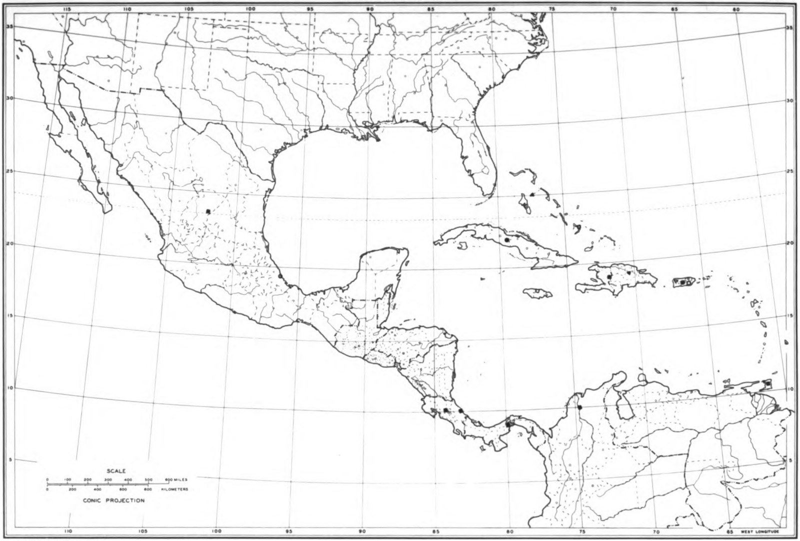
Prepared by Henry M. Leppard
Published by the University of Chicago Press, Chicago, Illinois

Distribution map of:

Coenogonium acrocephalum Müll. Arg. (dark circles);
Coenogonium botryosum Knight (light circles);
Coenogonium complexum Nyl. (dark squares);
Coenogonium curvulum A. Zahlbr. (light triangle);
Coenogonium pannosum Müll. Arg. (light squares);
Coenogonium tomentosum Müll. Arg. (dark triangles).

CARIBBEAN AMERICA

No. 213



GOODE'S SERIES OF BASE MAPS
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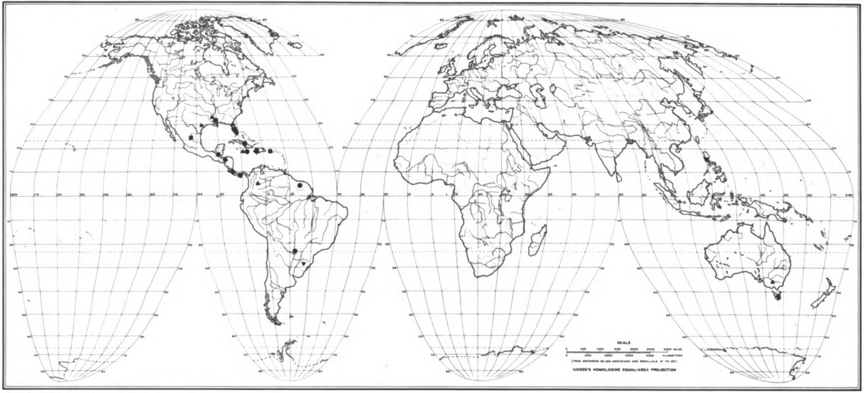
Distribution map of:

Coenogonium disjunctum Nyl. (dark squares);
Coenogonium implexum Nyl. (dark triangles); and
Coenogonium moniliforme Tuck. (dark circles).

WORLD, CONTINENTS

No. 201HC



GOODE'S SERIES OF BASE MAPS
HENRY M. LEPPARD, EDITOR

Prepared by Henry M. Leppard
Published by the University of Chicago Press, Chicago, Illinois

Distribution map of:

Coenogonium interplexum Nyl. (dark circles); and
Coenogonium ornatum Müll. Arg. (dark triangles).

GOODE'S SERIES OF BASE MAPS

HENRY M. LEPPARD, EDITOR

Distribution maps of:

Coenogonium interpositum Nyl. (dark triangles) and
Coenogonium Leprieurii Nyl. (dark circles.

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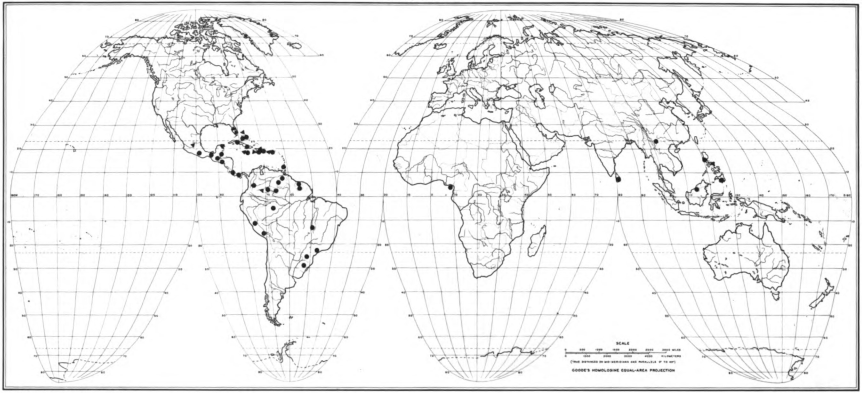

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Distribution maps of:

Coenogonium velutinum A. Zahlbr. (dark circles); and
Coenogonium Linkii Ehrenb. (black squares).

WORLD, CONTINENTS

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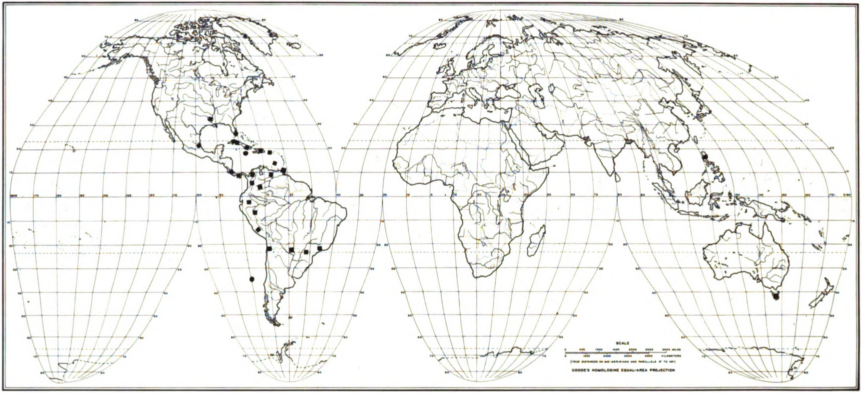

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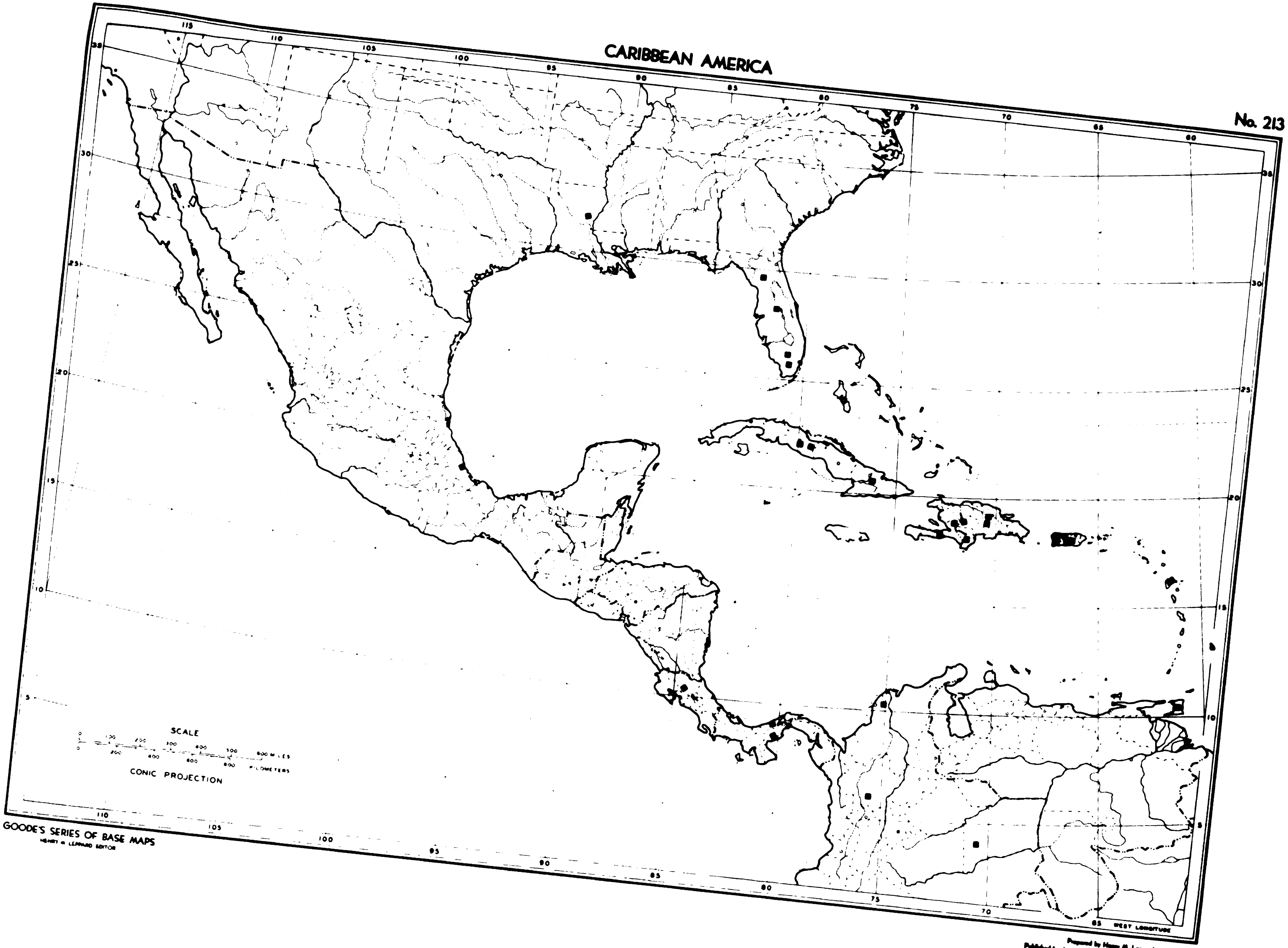

CONIC PROJECTION

GOODE'S SERIES OF BASE MAPS
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Plate 1

Fig. 1. Convex, stalked apothecium with thin margin. (*Coenogonium* *Leprieurii* Nyl.)

Fig. 2. Convex, sub-sessile apothecium (*C*. *interplexum* Nyl. or *C*. *interpositum* Nyl.)

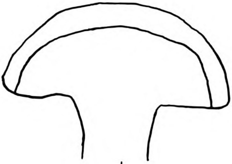
Fig. 3. Flat, stalked apothecium with thick margin. (*C*. *disjunctum* Nyl.)

Fig. 4. Convex apothecium with thin margin. (*C*. *Linkii* Ehrenb. or *C*. *pannosum* Müll. Arg.)

Fig. 5. Flat, sessile apothecium with thick margin. (*C*. *implexum* Nyl. or *C*. *acrocephalum* Müll. Arg.)

Fig. 6. Concave, subsessile apothecium. (*C*. *complexum* Nyl.)

Fig. 7. Longitudinal section of a mature apothecium showing the hymenium, excipulum and the hypothecium (*C*. *Linkii*). x 100.



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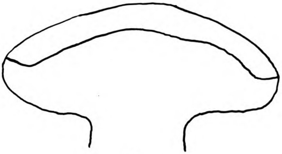

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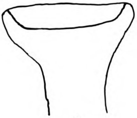

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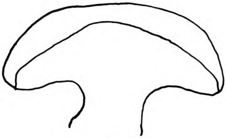

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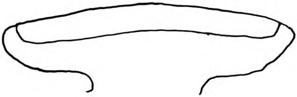

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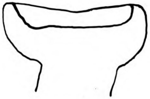

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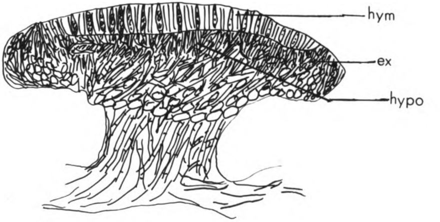


7

Plate 2

Fig. 1. Ascus and paraphysis of _C_. _Leprieurii_ Nyl. with simple, ovate and linear spores; paraphysis septate with clavate apex. x 1000

Fig 2. Ascus and paraphysis of _C_. _velutinum_ A. Zahlbr. with fusiform-elliptic and irregularly biseriate spores; paraphysis simple with apex not wider than main filament. x 1200

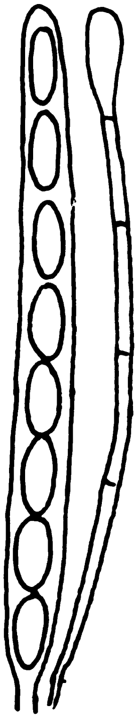
Fig. 3. Ascus and paraphysis of _C_. _moniliforme_ Tuck. with 1-septate, fusiform and biseriate spores; paraphysis septate, with globose-clavate and capitate apex. x 875

Fig. 4. Ascus and paraphysis of _C_. _implexum_ Nyl. with 1-septate, elliptic, oblique and uniseriate spores; paraphysis septate, apex globose and capitate. x 1125

Fig. 5. Ascus and paraphysis of _C_. _Linkii_ Ehrenberg with 1-septate, short-fusiform and biseriate spores; paraphysis septate, apex sub-globose. x 889

Fig. 6. Ascus and paraphysis of _C_. _curvulum_ A. Zahlbr. showing arcuate spores. x 1500

Fig. 7. Conidia and conidiophores. x 1000



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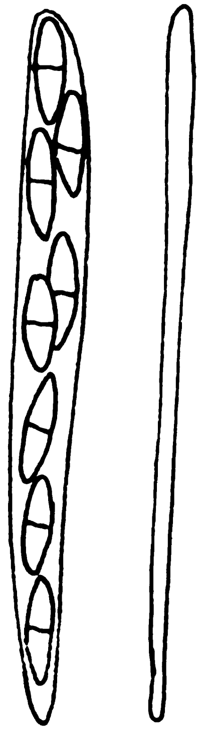

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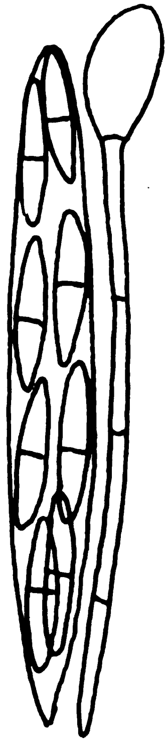

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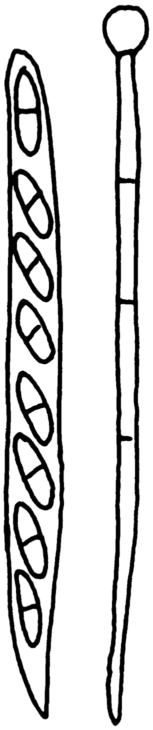

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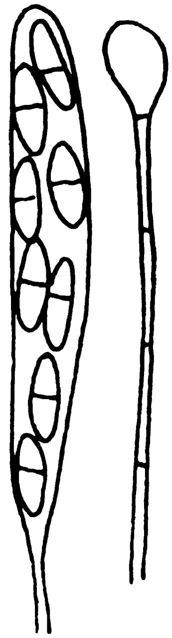

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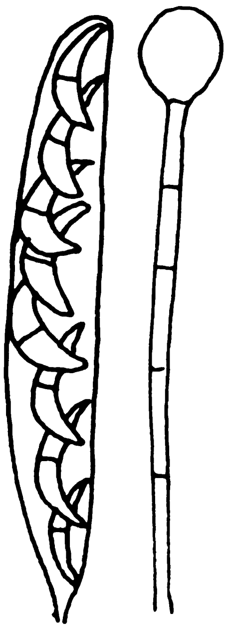

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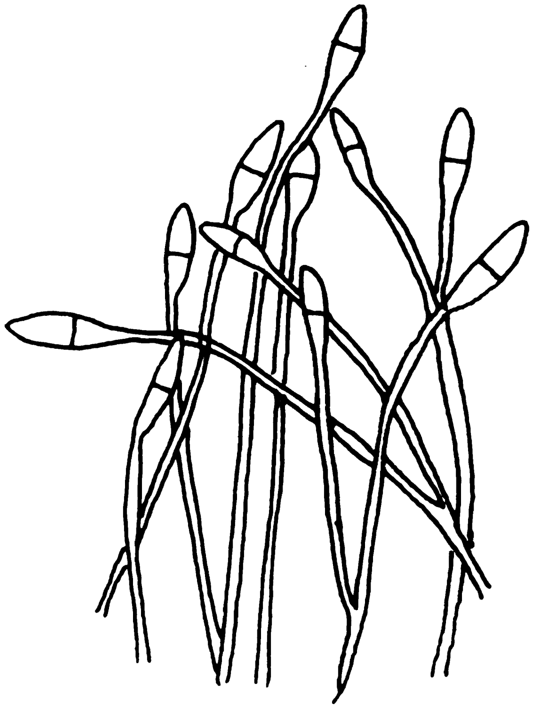

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Plate 3

Fig. 1. Portion of a filament of *T. arborum* (Ag.) Hariot with three sporangia attached to stalk cells. x 600

Fig. 2. *Trentepohlia abietina* (Flot.) Hansgirg phycobiont of *C. interplexum*, showing lateral and terminal sporangia. x 300

Fig. 3. *Trentepohlia aurea* (Linn.) Mart., phycobiont of *C. Linkii*, showing young, globose gametangia. x 706

Fig. 4. Portion of a filament of *Trentepohlia umbrina* (Kütz.) Born. showing lateral, globose sporangia. x 900

Fig. 5. *T. aurea*, phycobiont of *C. interplexum*, with terminal stalk cell bearing sporangium. x 590

Fig. 6. *T. aurea*, phycobiont of *C. Linkii*, showing right-angled branching habit of the filament and the pectose cap on the tip cell. x 756

Plate 4

Fig. 1. Portion of a filament of T. elongata, symbiont of C. interplexum, showing a young branch and lateral, globose sporangia at different age stages. x 1064

Fig. 2 T. abietina (Flot.) Hansgirg, with terminal, globose sporangia. x 300

Fig. 3. T. elongata, phycobiont of C. Linkii. x 750

Fig. 4. T. elongata, phycobiont of C. interplexum. x 526

Fig. 5. Portion of a filament of Physolinum monilia (De Wildem.) Printz, showing sporangia containing aplanospores. x 1000

Fig. 6. Lichenized algal filaments with two apothecial initials. x 500

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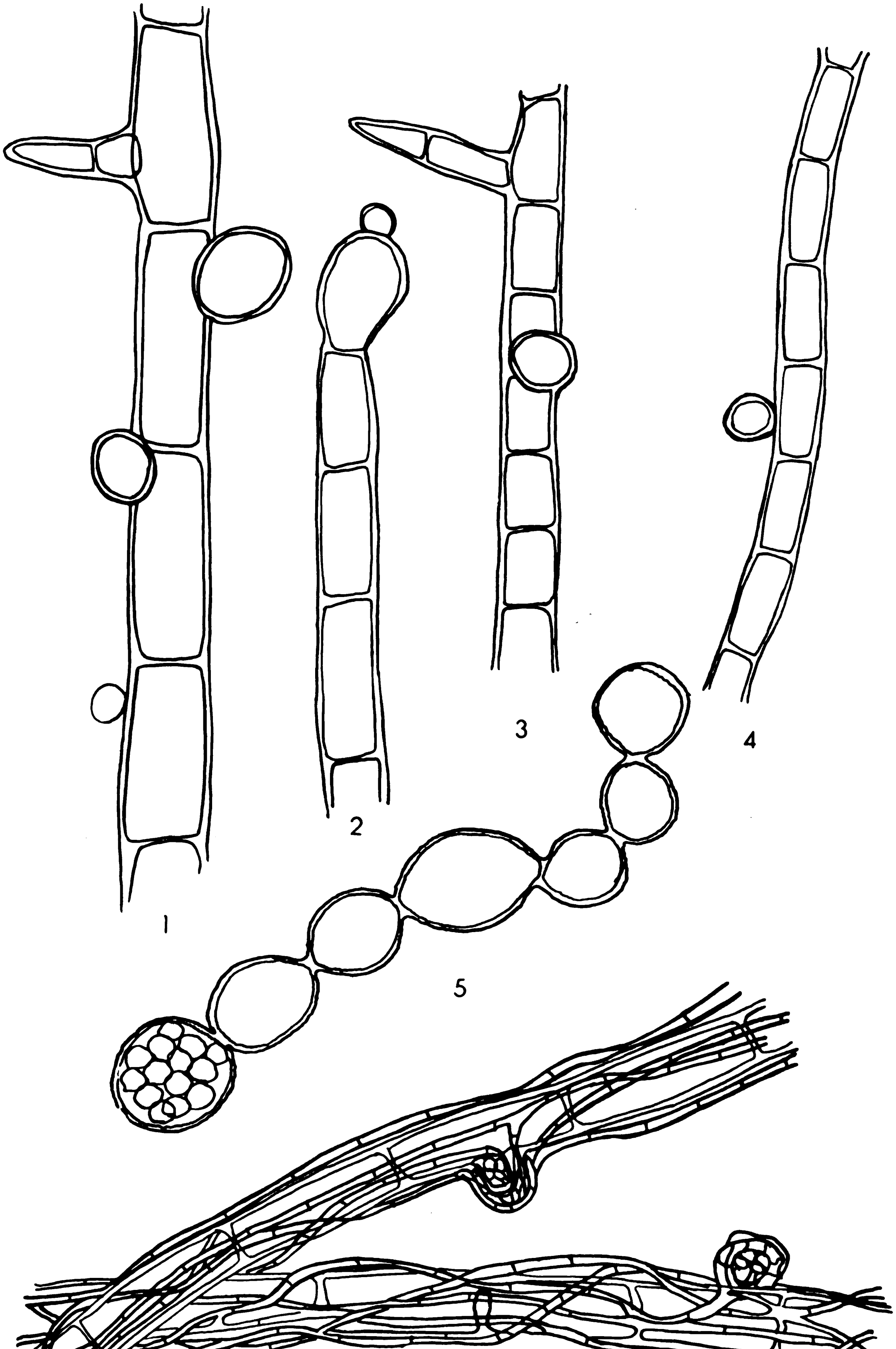


Plate 5

Fig. 1. A portion of a filament of *T. arborum* showing an empty gametangium. x 600

Fig. 2. Young isogametes. x 1000

Fig. 3. A single zoospore. x 778

Fig. 4. Isogametes gametes in contact prior to fusion. x 750

Fig. 5. Zygote. x 750

Fig. 6. Young isogametes of *T. aurea*. x 1500

Fig. 7. Isogametes in contact prior to fusion. x 1125

Fig. 8. Zoospores of *T. elongata*, phycobiont of *C. Linkii*. x 1000

Fig. 9. Portion of a filament of *T. aurea* showing sessile, globular gametangium. Note germinating spores in vicinity of the filament. x 750

Fig. 10. *Trentepohlia odorata* (Wiggers) Wittrock with rough wall and terminal and lateral sporangia. x 900

Plate 6

Coenogonium Linkii Ehrenb. showing shelf-like habit of thallus and apothecia on the upper surface. x 2.5 Azael, 5 February 1938 (US).

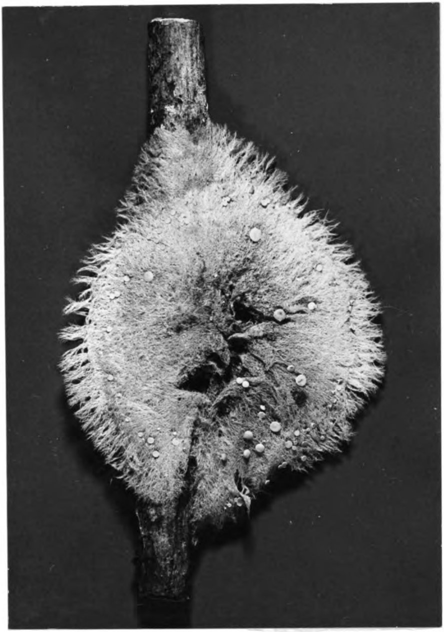


Plate 7

Coenogonium Leprieurii Nyl. showing shelf-like habit of thallus and apothecia on the lower surface. x 2. 2676 1 April 1905 (NY).

Plate 8

Coenogonium *Leprieurii* showing zonate appearance of thallus. x 2. *Spruce* *228* (NY).

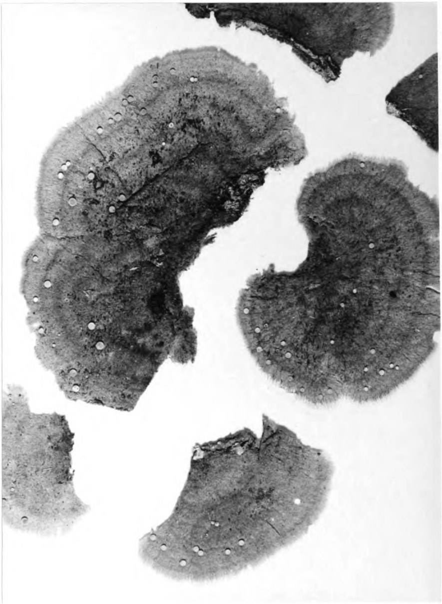


Plate 9

Fig. 1. *Trentepohlia aurea* (phycobiont of *Coenogonium interplexum*) with young apothecial initial and a young branch.

Fig. 2. *T. aurea* with older apothecial initial.

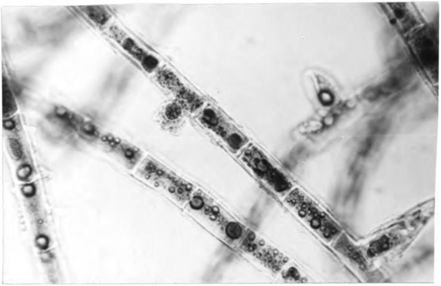
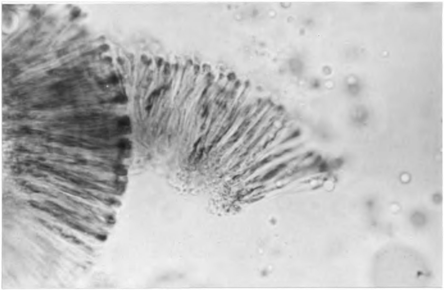


Plate 10

Fig. 1. Hymenium of Coenogonium Linkii showing asci and paraphyses with globose apices.

Fig. 2. Trentepohlia arborum (phycobiont of Coenogonium Linkii) with young sporangium.



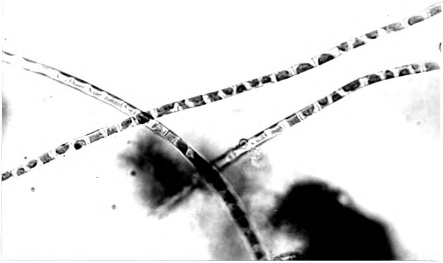


Plate 11

Fig. 1. Trentepohlia elongata filaments grown in culture. Note extended tip cells of filaments (Low power objective).

Fig. 2. Lichenized filaments of T. elongata showing hyphae surrounding vegetative cells. (High power objective).