THE BARK OF LIVING TREES AS A SUBSTRATE FOR REPRESENTATIVES OF THE ORDER MYXOBACTERIALES

Thesis for the Degree of Ph. D.
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John Edward Peterson, Jr.
1957

THESIS

This is to certify that the

thesis entitled

The Bark of Living Trees as a Substrate for Representatives of the Order Myxobacteriales.

presented by

John E. Peterson, Jr.

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Major professor

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Date March 1, 1957

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THE BARK OF LIVING TREES AS A SUBSTRATE FOR REPRESENTATIVES OF THE ORDER MYXOBACTERIALES

By

JOHN EDWARD PETERSON, JR.

AN ABSTRACT

Submitted to the School for Advanced Graduate Studies of
Michigan State University of Agriculture and
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the requirements for the degree of

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DOCTOR OF PHILOSOPHY

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1957

John Edward Peterson, Jr.

ABSTRACT

Organisms identified as belonging to Order Myxobacteriales Jahn of the Schizomycetes were found frequently on bark of living trees in moist chamber culture, on which other organisms were being studied by the writer. A search of the literature indicated that the bark of living trees was an undescribed habitat for myxobacteria; that myxobacteria had not been reported extensively on woody material; and that the total literature concerning the myxobacteria was scanty. Two questions were immediately suggested: (1) How frequently do myxobacteria occur on the bark of living trees? (2) What species of myxobacteria are to be found in this habitat?

Study of 1081 random bark collections from 95 different trees, representing 32 different species, growing in various habitats in Missouri, yielded 267 pieces of bark on which myxobacteria were found, or 24.7% occurrence. In addition to the 1081 pieces of bark included in the frequency study, approximately 100 pieces of bark of various species of trees from Michigan, Illinois, Florida, Jamaica and Greece, on all of which myxobacteria had been found, were examined. A total of 30 species of myxobacteria were observed and studied, with 24 of these organisms being identified as previously described species and six being designated as new species.

The descriptive literature concerning many of the representatives of the Order Myxobacteriales is meager. In several instances, a species has been reported only by the original observer or, perhaps, one or two subsequent workers. Consequently, character ranges have been extended for most of the organisms included in this study and total descriptions have been compiled for the 30 species considered. Cultural trials were made whenever possible on the species concerned and some meager information in this direction has been added to the literature. Further study in this area is necessary and is planned for the near future.

It is concluded that the bark of living trees is a natural habitat for members of the Order Myxobacteriales and that this habitat is equal in importance to any of the substrates of isolation previously known for the group. This conclusion is predicated on (1) the frequency of occurrence of myxobacteria on the bark of living trees, and (2) the number of species found on this substrate in proportion to the total number of species currently known; i.e., over one-third of the 85 described species. Because of the scope of the bark of living trees as a habitat for myxobacteria, all of the habitats of all of the members of the Order Myxobacteriales have been reviewed and tabulated, with the bark of living trees, as a habitat, included in the review.

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Dr. I. Mackenzie Lamb, Director, Farlow Herbarium of Cryptogamic Botany, and Dr. Donald P. Rogers, Curator, Cryptogamic Herbarium, New York Botanical Garden, have been extremely helpful and their loaning of specimens is gratefully acknowledged.

Finally, the writer wishes to acknowledge the correspondence and suggestions of workers, past and present, here and abroad, who have graciously answered his letters and queries.

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INTRODUCTION

During the months between October 1950 and August 1951, while studying the Myxomycetes developed on the bark of living trees in moist-chamber cultures, orange and red structures which suggested myxomycetous plasmodia and immature fruiting bodies were occasionally encountered. When these masses were observed microscopically, they proved to be composed of rod-shaped cells of a size which indicated that they were bacterial. Further observations resulted in identifying these structures as masses of vegetative cells and fruiting bodies of organisms consigned to Order Myxobacteriales of the Schizomycetes.

Some 60 moist chambers containing pieces of bark which appeared to bear myxobacteria were set aside during the course of observation of over 3000 pieces of bark from Michigan trees. Later, a few pieces of bark from Illinois, Florida, Jamaica, and Greece, which also had similar structures on them, were added to the collection.

A survey of the literature yielded only the briefest reference to myxobacteria having been reported on bark or woody substrates and, indeed, yielded very little in the way of total knowledge concerning this group. The Myxobacteriales, then, appeared to be a group of organisms which would well afford interesting study in a broad sense and, in particular, on this relatively unreported substrate--the

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bark of living trees. Two primary questions presented themselves in this regard. First, how frequently and profusely to myxobacteria occur on the bark of living trees? Second, what myxobacteria species occur on this particular substrate? The purpose of the study reported in this paper, then, is to provide at least partial answers to these questions.

REVIEW OF THE LITERATURE

This study has two rather distinct facets: (1) An undescribed habitat of the organisms in the Order Myxobacteriales; (2) Descriptive data on the organisms of this order found in this habitat. It is necessary, therefore, to consider the literature relating to both of these facets. That which is descriptive in nature will be considered first.

A review of the habitats and isolation substrates of all representatives of the Order Myxobacteriales, including those found on the bark of living trees and those found in other habitats, is a part of this paper. Since this is a review, and since all pertinent literature citations are included, no purpose would be served in treating citations which refer only to habitats in this REVIEW OF THE LITERATURE chapter.

In the opinion of the writer, there have been seven major contributions to descriptive knowledge on the myxobacteria, in addition, of course, to various short and scattered contributions. The order originated with Roland Thaxter (1892) when he wrote "On the Myxobacteriaceae, A New Order of Schizomycetes." Thaxter's 1892 paper was not the first reference to organisms now consigned to the Order Myxobacteriales, but it was the initial paper treating these organisms according to our present concepts. Link

published on Polyangium vitellinum in 1809 and Berkeley and Curtis recorded and described a member of the order in 1857, although they described it as a member of what is now Family Stilbellaceae of the Fungi Imperfecti. Between 1857 and Thaxter's first paper in 1892, there were two or three other descriptions of what appear to be myxobacteria, but which were originally described as true fungi, myxomycetes or true bacteria. These are somewhat questionable and are of no particular concern in the present consideration. It suffices to cite Thaxter's four papers (1892, 1893, 1897 and 1904), published in the Botanical Gazette, as the first of these seven major descriptive contributions.

In the 20 years following Thaxter's works, descriptive contributions were made primarily by German workers, but, with one exception, these were in the nature of descriptions and reports of one to a few organisms per paper. The one exception was the publication of a paper by Quehl (1906) in Centralblatt fur Bakteriologie. Quehl includes 16 species in this paper, which describes not only his own findings, but those of his predecessors. This paper is the second of the seven major descriptive contributions.

Jahn (1911, 1924) produced the next two works which can be considered comprehensive, the first in Kryptogamenflora der Mark Brandenburg V, Pilze I, Lief 2 and the second in Beitrage zur botanischen Protistologie I. Die Polyangiden. Since both these works were monographic as concerns the myxobacteria,

they are held to be the third and fourth of the seven major contributions.

Soon, chronologically, after Jahn's 1924 contribution, the Polish husband and wife team of Helene and Seweryn Krzemieniewsky made excellent contributions to the knowledge of the myxobacteria (Krzemieniewski and Krzemieniewska 1926, 1928, 1930, 1937, 1947 and Krzemieniewska 1930, 1933). These contributions include life cycle and cytological work with selected species of the group, but, while studying the myxobacteria found in Polish soils, much descriptive knowledge was contributed by these workers. They are the fifth contribution.

Hutchinson and Clayton (1919), Winogradsky (1929), Stapp and Bortels (1934), Imsenecki and Solntzeva (1936) and Stanier (1940) had assigned organisms to groups other than the Order Myxobacteriales. Stanier (1942) pulled together these organisms in an excellent comprehensive work on the myxobacteria which do not produce fruiting bodies. We know these organisms today as Family Cytophagaceae and as Genus Sporocytophaga of Family Myxococcaceae. Stanier's paper is the sixth of the seven major contributions to the knowledge of the Order Myxobacteriales.

The seventh such contribution is to be found in Bergey's Manual of Determinative Bacteriology (1948) where the most modern and complete descriptive concepts of the group appear. The section in Bergey's Manual relating to the Order Myxo-

bacteriales was first prepared for the Fourth Edition of the Manual by Professor R. E. Buchanan, Iowa State College, Ames, Iowa, in 1934. It was revised by Buchanan in 1939 for the Fifth Edition and, finally, put into the present form for the Sixth Edition by Dr. J. M. Beebe, Professor Buchanan, and Dr. R. Y. Stanier. Although a review, rather than publication of original work, this treatment is currently the most usable and comprehensive for a worker interested in the myxobacteria, and the systematic treatment presented in Bergey's Manual shall be the one considered authoritative as to taxonomical methodology and recognition of validity of species for the purpose of this paper.

The second facet of the literature to be reviewed concerns those references to habitats, or substrates, which approximate the one now under consideration; namely, the bark of living trees. Such references can be attributed to only a small group of workers and these workers are those who were particularly interested in the flora of decaying woody substrates, as opposed to other workers who were primarily interested in soil, dung or other substrates.

The Krzemieniewskys (1947) write: "It was only in 1936 that we received specimens of Ch. crocatus obtained in 1935 on bark of a tree in the environs of Santa Maria in Columbia thanks to the good offices of Professor G. W. Martin of Jova City (U.S.A.)." In view of Dr. Martin's interests, such an occurrence was undoubtedly on the same substrate as the one

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under consideration in the current study. Quite probably, the myxobacterium may even have occurred in moist-chamber culture.

Jahn (1924) reported having found both Polyangium vitellinum Link and Polyangium fuscum (Schroeter) Thaxter on poplar bark kept moist in a dish. Such methodology, of course, is exactly the same as that used in the current study except that Jahn's bark may not have been plucked off a living tree. Jahn also reported P. vitellinum on old wood in moist ditches and P. fuscum on decaying lichens. Thaxter (1892) reported P. vitellinum on very wet wood and bark in swamps. In the same paper, Thaxter described Podangium lichenicolum (Thaxter) Jahn on lichens on the trunks of elm and maple trees along city streets. In a later paper, Thaxter (1904) reported Stelangium muscorum (Thaxter) Jahn "on hepatics on trunks of living beech trees, Crawfordsville, Indiana." Jahn (1924) described Podangium erectum (Schroeter) Jahn on bark covered with lichens. These references concern myxobacteria from like, or very similar, substrates to the one considered in the present paper.

In addition to the above pertinent references, there are others which must be cited because they refer to similar substrates. Jahn (1924) referred to observing Archangium gephyra Jahn on old decaying lichens. Thaxter (1892) found Archangium serpens (Thaxter) Jahn on decaying lichens, but he described this species as appearing in company with Podangium

lichenicolum (Thaxter) Jahn, cited above, as being on bark of elm and maple trees. It must, therefore, be assumed that Thaxter's decaying lichens were, in turn, on bark. Polyangium simplex Thaxter has been described by him (1893) on very wet wood and bark in swamps and, in a later paper, he (1904) found Synangium sessile (Thaxter) Jahn on decaying wood from Florida.

Chondromyces aurantiacus (Berkeley and Curtis) Thaxter has been described by Berkeley (1857) on lichen, by Berkeley and Brown (1873) on rotten wood from Ceylon, and by Thaxter (1892) on old wood and fungi. Thaxter (1904) described Chondromyces catenulatus Thaxter on decaying poplar wood from New Hampshire. Myxococcus fulvus (Cohn emend. Schroeter) Jahn was reported by Thaxter (1892) on various decaying substances, including lichens and paper, and by Jahn (1924) on bark, decaying wood and lichens. Chondrococcus coralloides (Thaxter) Jahn was reported by Thaxter (1892) on lichens and by Jahn (1924) on old bark and old lichens.

All the substrates in the references reviewed above approximate the habitat considered in the study reported in this paper. Some do so very closely and some do so only vaguely. In all cases, however, it appears that these substrates have been considered only as substrates and never as an actual habitat for certain species of the Order Myxobacteriales. The present paper shall present the thesis that the bark of living trees is an actual habitat for representatives of this group of organisms.

MATERIALS AND METHODS

Mycologists and other workers interested in the flora to be found on various substrates have been using moist-chamber techniques for many years to enhance their observations of such microflora. References to dung, decaying wood, leaves and various other such materials placed in moist chambers in order to further the growth of organisms contained thereon are to be found in the literature from the beginning of microbiological history. The first reference to the use of moist chambers in order to provide adequate laboratory conditions for the completion of the life cycle of organisms on the bark of living trees, however, appears to be that of Gilbert and Martin (1933) in the study of myxomycetes. This same technique was used by the author in the study of myxomycetes referred to in the Introduction of this paper and was employed again in the observation of representatives of the Order Myxobacteriales.

Bark from various living trees was collected on a random sampling basis. Only bark which was in intimate contact with the tree was collected. This statement is made, not with the intention of implying that the actual bark substrate is anything other than non-living material, but rather to emphasize that the bark studied was always as different from decaying back and wood as possible. Effort was made to collect

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bark on all sides of the trunk of each tree sampled and from as many levels as possible, but no attempt was made to chart these collection positions. The number of pieces of bark gathered from any one tree was quite indefinite, ranging from four to twenty-four pieces per tree, with about ten pieces per tree most commonly collected.

The trees from which bark was collected were, again, selected strictly at random. As many different species of trees as reasonably possible were sampled, as were trees in different habitats. For the purpose of this study, no attempts were made at correlating occurrence of species of myxobacteria with species or habitats of trees, although indications were found that there would be merit in seeking such correlations.

After collection, the pieces of bark were taken into the laboratory, placed in moist chambers which were usually Petri dishes with a disc of filter paper in the bottom, and soaked well with distilled water. After soaking for about 24 hours, the excess water was poured off and the chambers set aside for from three to four weeks. At the end of this period of time, the bark was examined under a stereoscopic microscope at magnifications of 15, 45 and 90 diameters.

Specimens for study under the compound microscope were mounted in lactophenol, both plain and with aniline blue. Therefore, all references to color, opacity, etc., in transmitted light refer to these characters when the specimens are mounted in this medium.

An attempt was made to culture most of the organisms found during the course of this study, primarily for the purpose of obtaining data concerning the vegetative stage. A reasonable amount of success was had in this respect and information is presented concerning the vegetative phase of about half of the organisms reported. It is emphasized that these cultural attempts in no way constituted a full-scale nutritional or physiological study of the organisms involved. Such knowledge has been fairly well worked out for only a few of the myxobacteria and a great void exists in the literature for the remainder. It is proposed to launch a detailed physiological study on the myxobacteria in the near future for the purpose of filling some of this void.

It is unfortunate that organisms produced on bark in moist chambers often occur in very limited numbers. This was the prime reason for not making cultural attempts on all of the myxobacteria involved. After a great number of inquiries to institutions and workers over the world, it has become apparent that there are very few specimens of any myxobacteria, much less Type Specimens, in existence. Because of this lack, because this study is primarily descriptive, and because the taxonomy of the Order Myxobacteriales is based strictly on the fruiting stages, it is felt that the building of a collection of preserved myxobacteria fructifications is the first consideration at this time. Consequently, when only a limited amount of material was available, these specimens were pre-

served as such, at the expense of cultural attempts.

Seven substrates for culture were decided upon as follows: (1) Rabbit Dung Decoction Agar; (2) Rabbit Dung Pellet Plates; (3) Killed Bacterial Cell Agar; (4) Bark Decoction Agar; (5) Homogenized Bark Agar; (6) Sterilized Elm Bark; and, (7) Sterilized Oak Bark. The first three of these substrates were prepared according to Beebe (1941b). The Bark Decoction Agar was made by slowly boiling a bucket of American Elm and White Oak bark for about two hours, after which the supernatant was filtered through several layers of cheese cloth. Sufficient Bacto-Agar was added to make a resultant medium of about 2.5% and this was sterilized in routine fashion. Homogenized Bark Agar was prepared by pulverizing American Elm and White Oak bark in a Waring Blender. The homogenate was filtered through two layers of cheese cloth, sufficient agar added to make a 2.5% medium, and sterilized in the autoclave in routine manner.

The bark substrates were prepared by placing small pieces of Ulmus americana and Quercus alba bark on filter paper in Petri dishes. Enough distilled water to moisten the bark and paper was added and the dishes were sterilized in the autoclave for something over 30 minutes at 121°C. Bark of U. americana and Q. alba was selected because the greatest number of myxobacteria in the greatest profusion had been found on bark from these tree species during the course of the study.

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In addition to these seven substrates, Van Tieghem cells with hanging-drops of five different solutions were employed. These five solutions were: (1) Sterile distilled water; (2) Nutrient broth; (3) Yeast extract; (4) Bark decoction; and, (5) Nutrient broth plus a killed bacterial suspension. It was hoped that germination of fruiting bodies could be observed in such hanging-drop preparations and fruiting bodies, or cysts, of nine different species were transferred as aseptically as possible into each of these five hanging-drop solutions. These 45 hanging-drop preparations were failures and the method was abandoned for the remaining organisms.

It has been stated previously in this chapter that many inquiries concerning the existence of Type Specimens, other specimens, and cultures of myxobacteria were made of various workers, herbaria, museums and other institutions over the world. Since the use of such specimens is part of the taxonomical methodology employed, this chapter is the logical place in which to elaborate on this topic.

About 40 such inquiries were made with meager results. The Farlow Herbarium of Harvard University possesses 20 specimens of myxobacteria representing 11 different species, six of which were pertinent to the present study. Only a few of these specimens were designated as "Type," but they were all specimens originally from the collection of Roland Thaxter and, consequently, can be considered as valid as

Type Specimens. All of this collection was borrowed from the Farlow Herbarium and critically studied.

The New York Botanical Garden possesses seven specimens representing four different species, three of which were pertinent to this study. Fortunately, these are different species from those in the Farlow collection. None of these are designated as Type Specimens, but, again, they all appear to have originated from Thaxter's collection and, therefore, may be considered as valid designations. This collection was also borrowed and studied.

The British Museum of Natural History has indicated that it possesses three specimens representing two species of myxobacteria, but since both of these species are included in the other two collections, no attempt to borrow these specimens was made. The American Type Culture Collection possesses several strains of six different species of myxobacterial cultures although they are not currently included in the published listing of cultures available. Three of these six species were pertinent to the present study and these three cultures were obtained for comparison studies.

The collections of Jahn, the Krzemieniewskys and other past European workers were traced as far as possible and none were located. Current European workers, none of whom are at present actually concerned with comprehensive descriptive work, were contacted and could offer no helpful suggestions.

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RESULTS

Frequency Study

Since one of the purposes of this study was to procure some information on the frequency of occurrence of species of the Order Myxobacteriales on the bark of living trees and since the original pieces of bark with myxobacteria on them which had been gathered over a five year period could not be used to indicate any such frequency, collections of bark of known numbers were made in Missouri, between March 2, 1955, and June 5, 1956.

A total of 1081 pieces of bark were collected from 95 different trees, representing 32 different species. The species of trees sampled and the number of times each species was sampled are shown in Table No. 1. These trees were growing in fourteen different locations in nine different Missouri counties. Six of the locations were in Boone County in central Missouri and the remaining eight locations were each in a different county as follows: (1) Sinkin Forest, Dent County, in south central Missouri; (2) Perryville, Perry County, in eastern Missouri; (3) St. Louis County, in eastern Missouri; (4) St. Louis (the municipality of St. Louis is a separate entity and acts as a county in its own right), in eastern Missouri; (5) Senath, Dunklin County, in the "Boot-heel" region of deep southeastern Missouri; (6) Cook Station,

Table No. 1 - Trees sampled and the number of samples included in frequency study.

	Tree Species	Number of Collections
1.	Acer rubrum Linnaeus	1
2.	Acer saccharinum Linnaeus	2
3.	Acer saccharum Marshall	9
4.	Carya illinoensis (Wangenheim) K. Koch	1
5.	Carya ovata (Miller) K. Koch	6
6.	Castanea mollissima Blake	1
7.	Celtis occidentalis Linnaeus	1
8.	Cercis canadensis Linnaeus	1
9.	Cornus sp.	1
10.	Diospyros virginiana Linnaeus	1
11.	Fagus grandifolia Ehrhart	2
12.	Fraxinus americana Linnaeus	3
13.	Gleditsia triacanthos Linnaeus	1
14.	Juglans nigra Linnaeus	3
15.	Juniperus virginiana Linnaeus	3
16.	Liriodendron tulipifera Linnaeus	1
17.	Nyssa sylvatica Marshall	3
18.	Pinus echinata Miller	9
19.	Platanus occidentalis Linnaeus	2
20.	Populus deltoides Marshall	2
21.	Quercus alba Linnaeus	13
22.	Quercus falcata Michaux	1
23.	Quercus macrocarpa Michaux	1
24.	Quercus muehlenbergii Engelmann	2
25.	Quercus rubra Linnaeus	4
26.	Quercus velutina Lamarck	2
27.	Robinia pseudoacacia Linnaeus	1
28.	Sassafras albidum (Nuttall) Nees	3
29.	Ulmus alata Michaux	1
30.	Ulmus americana Linnaeus	8
31.	Ulmus pumila Linnaeus	2
32.	Ulmus rubra Muhlenberg	4

Crawford County, in south central Missouri; (7) Round Spring, Shannon County, in south central Missouri; and, (8) Holstein, Warren County, in central Missouri.

A piece of bark, for the purposes of this study, is defined as being about two square inches in area. Whenever possible, one piece of bark of this approximate size was collected and recorded, but, in several instances, the nature of a particular bark made it impossible to collect single pieces of this size. In these instances, two or more smaller pieces, making a total area of about two square inches, were treated and recorded as "one piece" of bark.

Of the 1081 pieces of bark collected, 267 proved to be positive for myxobacteria. This is a percentage of 24.7% occurrence. On the basis of this study, it can be stated that one out of every four pieces of bark gathered at random from living trees is positive for myxobacteria. It must be pointed out, however, that this gives no indication of profusion of myxobacteria. For example, some pieces of bark on which only one or two fruiting bodies were found, were recorded as positive just as were those on which hundreds of fruiting bodies of three or four different species were found. A positive recording simply indicates that myxobacteria of some sort were found on the piece of bark in question.

Table No. 2 lists the 26 species of myxobacteria which were found on the pieces of bark included in the frequency study and the number of times each species was found out of

Table No. 2 - Myxobacteria species observed in frequency study.

	Name of Organism	Number of Occurrences
1.	Archangium primigenium (Quehl) Jahn	49
2.	Archangium flavum (Kofler) Jahn	2
3.	Archangium serpens (Thaxter) Jahn	1
4.	Archangium thaxteri Jahn	1
5.	Stelangium muscorum (Thaxter) Jahn	1
6.	Stelangium vitreum n. sp.	12
7.	Sorangium sorediatum (Thaxter) Jahn	3
8.	Polyangium vitellinum Link	24
9.	Polyangium cellulosum Imsenecki & Solntzeva	6
10.	Polyangium fuscum (Schroeter) Thaxter	4
11.	Polyangium luteum Krz. & Krz.	1
12.	Haploangium minor n. sp.	32
13.	Haploangium rugaseptum n. sp.	27
14.	Haploangium simplex (Thaxter) n. comb.	3
15.	Podangium erectum (Schroeter) Jahn	15
16.	Podangium lichenicolum (Thaxter) Jahn	1
17.	Podangium gracilipes (Thaxter) Jahn	16
18.	Podangium alboracemum n. sp.	2
19.	Chondromyces crocatus Berkeley & Curtis	2
20.	Chondromyces cylindricus Krz. & Krz.	10
21.	Chondromyces apiculatus Thaxter	4
22.	Myxococcus virescens Thaxter	3
23.	Myxococcus fulvus (Cohn emend. Schr.) Jahn.	1
24.	Chondrococcus coralloides (Thaxter) Jahn.	41
25.	Chondrococcus blasticus Beebe	1
26.	Angiococcus moliroseus n. sp.	1
	Unidentifiable	35

the total of 1081 pieces of bark. Many of the species of myxobacteria were also found on previously collected bark from other localities and these final totals are stated in the descriptions of each species and in Table No. 3. In addition to these 26 species of myxobacteria, a final item included in Table No. 2 consists of definite, but unidentifiable myxobacterial structures. They were unidentifiable because of malformation, overgrowth by filamentous fungi, or extreme scantiness of production. Although there were 35 such recordings, this does not mean that 35 of the total of 267 recorded positives were unidentifiable because many of these unidentifiable structures were found on a piece of bark along with identified fruiting bodies.

It should be pointed out that Table No. 2 does not include all of the species found during the course of this entire study. Only those which were on bark collected for the purpose of establishing some information on frequency of occurrence are included, although the majority of all the species represented in the entire study do happen to be included here.

There are some interesting aspects of myxobacterial distribution on the bark of living trees which are not indicated in the preceding tables or discussion. The first of these centers around a collection made in the Sinkin Forest, Dent County, Missouri. This collection, consisting of 93 pieces of bark from Pinus echinata (Missouri's only native

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pine) and 32 pieces of Quercus velutina bark, was included in the frequency study because the mixed shortleaf pine-oak complex is an important and extensive forest component of south central Missouri.

Not a single myxobacterial-positive piece of Pinus echinata bark was found of the 93 samples. However, 15 of the 32 pieces of Quercus velutina bark, collected from trees sometimes immediately adjacent to the pines, were positive for myxobacteria. Certainly, myxobacteria exist in that particular forest area, as evidenced by the Quercus velutina bark, and probably myxobacterial cysts and resting cells were to be found lodged on Pinus echinata bark. On the basis of these meager data, it appears that growth and the completion of the life cycle are inhibited on this particular bark and, in this case, the bark would not be a habitat for myxobacteria.

In opposition to the low-productivity bark collected from the Sinkin Forest, a collection of 192 pieces of bark from 19 trees, representing seven different species, was made from a location known as Wagner's Woods near Holstein, in Warren County, Missouri. Wagner's Woods is one of the few areas of native forest remaining in the state and consists of an overstory of mostly oaks and hickories from 250 to 400 years old. The forest is a rather mesic, undisturbed area of the type that one would expect to be rather productive of microflora.

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Seventy-six of the 192 pieces of bark from Wagner's Woods were positive for myxobacteria for a percentage of 39.6%. Since Carya ovata was a prominent member of this forest, 10 pieces of bark were gathered from each of three hickory trees, although past experience has shown hickory bark to be quite barren of any type of microflora. Only two of these 30 pieces of hickory bark were positive for myxobacteria and, if adjustments are made in this collection to exclude Carya ovata, the percentage of myxobacterial positives for the Wagner's Woods collection becomes a lofty 45.7%.

Whereas Carya ovata bark was, of course, the lowest of the seven tree species sampled in this collection, there were species which showed an outstanding number of positives. The foremost example of this was that 26 pieces of a total of 30 pieces of Ulmus rubra bark were positive for myxobacteria. Only 12 pieces of Quercus rubra were gathered from this location, but eight of these 12 were positive for myxobacteria. Thirteen pieces of a total of 30 of Fraxinus americana bark from Wagner's Woods proved to be positive for myxobacteria.

The above citations of the high and low points of productivity observed during the frequency portion of this study are not construed to be conclusive in any fashion. The study was not designed to give adequate data regarding such correlations. The observations cited, however, are indicative that further study in the directions suggested could prove very interesting.

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A total of 24 species of myxobacteria, which have been previously described, were found on bark from living trees during the course of the study being reported. In addition, two described varieties of one of these species, Chondrococcus coralloides (Thaxter) Jahn, two different described varieties of Polyangium cellulosum Imsenecki & Solntzeva, and a described variety of Archangium primigenium (Quehl) Jahn, were observed.

Six other distinct species of myxobacteria, which, at this writing, cannot be attributed to any published description, were also observed and described, making a total of 30 species reported in this paper. These latter six organisms are described as new species in this paper. Two of them have been assigned to Genus Podangium Jahn and two others have been designated as belonging to a newly erected genus, Haploangium, which will encompass these two new species and, at least, one species now assigned to Genus Polyangium. Both Podangium and Haploangium are genera of Family Polyangiaceae Jahn. The fifth new species has been diagnosed as a second species of Genus Stelangium Jahn of Family Archangiaceae and the final organism has been assigned to Genus Angiococcus Jahn of Family Myxococcaceae.

Of the five families of the Order Myxobacteriales recognized in Bergey's Manual (1948), representatives of four

families were found on the bark of living trees. Because of the methodology employed, it is not surprising that no representatives of Family Cytophagaceae Stanier were found. Since the organisms consigned to this family do not produce fruiting bodies, it is quite apparent that they would not generally be detected in a microscopic observation even if they did exist on bark. Other isolation methods which would allow recognition of species of Cytophaga are planned for the future.

The Family Sorangiaceae Jahn was represented by three occurrences of only one species, Sorangium sorediatum (Thaxter) Jahn. It is interesting to note that of the eight species of Sorangium, the lone genus in the family, none has previously been reported from any isolation substrate other than dung or soil.

Of the two genera comprising the Family Archangiaceae Jahn, both were represented in findings on bark. Five species of Genus Archangium Jahn are recognized in Bergey's Manual and four of these were found in the present study. Only one species comprises the Genus Stelangium Jahn, Stelangium muscorum (Thaxter) Jahn. This organism was described by Thaxter as occurring on liverworts on living beech trunks in Indiana and, therefore, might have been expected to appear in this study. It did appear, in some profusion, on only one piece of bark, but a second organism which obviously is a second member of this genus was found several times.

Of the five genera recognized by Bergey's Manual as

comprising Family Polyangiaceae Jahn, three were represented in this study. The first of these genera, Polyangium Link, was represented by five species and one of these five includes two distinct varieties, both previously reported. All three of the recognized species of Genus Podangium Jahn were found during the course of this study and two new species have been added. The third genus of Family Polyangiaceae of which representatives were found in this study, Chondromyces Berkeley and Curtis, contains eight recognized species. Six of these eight species were observed in the present study. Finally, a new genus, Haploangium, which will be placed in Family Polyangiaceae, will encompass two new species and one species currently assigned to Genus Polyangium.

The final family of the Order Myxobacteriales is Family Myxococcaceae Jahn, to which four genera are assigned in Bergey's Manual. One of these genera, Sporocytophaga Stanier, produces no fruiting bodies and, therefore, the comments made for Family Cytophagaceae also apply to this genus. As might be expected, no representatives of this genus were found. Of the six recognized species assigned to Myxococcus Thaxter, two are reported in this study. Genus Chondrococcus Jahn is composed of seven species and two varieties in Bergey's Manual. Two of these species and both of the varieties were found during the course of this study. The final genus, Angiococcus Jahn, is composed of only two species. Neither of these was found on the bark of living trees, but an undescribed organism which is assigned to this genus did occur.

Table No. 3 is a summation of all of the species found during the course of the study. They are arranged systematically, with Bergey's Manual being considered authoritative for the taxonomical treatment. The number of pieces of bark on which each species occurred is recorded. No data concerning the profusion of fruiting bodies in each occurrence are included since they will be discussed in the description of each species in the following chapter.

Table No. 3 - Species of myxobacteria found; in systematic arrangement and with number of occurrences.

	Name of Organism	Number of Occurrences
Family Cytophagaceae	No representatives	
Family Archangiaceae	6 representatives	
1.	Archangium primigenium (Quehl) Jahn	56
2.	Archangium flavum (Kofler) Jahn	2
3.	Archangium serpens (Thaxter) Jahn	1
4.	Archangium thaxteri Jahn	1
5.	Stelangium muscorum (Thaxter) Jahn	1
6.	Stelangium vitreum n. sp.	15
Family Sorangiaceae	1 representative	
7.	Sorangium sorediatum (Thaxter) Jahn	3
Family Polyangiaceae	18 representatives	
8.	Polyangium vitellinum Link	23
9.	Polyangium cellulosum Imsenecki & Solntzeva	8
10.	Polyangium fuscum (Schroeter) Thaxter . . .	4
11.	Polyangium luteum Krz. & Krz.	1
12.	Haploangium minor n. sp.	32
13.	Haploangium rugaseptum n. sp.	27
14.	Haploangium simplex (Thaxter) n. comb. . .	3
15.	Podangium erectum (Schroeter) Jahn	15
16.	Podangium lichenicolum (Thaxter) Jahn . . .	1
17.	Podangium gracilipes (Thaxter) Jahn	26
18.	Podangium alboracemum n. sp.	2
19.	Podangium cylindricum n. sp.	1
20.	Chondromyces crocatus Berkeley & Curtis . .	3
21.	Chondromyces cylindricus Krz. & Krz. . . .	10
22.	Chondromyces apiculatus Thaxter	5
23.	Chondromyces medius Krz. & Krz.	4
24.	Chondromyces minor Krz. & Krz.	1
25.	Chondromyces catenulatus Thaxter	1
Family Myxococcaceae	5 representatives	
26.	Myxococcus virescens Thaxter	4
27.	Myxococcus fulvus (Cohn emend. Schr.) Jahn.	3
28.	Chondrococcus coralloides (Thaxter) Jahn .	57
29.	Chondrococcus blasticus Beebe	1
30.	Angiococcus moliroseus n. sp.	1

DISCUSSION

As an introduction to the following systematic account, it is emphasized that a large number of the currently known members of the Order Myxobacteriales have been reported in the literature and, apparently, observed only on a minimum of occasions. Several of these organisms have been reported only by the original describer. The bulk of the remainder have been reported only by the original describer and one, or perhaps two, succeeding workers. Consequently, in view of the meager number of observations on most of these organisms, such characters as size, color gradations, etc. are much too limited in range. Therefore, certain discrepancies in such characters have not been considered too important in many of the following identifications. Rather, the opinion is held that the current observations extend the known ranges of these characters more nearly to what these ranges actually are. Such range extensions have been incorporated into previous descriptions and the emended characterizations for the 30 species considered in this study are given in the following section.

Systematic Account

Order Myxobacteriales Jahn

Kryptogamenflora der Mark Brandenburg, 5, Pilze 1:187. 1911.

Key to the families on bark of living trees

1. Encysted cells rod-shaped

    2. Fruiting bodies indefinite in shape; encysted cells in columns, tubules or globose masses; no definite wall generally present ..... Archangiaceae

    2. Fruiting bodies composed of definite cysts with definite walls

        3. Cysts polygonal; small, less than 15μ ..... Sorangiaceae

        3. Cysts rounded; larger than 15μ .. Polyangiaceae

1. Encysted cells coccoid in shape ..... Myxococcaceae

Family Archangiaceae Jahn

Beit. z. botan. Protist., I. Die Polyangiden. Leipzig. 1924.

Key to the genera on bark of living trees

1. Fruiting bodies consisting of tubular components, irregularly delimited.. *Archangium*

1. Fruiting bodies simple and columnar ..... *Stelangium*

Genus *Archangium* Jahn

Beit. z. botan. Protist., I. Die Polyangiden. Leipzig. 1924.

Key to the species on bark of living trees

1. Encysted rods borne in prominent tubules

2. Tubules without persistent membranous walls

3. Fruiting bodies bright orange-red.. A. primigenium

3. Fruiting bodies yellow ..... A. thaxteri

2. Tubules with membranous walls ..... A. serpens

1. Encysted rods borne in rounded segments in a globular mass ..... A. flavum

Archangium primigenium (Quehl) Jahn

Centralblatt f. Bakteriologie, 16:16. 1906.

Polyangium primigenium Quehl, as cited above.

Archangium primigenium (Quehl) Jahn, Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Neotype: A specimen, unattached to any substrate, on deposit in the Farlow Herbarium. Collected and determined by Finkenkrug, Berlin, and bearing Thaxter's Accession No. 4616.

Fruiting body bright red-orange, in both fresh and desiccated condition; irregularly humped cushion; up to 1 mm or larger. In transmitted light, fruiting body flesh-red to yellowish; composed of encysted rods held together in tubular forms; several tubules held together by hyaline slime. Tubules variable in size; constricted and attenuated; lacking in bounding wall or membrane, but receiving characteristic form from bounding slime. Desiccated specimens, in transmitted light, do not show tubular appearance or bound-

ing slime and such specimens appear only as a mass of cells in segments of various sizes and shapes. Encysted rods (spores) 0.8 x 3-4μ. Vegetative cells 1.0 x 4-8μ, averaging 5-6μ; slightly tapering toward both ends.

Material examined: One collection, although not a "type," was borrowed from the Farlow Herbarium and examined. The collection consisted of only one fruiting body loose in a packet of soft paper. It had been collected and determined by Finkenkrug in Berlin and incorporated into Thaxter's collection. No mount could be made for study. A. primigenium occurred on a total of 56 pieces of bark, all of which were examined, during the course of this study.

Recorded collections: Quehl, Berlin, 1906; Kofler, Vienna, 1913; Jahn, Berlin, 1911, 1924; Krzemieniewski and Krzemieniewska, Poland, 1927; Current study, Missouri, Michigan, Illinois, Florida, Greece.

This organism was probably the first myxobacterium to be observed on bark by the writer, but almost the last one to be correctly identified. During the intervening four years, it has been recorded simply as "X" and considered to be either masses of desiccated vegetative cells or malformed fruiting bodies. The explanation of this was that the fruiting bodies were always observed in a dry, or nearly dry, state and the characteristic tubular structure was then lost. After seeing

the Farlow Herbarium specimen, which, of course, was also dried, and after culturing the organism and, thus, observing it in a fresh, moist state, little doubt remained as to what "X" really was.

It is interesting to note that Jahn (1924) and the Krzemieniewskys (1927) consider A. primigenium rare on dung and in Polish soils, but that it occurred a total of 56 times during the course of this study. It occurred on bark from a great variety of trees growing in a great variety of habitats. In some instances, only a single fruiting body was found on a piece of bark, but up to two and three dozen occurred on other pieces. Most commonly, five to ten fruiting bodies were scattered over a piece of bark. A. primigenium was very often found in conjunction with Podangium gracilipes. So much so, in fact, that it was at first thought that these were not fruiting bodies at all, but, rather, desiccated masses of vegetative cells of Podangium gracilipes. The two species grow readily together in culture, separating from one another as growth progresses, but they never show any apparent competitive effects.

A. primigenium was easily and profusely cultured on Rabbit Dung Pellet medium and transfers to new pellets every week or so were made with continued success for a long period of time. Fruiting was very profuse, both on the pellets and, to a lesser extent, on the water agar itself. Some growth and limited fruiting was also observed on Rabbit Dung Decoc-

tion Agar and on Bark Decoction Agar. The active vegetative colony is faint pinkish in color and strongly spreading.

Jahn (1924) has described a variety, assurgens, of A. primigenium and has stated that races and variations are prominent. Some of this variation has been observed, although it does not seem necessary to designate any such variants as separate varieties. One form of what was finally identified as A. primigenium, in fact, was originally considered to be a species of the Genus Polyangium during the earlier portions of this study.

Type specimens to accompany Quehl's original description have not been located. In view of this absence, the single fruiting body now in possession of the Farlow Herbarium is designated as the neotype. Although the date of Finkenkrug's specimen is not recorded, other specimens sent to Thaxter by Finkenkrug are dated 1912 and it is assumed that the specimen of A. primigenium is of that general vintage. If this is true, Quehl and Finkenkrug worked in the same general chronological time and in the same geographical location and it would be quite possible that Quehl had examined Finkenkrug's specimens of A. primigenium.

Archangium flavum (Kofler) Jahn

Sitzber. d. Kais. Akad. Wiss. Wein Math.-Nat. Klasse, 122:845. 1913.

Polyangium flavum Kofler, as cited above

Archangium flavum (Kofler) Jahn, Beit. z. botan. Protist., I. Die Polyangiden. Leipzig. 1924.

Neotype: Specimens on bark of Quercus ellipsoidalis (Peterson No. 216-c-2) on deposit in the University of Missouri herbarium.

> Fruiting bodies orange-yellow, irregularly spherical or oval masses; 35-500μ in diameter. In transmitted light, faint orange-pink in color; no membrane or slime sheath apparent, but rods adhere well together; further pressure causes the rods to break up into rounded sections. Spores 0.5-0.7 x 2.0-4.5μ; mostly about 4.0μ long; ends squarish; uniformly either straight or very gently curved; strong affinity for analine blue dye, staining uniformly. Vegetative cells undescribed.

Material examined: Two occurrences on bark during the course of the current study.

Recorded collections: Kofler, Vienna, 1913; Krzemieniewski and Krzemieniewska, Poland, 1926, 1928; Current study, Missouri.

The first occurrence of this organism was found on a piece of Quercus ellipsoidalis bark collected in April, 1955. The tree from which it was collected was growing on the top of a high rocky ridge at Duly Mill, Missouri, in a barren, windy, dry, difficult habitat. The occurrence of A. flavum consisted of approximately two dozen well-formed fruiting

bodies in an area of about six square millimeters. A second myxobacterium, Polyangium cellulosum Imsenecki and Solntzeva, was also found on this same piece of bark. A second occurrence of A. flavum was found on a piece of bark collected from a Juglans nigra growing in a farm yard near Senath, Missouri, and collected in March, 1956.

Although A. flavum has been reported by both Kofler (1913) and the Krzemieniewskys (1926, 1928), the description of the fruiting body is sparse and that of the vegetative stage is completely lacking. The organisms reported by the above-named authors produce fruiting bodies approximately five times the size of those observed in this study and the color apparently is slightly different. There is no doubt, however, that the organisms observed on bark are correctly identified as A. flavum.

Attempts to culture A. flavum were made on all seven substrates without success. Further attempts were not possible because of the limited amount of material available.

It is difficult to understand why this species and, to a lesser extent, the following one, A. serpens (Thaxter) Jahn, have been placed in Genus Archangium by Jahn (1924). After studying four representatives of the genus, A. primigenium, A. flavum, A. serpens and A. thaxteri, it seems that A. flavum has little in common with the other three. Jahn apparently never personally observed A. flavum and A. serpens, but included them in his Genus Archangium on the basis of the

descriptions of Kofler (1913) and Thaxter (1892). It is the writer's opinion that A. flavum holds closer affinities to Genus Stelangium Jahn than to Genus Archangium. A. serpens does appear to have some affinities to both genera and, because of the tubular form of the fruiting bodies, can reasonably be included in Genus Archangium. Future study and reflection will substantiate or eliminate these opinions.

No specimens of A. flavum have been located. Consequently, the specimens found during the course of this study are designated as the neotype material. These specimens are deposited in the University of Missouri herbarium.

Archangium serpens (Thaxter) Jahn

Bot. Gaz., 17:403. 1892.

Chondromyces serpens Thaxter, as cited above

Archangium serpens (Thaxter) Jahn, Beit. z. botan. Protis., I. Die Polyangiden. Leipzig. 1924.

Type: Specimens on rabbit dung; collected by Wolfe at Sandy Run, South Carolina, and determined by Thaxter on laboratory culture in March, 1904; bears Thaxter's Accession No. 4488; on deposit in Farlow Herbarium.

Fruiting body an aggregate of branching, anastomosing tubules; flesh-colored when fresh, copper-orange to red when dry; 150-1000μ in size. Tubules 15-50μ in width; length indeterminate; bounded by

tough, glistening membranes of dried slime, difficult to break open. No slime discernible between tubules. Spores small, variable from spheres to short rods; some definitely spherical and 0.7μ in diameter, others 1.0 x 2.5μ, with various gradients between these extremes; stain readily with aniline blue. Vegetative rods cylindrical; 0.6 x 5-7μ.

Material examined: One collection of Thaxter's material labeled "type," which was borrowed from the Farlow Herbarium. One occurrence on bark during the current study.

Recorded collections: Thaxter, Massachusetts, 1892, 1904; Zukal, Austria, reported by Thaxter in his 1904 paper; Current study, Missouri.

Only a single occurrence of A. serpens was found during the course of this study and this consisted of only two or three dozen fruiting bodies scattered over an area about two centimeters square. This occurrence was on a piece of bark from Ulmus americana growing in an open, dry, old-field ridge at a location known as "The Pinnacles," Missouri. The bark was collected in April, 1955.

This organism has previously been reported by Thaxter (1892) as occurring once on decaying lichens at Cambridge, Massachusetts, by Thaxter (1904) again, but as occurring on old dung, and, finally, Thaxter states (1904) that Zukal had found it in Austria, although Zukal apparently did not pub-

lish this find. In the current study, A. serpens was found occurring on mosses, on badly decomposed lichens and, in some instances, directly on the bark. All of these were on the same piece of bark.

Archangium thaxteri Jahn

Beit. z. botan. Protis., I. Die Polyangiden. Leipzig. 1924.

Neotype: A microscope slide with two fruiting bodies mounted on it; collected and determined by Finkenkrug in Berlin in 1912; bearing Thaxter's Accession No. 4595; on deposit in the Farlow Herbarium.

Fruiting bodies 250-750μ in diameter; irregularly rounded to cushions with finger-like projections; sulphur-yellow to reddish-orange in color; sometimes tapered at base to appear stalked. In transmitted light, pinkish to red tubules are seen imbedded in yellow-brown slime; tubules 10-50μ in width, but width is irregular within any one tubule; length indeterminate; tubules possess cross-walls and constrictions at random over their length; tubule wall definite, turgid and smooth. Spores both within tubules and in the surrounding slime; slender, 0.5 x 1.8-3.0μ; generally slightly curved and slightly tapered to both ends; uniformly and avidly stained with analine blue; adhering tenaci-

ously together in packets or sheaths. Vegetative cells not known.

Material examined: One slide with two fruiting bodies mounted on it from the Farlow Herbarium. Only one piece of bark from the current study.

Recorded collections: Jahn, Berlin, 1924; Krzemieniewski and Krzemieniewska, Poland, 1926; Current study, Missouri.

Only five fruiting bodies of A. thaxteri were found scattered over one piece of bark of Juniperus virginiana collected in March, 1955. This tree grew near the edge of a bluff above the Missouri River at Providence, Missouri. The habitat was extremely dry, windy and unfavorable for any organism or plant. The piece of bark in question was practically devoid of all other flora.

Jahn (1924) first described this organism as being rare on rabbit dung. He described his specimens as being sulphur-yellow and irregularly rounded whereas the specimens observed on bark are reddish-orange cushions with definite finger-like projections. Jahn also refers to a suggestion of a stalk for his specimens, but no such indication was observed in the specimens found on bark.

According to Jahn, the tubules contain the spores. In the present observations, many tubules which did not contain spores, but which did contain a watery material, were seen. Other tubules definitely do contain spores which can be easily

seen through the tubule wall. Furthermore, many spores, exactly the same in appearance as those which are seen within the tubules, were found in the surrounding slime outside of the tubules.

Jahn states that no membrane surrounds the tubules. It is difficult to understand this statement because the slime envelope dries down to become a rather hard, membranous covering around the tubules, which can definitely be interpreted as being a membrane.

Because of the presence of the yellow slime envelope and the tubules, there is no hesitation in identifying these specimens as A. thaxteri. One of the specimens on deposit in the Farlow Herbarium is A. thaxteri, collected and determined by Finkenkrug in Berlin in 1912, and, apparently, sent to Thaxter, since the specimen was originally in Thaxter's collection. The specimen consists only of a microscope slide with two fruiting bodies mounted on it. The structure of these fruiting bodies is not at all discernible and the slide was of no value in verifying the identification of A. thaxteri found on bark. In spite of the inadequacy of this material, the rules of nomenclature dictate that it must be designated as the neotype in the absence of type material.

Genus Stelangium Jahn

Kryptogamenflora der Mark Brandenburg, 5, Pilze 1:205. 1911.

Key to the species on bark of living trees

1. Fruiting bodies opaque or translucent ..... S. muscorum

1. Fruiting bodies crystalline ..... S. vitreum

Stelangium muscorum (Thaxter) Jahn

Bot. Gaz., 37:411. 1904.

Chondromyces ligulatus Thaxter, unpublished, but on Type in Farlow Herbarium

Chondromyces muscorum Thaxter, as cited above

Stelangium muscorum (Thaxter) Jahn, Beit. z. botan. Protist., I. Die Polyangiden. Leipzig. 1924.

Type: On pieces of bark from beech trunks; collected from Crawfordsville, Indiana, by E. W. Olive and determined by Thaxter in 1897; labelled Chondromyces ligulatus Thaxt.; bearing Thaxter's Accession No. 4522; on deposit in the Farlow Herbarium.

Fruiting bodies typically long, finger-like columns, 20-35 x 120-300μ, but varying to those which are oval-globose, 40 x 50μ; typically individual, but several arising from the same general area to form a coralloid structure can be found; yellow-orange; no hypothallus or stalk; rounded at apical end and generally slightly tapered toward apex. In transmitted light, a hyaline mass of rods surrounded by a faintly orange, almost indiscernible membrane of dried slime. Spores

straight with slightly rounded ends, 1.0-1.3 x 3.5-6μ; highly refractile when unstained; strong affinity for aniline blue, staining evenly with only a few showing a "beady" effect; easily separable one from another. Vegetative cells not described.

Material examined: Type material from the Farlow Herbarium. One occurrence from the current study.

Recorded collections: Thaxter, Indiana, 1904; Current study, Missouri.

About 100 fruiting bodies of S. muscorum occurred once on a piece of bark gathered in March, 1956, from a Quercus velutina growing on the top of a relatively dry ridge in a semi-dense shortleaf pine-oak forest in Missouri. These fruiting bodies were spread over an area of bark about 5 mm. square, but very unequally so because they were generally in clusters. Because of the meager amount of material available, no attempts to culture S. muscorum were made.

One collection, labelled "Type," is currently on deposit at the Farlow Herbarium. This collection is designated as Chondromyces ligulatus Thaxter, a name which does not appear in the literature at any time. However, there is no doubt but that this is Thaxter's type material for his Chondromyces muscorum (1904). The fruiting bodies present on the material, in all respects except the color, which has

faded over 60 years, check with his original description and with his drawings of C. muscorum and, in addition, other information on the herbarium sheet checks with Thaxter's published records.

Stelangium vitreum n. sp.

Etymology: Latin, vitreum, glassy.

Fruiting bodies crystalline orange; sessile on substrate; simple, either globose or columnar, generally unbranched; 60-70μ in diameter, ranging up to 150-200μ for the more complex, columnar forms. In transmitted light, no membrane or wall discernible; spores lie parallel in packets, 6-12 per packet; adjacent packets perpendicular to each other in basket-weave fashion. Spores straight with squarish ends; uniform; 0.7 x 2.0μ; stain unequally with aniline blue dye to be darker at ends and in middle of rod, these three areas appearing to bulge. Vegetative cells 0.7 x 4.0μ.

Type substratum: Bark of Juniperus virginiana (Peterson No. 210-e-3)

Type locality: Providence, Missouri.

This organism was first observed on a piece of Juniperus virginiana bark which was collected in March, 1955, from a tree growing on a bluff high above the Missouri River at

Providence, Missouri, in a very difficult, xeric habitat. Only seven fruiting bodies scattered in an area about a centimeter square made up this occurrence. The organism was later found on bark of Ulmus americana (twice), Quercus alba (six times), Carya ovata (twice), Juglans nigra, Quercus velutina, and two other Juniperus virginiana collections. Most of these occurrences consisted of only four to eight fruiting bodies scattered rather widely on the bark surface, although two of them were composed of well over a dozen fruiting bodies in each occurrence.

The fruiting bodies of this organism are a lovely, delicate orange and glisten beautifully. The specific name given to the organism was selected because of this dominant characteristic. Both the color and the glistening appearance persist even after complete desiccation.

The closest relative to S. vitreum is, of course, the other member of the Genus Stelangium, S. muscorum. The only other possibly related species is Archangium flavum, which, as stated previously, the writer tentatively feels probably should be transferred to Genus Stelangium. S. vitreum differs markedly from both of these organisms in the persistent crystalline, almost transparent quality of the fruiting body. Both S. muscorum and A. flavum are essentially opaque in character. The spores of S. vitreum are smaller than those of the other two species, they exhibit a "three-beaded" appearance when stained, which the spores

of S. muscorum and A. flavum do not have, and they are arranged in distinct basket-weave packets which do not occur in either of the other two species.

When first mounted, the fruiting body is a pale pink in color in transmitted light. The lactophenol soon bleaches this color, however, and the mass becomes hyaline in appearance. In a cotton blue-stained preparation, there is a layer of amorphous material which takes stain and separates off from the spore mass proper giving the over-all illusion of a halo around the spore mass. Some of this material appears to be globules of an oily material. This material is interpreted to be the slime envelope, or residual of the slime envelope, around the spore mass, although such is not discernible in the intact, unstained mass.

Attempts to culture S. vitreum have not been completely successful and it has not been grown on any of the agar media. Fruiting bodies were produced on Sterilized Elm Bark two weeks after seeding and small yellowish-gray slimy areas on the bark yielded definite myxobacterial vegetative cells, which measured 0.7 x 4.0μ, in combination with other bacterial cells. There is little doubt that these vegetative cells belong to S. vitreum, but more critical study of the vegetative phase in pure culture is certainly a necessity for the future.

Type material of S. vitreum will be retained in the University of Missouri herbarium. Paratype material will be

deposited only in the Farlow Herbarium of Harvard University for the present.

Family Sorangiaceae Jahn

Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

(Only one species known on bark of living trees)

Sorangium sorediatum (Thaxter) Jahn

Bot. Gaz., 37:414. 1904.

Polyangium sorediatum Thaxter, as cited above.

Sorangium sorediatum (Thaxter) Jahn, Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Neotype: Specimens on bark from a living Ulmus americana (Peterson No. 217-d-2) on deposit in the University of Missouri herbarium.

Fruiting bodies small, irregularly rounded cushions of tiny cysts held together by evanescent slime envelope; from 30 x 30 x 15μ up to dimensions of about 100μ; bright reddish-orange when fresh, turning to dull brown-orange with desiccation. In transmitted light, cysts pale yellow in color; grossly oval to globose, but slightly polygonal under higher magnifications; ranging from 3μ up to 11.5μ in size; cyst wall of two layers, the inner smooth and hyaline, the outer brittle and cartilaginous; walls completely

impervious to aniline blue, but the spores within are discernible in unstained condition. Spores 18-24 per cyst; short, blunt, sometimes appearing coccoid; 0.8-1.0 x 3-5μ. Vegetative cells 0.8 x 3-5μ.

Material examined: Three occurrences on bark from current study.

Recorded collections: Thaxter, South Carolina, 1904; Quehl, Germany, 1906; Krzemieniewski and Krzemieniewska, Poland, 1927; Current study, Missouri.

S. sorediatum occurred three different times, on bark from three different trees growing at three widely separated locations in Missouri, and collected in three different months. The one point in common for all three of these collections was that they were all on bark from trees which were growing in moist, shady habitats.

The first occurrence of S. sorediatum was on a piece of bark of a Quercus alba growing at Providence, Missouri, collected in March, 1955, and consisting of only five fruiting bodies. The second occurrence consisted of about seven dozen fruiting bodies over an area approximately 14 mm. square on a piece of bark of Ulmus americana collected in April, 1955, at Duly Mill, Missouri. The final collection consisted of many dozens of fruiting bodies on two small pieces of bark of an Ulmus americana growing at a location known as Sand-

stone Bluffs, Missouri, and collected in May, 1955. In all, over 200 fruiting bodies of this organism were found on the above pieces of bark.

S. sorediatum is not included among any of the herbarium specimens known to the writer and, therefore, has not been studied comparatively. Four other species of the genus are in the Farlow Herbarium collection, however, and these have been seen and studied. Previous to such study, this organism, as found on bark, had been temporarily identified as an undescribed species of Genus Polyangium. Observations on the Farlow specimens, three of which are Thaxter's type specimens, make it absolutely certain that this organism is a member of Genus Sorangium. With this fact established, it is quite apparent that the proper designation is S. sorediatum. The only difference between the organism found on bark and the description of S. sorediatum is that the spores of the bark specimens are somewhat shorter. This certainly is a minor consideration. Since no other specimens are known to be in existence, those found on bark are designated as neotypes and will be deposited in the University of Missouri herbarium.

Attempts to cultivate this organism on all seven substrates were unsuccessful. They were repeated on the five agar substrates without success. It has been reported in the literature that previous attempts to cultivate have also failed, although the vegetative cells have been observed and described.

Family Polyangiaceae Jahn

Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Key to the genera on bark of living trees

1. Fruiting bodies sessile on substrate
    2. Fruiting bodies consisting of several cysts appressed together..... *Polyangium*
    2. Fruiting bodies consisting of a solitary cyst..... *Haploangium*
1. Fruiting bodies stalked
    3. Fruiting bodies consisting of a single cyst on each cystophore..... *Podangium*
    3. Fruiting bodies consisting of several cysts on each cystophore..... *Chondromyces*

Genus *Polyangium* Link

Mag. d. Ges. Naturforsch. Freude zu Berlin, 3:42. 1809.

Key to the species on bark of living trees

1. Slime generally deliquescent
    2. Cysts over 70μ in size
        3. Cysts yellow ..... *P. vitellinum*
        3. Cysts dark brown ..... *P. fuscum*
    2. Cysts under 50μ in size ..... *P. cellulosum*
1. Slime persistent; golden yellow ..... *P. luteum*

Polyangium vitellinum Link

Mag. d. Ges. Naturforsch. Freude zu Berlin, 3:42. 1809.

Myxobacter aureus Thaxter, Bot. Gaz., 17:403. 1892

Neotype: Collection on wood, labelled Cystobacter (Myxobacter) aureus Thaxter; collected and determined by Thaxter in 1892 at York, Maine; bearing Thaxter's Accession No. 4504; labelled "Type"; on deposit in the Farlow Herbarium.

This is herein designated as a "neotype" because it is not the type on which Link originally described P. vitellinum. This was Thaxter's type for his species Myxobacter aureus, which he later found to be identical with the organism Link had described some 83 years earlier.

> Fruiting bodies typically about one dozen golden yellow cysts appressed together, surrounded by white slime envelope; when fresh, a lobed cushion, reminiscent of half a mulberry, measuring up to 1 mm. in size; when dry, decreased in size, shrunken and irregularly wrinkled. Cysts 75-200μ in diameter. In transmitted light, fruiting bodies almost hyaline, with a faint yellow tinge in cyst walls; cyst walls 1.5-2.0μ thick in fresh material, gelatinous in texture, not discernible as such in dried material. Spores 0.7 x 2.5-3.0μ; irregular in shape, straight, curved and irregularly bent rods; taper slightly, more toward one end than the other, giving a club-shaped appearance; stain avidly and uniformly with aniline blue dye. Vegetative

cells cylindrical, rounded at the ends, 0.7-0.9 x 4-7μ; colony milky white at time of fruiting.

Material examined: Six different collections, one of which is "Type," from the Farlow Herbarium; 23 different bark occurrences from the current study.

Recorded collections: Link, Germany, 1809; Thaxter, Maine, Massachusetts, 1893; Zukal, Vienna, 1897; Quehl, Germany, 1906; Jahn, Germany, 1911; Current study, Missouri.

As had been the case with Archangium primigenium, this organism was found early in the study of myxobacteria on the bark of living trees, but was not actually identified properly until late in the study. Again, the reason for this discrepancy was that fruiting bodies of P. vitellinum were found in desiccated, or semi-desiccated, condition and had lost their characteristic structure. After studying herbarium specimens and observing the organism in an active, fresh condition, these structures, which had been recorded as "Y," were given their true designation of Polyangium vitellinum Link.

P. vitellinum was found a total of 23 times on bark from various species of trees growing in various habitats in various locations, but all in Missouri. There is no reason to list these various bark sources, since there are no indications or correlations to be seen in the data, other than that P. vitellinum is cosmopolitan on the bark of Missouri trees.

Thaxter (1892) mentions a yellow, oily material intermingled with the spore mass of P. vitellinum. An oily material is present in the specimens found on bark, more so in some than in others, but it is not prominent in any of them. The white, slimy envelope described as generally surrounding the entire fruiting body is, also, usually not discernible in the specimens found on bark.

Mixed colonies of P. vitellinum and unidentified Eubacteriales were cultivated on Killed Bacterial Agar and on Rabbit Dung Decoction Agar. Some of these colonies were yellow-white and others were gray-white, but this observation is of no value since the true bacteria undoubtedly influenced colony color. The vegetative colony of P. vitellinum has been described as being milky-white at time of fruiting. The myxobacterial vegetative rods in this mixed culture measure 0.8 x 5.0μ. They were in the minority in relation to the true bacteria and did not transfer successfully.

The Farlow Herbarium collection of myxobacteria includes six different packets of P. vitellinum, one of which is a "Type," and all of these have been examined. There are some differences, but they are not considered significant and there is no question about the 23 bark specimens being correctly identified. The Farlow specimens are all very plump and globose, although 60 years old and, of course, completely desiccated, whereas the specimens found in this study

are all wrinkled and shriveled when dry. It has been observed that myxobacterial slime often deliquesces in continued high moisture and perhaps that is the reason why these moist-chamber cultures--of other species as well as P. vitellinum--have shriveled and shrunken. The treatment to which the Farlow specimens were subjected, of course, is unknown, but most of the fruiting bodies probably occurred naturally.

Finally, the specimens found on bark did not always check with the Farlow specimens in color and texture. The color differences are not considered important, however, since even within the six Farlow packets (all of which were originally from Thaxter's collection) color differences were quite apparent. Those fruiting bodies of P. vitellinum from the Farlow were all opaque and dull, whereas those found on bark were all crystalline-translucent and shiny, but 60 years could well account for this difference.

Polyangium cellulosum Imsenecki & Solntzeva
Bull. Acad. Sci., U. S. S. R., Ser. Biol., 6:1115. 1936.

No type material in existence.

> Fruiting bodies an aggregate of rounded cysts on the surface of an indefinite mass of rods and slime; extremely irregular in shape and size; ranging from about 50μ in diameter to those which are 750-850μ in diameter, up to 100μ in height, but generally closely appressed to substrate; red-

orange to red-brown in color, with points of glittering irridescence on the surface. Surrounding slime indiscernible in dry specimens except as flakes of dried slime; some fruiting bodies loosely adhering together, others rather closely packed. Cysts oval to elongate, sometimes polygonal when tightly packed together; 20-85μ in diameter, with the elongate forms ranging up to 120μ long; some with constriction at basal portion; orange to brownish-yellow in transmitted light, the color localized in the slightly wrinkled wall. In transmitted light, the basal rod and slime mass is yellow-pink in color; no surrounding membrane, but rods are in rounded masses; these rods tend to be 0.5-1.0μ longer than spores within the cysts. Spores predominantly aligned perpendicular to cyst wall; apparent through the cyst wall; slightly curved with squarish ends; uniformly and strongly stained with aniline blue; 0.7-0.9 x 2.2-5.0μ in size. Vegetative cells thick, bent rods with rounded ends; 0.8-1.2 x 3.5-8.5μ; young rods possess one chromatin granule, older rods possess two; colonies orange and moist in appearance.

Material examined: Eight occurrences during the current study.

Recorded collections: Imsenecki & Solntzeva, Russia, 1936; Mishustin, Russia, 1938; Current study, Missouri, Greece.

This organism was found a total of eight times, but two of the eight occurrences were found on the same piece of bark. Such an "impossible" situation is explained by the statement that two distinct varieties, Polyangium cellulosum var. fuscum and Polyangium cellulosum var. ferrugineum, as described by Mishustin (1938), were found on one piece of bark. Both of these varieties have been treated here under the designation of Polyangium cellulosum Imsenecki & Solntzeva. Fruiting body color differences are the prime criteria for Mishustin's varieties, but the writer does not feel that he is familiar enough with this species and its apparent complexities to attempt to consider varietal differences.

What appears to be P. cellulosum var. ferrugineum was found on bark from Quercus ellipsoidalis, Juniperus virginiana, Juglans nigra and Ulmus pumila, all of which were growing in Missouri, and on a piece of bark gathered in September, 1954, from a Salix sp. growing on Mt. Parnes, Attica, Greece, by Dr. C. J. Alexopoulos. P. cellulosum var. fuscum occurred on bark of Ulmus rubra and on the same piece of Ulmus pumila indicated above, both from Missouri, and on a second piece of bark collected by Dr. Alexopoulos in Greece. This second collection made by Dr. Alexopoulos was from a

Salix sp. growing at Vasilika, Chalkidike, Greece, and was collected in October, 1954.

Originally, no attempts to culture P. cellulosum were planned because of the relatively limited amount of material. However, as identifications began to crystallize and as the possible color varieties of P. cellulosum presented themselves, it became apparent that it would be desirable to culture this organism in order to observe very fresh fruiting bodies and in order to check constancy of colors. Consequently, dry cysts were seeded onto Sterile Elm Bark, Rabbit Dung Decoction Agar and Rabbit Dung Pellet Plates. These attempts were unsuccessful and it was felt that no more of the material could be used for further attempts.

The writer does not think that neotypes should be designated for P. cellulosum at the present time, even though no existing specimens are known to him. There are two reasons for this opinion. First, although attempts have been made to contact the Russian workers responsible for P. cellulosum and its four varieties, no definite indication of the existence or absence of specimens has been attained. Second, this species and its varieties have been rather well worked out physiologically and the character of the fruiting body--quite indistinct, at best--consequently becomes of less importance. For the above reasons, the designation of neotypes will be relegated to the future.

Polyangium fuscum (Schroeter) Thaxter

Cohn, Kryptogamenflora v. Schlesien, 3:170. 1886.

Cystobacter fuscus Schroeter, as cited above.

Polyangium fuscum (Schroeter) Thaxter, Bot. Gaz., 37:414. 1904.

Neotype: Collection on jack rabbit dung; collected and determined by Thaxter in 1897 from southern California material; bearing Thaxter's Accession No. 4508; on deposit at the Farlow Herbarium.

Fruiting bodies composed of from a few to a great many cysts lying rather loosely together; flesh-colored to deep brown when fresh, chestnut-brown to almost black when dry; surrounding slime envelope extremely evanescent, generally indiscernible. Cysts irregularly globose; from 50-60μ in diameter up to those which are 300μ in size; bounded by a definite wall, heavy, but transparent enough so that the spore mass within may be seen; golden-brown in transmitted light, the color localized in the wall. Spores 0.8-1.5 x 3.0-3.5μ; straight with rounded ends; strong, uniform affinity for aniline blue dye. Vegetative cells slender, elongate; 0.6 x 5-12μ; Baur (1905) has described cells 15-20μ in length.

Material examined: Three collections, originally Thax-

ter's specimens, borrowed from the Farlow Herbarium. Four occurrences on bark from current study.

Recorded collections: Schroeter, Germany, 1886; Thaxter, California, 1897; Baur, Germany, 1905; Quehl, Germany, 1906; Kofler, Vienna, 1913; Jahn, Germany, 1924; Krzemieniewski and Krzemieniewska, Poland, 1926; Current study, Missouri.

P. fuscum occurred on four different pieces of bark, three of them from the same Ulmus americana growing at Round Spring, Missouri, in a moist river bottom habitat. The fourth occurrence was on a piece of Quercus alba bark collected from a tree growing in a deep forest situation at Holstein, Missouri.

When the four pieces of bark on which P. fuscum was found were still moist, a total of approximately seven dozen fruiting bodies were counted. However, after drying out, not more than two dozen were discernible because of the darkening and shriveling which the fruiting bodies undergo. Consequently, these remaining fruiting bodies were kept as specimens and no cultural attempts were made with P. fuscum.

Although P. fuscum was originally described by Schroeter (1886), no specimens of this vintage appear to be in existence. Two of the three collections in the Farlow Herbarium are dated 1897 and the third is dated 1904. One of the two dated 1897 is labeled "Lab. Culture. Cambridge," and probably was a transfer of the other one labeled, "On jack rabbit

dung. S. California." This collection, then, bearing Thaxter's Accession No. 4508 and now on deposit in the Farlow Herbarium is designated as the neotype of P. fuscum.

Polyangium luteum Krzemieniewski and Krzemieniewska
Acta Soc. Bot. Poloniae, 5:98. 1928.

Neotype: Specimens on a piece of bark from a living Quercus ellipsoidalis (Peterson No. 216-b-2); on deposit in the University of Missouri herbarium.

Fruiting bodies unspectacular, orange-brown, dull, but glistening slightly when moist; ranging in size from those composed of only a few cysts to those 300 x 300μ in size, generally not nearly as high as they are long or wide. Cysts averaging 70 x 90μ, but ranging from 45-80 x 75-100μ; generally slightly elongate; usually smooth and turgid in appearance; golden yellow in transmitted light, the color in the cyst wall which measures 2.5-3.0μ thick and is the agency of binding the cysts into the fruiting body unit; spores within readily seen as stipples. Spores 0.7-1.0 x 2.0-5.8μ; extremely variable in shape, ranging from ovals about 1.0 x 2.0μ to definite rods, with comma-shaped, crescent-shaped, convex and concave tapering rods, and practically square rods in between; stain well with aniline blue, occasionally showing a central area

of less dense staining. Vegetative cells not described.

Material examined: One occurrence on bark from current study.

Recorded collections: Krzemieniewski and Krzemieniewska, Poland, 1928; Current study, Missouri.

This organism was found on only one piece of bark during the current study. This piece of bark was collected from a Quercus ellipsoidalis growing on the top of a high, barren, windy ridge at Duly Mill, Missouri, in April, 1955. The one occurrence consisted of about three dozen fruiting bodies scattered randomly over an area of about three inches by one-half inch. No attempts to culture P. luteum were made.

The only previous report of this organism has been by the Krzemieniewskys in their original description. They described the cyst wall as being a thin, colorless membrane with a thick, yellow slime envelope surrounding the cysts. The description given above states that the wall is thick and yellow. Such a discrepancy is simply a matter of interpretation as to what is cyst wall and what is slime envelope. The Krzemieniewskys also described the spores of P. luteum as being about twice as long as were any of the spores observed in the bark specimens.

Inquiries to Madame Krzemieniewska have not indicated the existence of any specimens of P. luteum. Therefore, the

specimens found on bark are designated as neotype material and are deposited in the University of Missouri herbarium.

Genus Haploangium n. gen.

Etymology: Greek, haplo, single; Greek, angion, vessel

Fruiting body consisting of a single, solitary cyst; sessile on substrate. Cyst wall well developed and distinct; may or may not be imbedded in further slime layers.

A new genus of the Family Polyangiaceae is erected to include two new species of myxobacteria which have been found on the bark of living trees during the course of this study and a third species, Polyangium simplex Thaxter, which is herein transferred into this new genus. Polyangium ochraceum Krzemieniewski and Krzemieniewska (1926) has been recorded only by those authors and is described as being of solitary cyst habit in fruiting body character. As pointed out in the discussion of Haploangium rugaseptum n. sp., the writer is not currently convinced that P. ochraceum is a valid species, but, if it should prove to be valid, it also should be transferred to Genus Haploangium.

Key to the species on bark of living trees

1. Spores arranged in spherical packets ..... H. minor
1. Spores in no particular arrangement
   2. Mature cyst wall prominently wrinkled..H. rugaseptum

2. Mature cyst wall essentially smooth; sometimes with persistent slime envelope ..... H. simplex

Haploangium minor n. sp.

Etymology: Latin, minor, less or small

Fruiting bodies solitary cysts, sessile in groups of 4-10, but with no contact or clustering; globose, oval or bean-shaped; 60-140μ; turgid, smooth, dull orange-brown when fresh; collapsed, wrinkled, more glistening and orange when desiccated. Spore mass not readily discernible through cyst wall; wall bright yellow-orange in transmitted light; about 2μ thick. Spores 0.7 x 2.5-3.5μ; irregular in shape; arranged in distinct spherical groups which are difficult to break up. An amorphous material also present in cysts. Vegetative cells with squarish ends; 0.7 x 3.0-4.5μ.

Type substratum: Bark of Ulmus rubra (Peterson No. 283-3)

Type locality: Holstein, Missouri.

This undescribed species was found only on bark collected near Holstein, Missouri, in early June, 1956, but it was found a total of 32 times, to rank only behind Chondrococcus coralloides and Archangium primigenium in total number of occurrences. The 32 occurrences were all found on only seven

different trees, representing four different species. Of three collections from three different Ulmus rubra trees, Haploangium minor was found on eight of ten pieces from one tree and on seven of ten pieces from each of the other two trees. It occurred on one piece of Quercus alba bark, on six pieces of Quercus rubra bark, all from the same tree, and three times on bark from two different Fraxinus americana trees. The occurrences ranged in profusion from only two or three fruiting bodies on some pieces of bark to uncountable numbers on others.

The fruiting bodies of Haploangium minor are solitary cysts in practically all cases, although an occasional clustering of two or more to give a Polyangium-like effect can be observed. The solitary cysts are usually found in groups of from four to ten cysts close together, as if they all arose from the same vegetative cell mass, but there is no contact between the individuals and no connections between them. The cysts are sessile on the substrate, without any suggestion of a hypothallus or stalk, and the cysts are not closely appressed or attached to the substrate.

Cysts of H. minor were seeded into all five Van Tieghem preparations and onto all seven substrates. Grayish-yellow colonies were produced on Homogenized Bark Agar and on Rabbit Dung Pellet Plates in four days. Examination showed that these colonies were composed of myxobacterial rods, measuring 0.7 x 3.0-4.5μ, and at least one representative of

the Eubacteriales. The true bacteria predominated and, eventually, no myxobacterial cells were to be found. Attempts to transfer and purify the myxobacterial cells were unsuccessful and further seedings with cysts on new substrates only repeated the same mixed-culture situation.

The following species, Haploangium rugaseptum, is the closest relative of H. minor. The differences between these two new species will be considered in the following discussion.

Type material of H. minor has been deposited in the University of Missouri herbarium. Paratype material will be placed in the Farlow Herbarium in the near future and probably in one or two other herbaria in the more distant future.

Haploangium rugaseptum n. sp.

Etymology: Latin, ruga, wrinkled; Latin, saeptum, enclosure

Fruiting bodies solitary globose, or oval, cysts; sessile on substrate; glistening orange-red; heavily wrinkled when dry; up to 200μ in size, but averaging about 85μ. Cyst wall of two indistinct layers; inner, smooth and yellow; outer, irregular and dark orange. Fatty globules and amorphous mass sometimes within cyst in addition to the spores. Spores 0.8 x 4-6μ; curved once or twice; appearing knobby along their length. Vegetative cells not described.

Type substratum: Bark of Populus deltoides (Peterson No. 215-b-2)

Type locality: Duly Mill, Missouri

With the exception of Chondrococcus coralloides, Archangium primigenium and Haploangium minor, this organism occurred more times than any of the 30 species being reported in this paper. Although it appears to be quite common on the bark of living trees, it undoubtedly is an unreported species of the myxobacteria. Perhaps it is unreported because it is peculiar to the habitat under consideration in the present study, although there is no real evidence to substantiate this statement other than that it has not previously been described and that it appears to occur on bark in some profusion.

H. rugaseptum occurred a total of 27 times, on bark from 16 different trees representing 10 different species, and on bark collected in nine different geographical locations in Missouri. Enumerating the tree species and the habitat and location for each of these 27 occurrences would serve no useful purpose. However, enough occurrences of this organism were observed so that some meager indications concerning its range can be stated. It was found on bark of trees growing in widely divergent habitat types, to be sure, but preponderantly it was found on bark from trees growing in shady, moist situations. Moreover, bark from those trees which grew in moist, shady situations produced

a greater profusion of fruiting bodies per occurrence than did those pieces from trees in drier, more unfavorable habitats.

The fruiting bodies of H. rugasertum are individual, sessile cysts which occur without any apparent hypothallus-like attachment. They are extremely easy to remove from the substrate and, in fact, they are prone to flip away from the dissecting needle at a very slight touch when they are dry, indicating that they are not at all appressed to the substrate as are most of the similar forms. In reflected light, the fruiting bodies are bright, glistening orange-red. When fresh, they are quite plump, unwrinkled, and more orange than red in color, but when fully mature and dessicated, they are very wrinkled and more red than orange. The wrinkles on the dried cysts are so prominent that they are readily seen at 90X magnification under the dissecting microscope and it is this characteristic which suggested the specific name given to the organism.

A rather considerable amount of material was available and cysts were sown on all seven of the substrates used and into all five of the Van Tieghem cell hanging-drop solutions with no success. Four more attempts to culture this organism were made on all seven of the substrates, again without success. At least one cyst had been placed in at least two spots on each substrate so that a total of more than 70 cysts were seeded during these trials. Further attempts to germin-

ate and grow mature cysts, and plans to catch vegetative masses as they arise on fresh bark, are underway, but at this writing, the vegetative stage of H. rugaseptum has not been observed.

Two species of myxobacteria, Polyangium simplex Thaxter and Polyangium ochraceum Krzemieniewski and Krzemieniewska, which produce solitary-occurring cysts, had been reported in the literature previous to the current study. Two more species, Haploangium minor and Haploangium rugaseptum, have been found during the course of the current study. Genus Haploangium, as erected in this paper, then, should include all four of these species on the basis of their solitary cyst habit of fruiting. However, as stated in the following discussion of Haploangium simplex (Thaxter) n. comb., the writer holds the opinion that P. simplex Thaxter and P. ochraceum Krzemieniewski and Krzemieniewska are probably one and the same organism. In any event, the writer has found and studied three distinct solitary-cysted organisms and these three have been consigned to Genus Haploangium.

H. rugaseptum and H. minor undoubtedly are rather closely related species. However, when one observes the two comparatively, there is no question but that they are different organisms, even though it is sometimes difficult to enumerate precise differences between the two. H. minor is consistently smaller and more brownish-orange in color in reflected light than H. rugaseptum. When dry, both species

have a similar collapsed, heavily wrinkled appearance, but the differences in size and color are still apparent. The oil globules described for H. rugaseptum have never been seen in H. minor. The spores of H. minor are smaller than those of H. rugaseptum and they are in distinctly characteristic globular packets whereas no such formations have been seen in H. rugaseptum.

In addition to H. minor, the only other species to which H. rugaseptum appears to be closely related is the "Polyangium simplex - Polyangium ochraceum" complex mentioned above. The writer has seen an organism which he identified as P. simplex after comparison with some of Thaxter's specimens in the Farlow Herbarium. This organism is strikingly different from the one here described as Haploangium rugaseptum. The Krzemieniewskys (1926) characterized their Polyangium ochraceum as possessing a constricted cyst wall. Such has never been seen in any of the specimens described as H. rugaseptum. The Krzemieniewskys make no mention of either oily globules or an amorphous mass in P. ochraceum, as has been seen in some of the specimens of H. rugaseptum.

In summation of the above comparative discussion, the writer has seen three distinctly different single-cysted myxobacteria, two of which are described as new species. The third organism has been identified as Thaxter's Polyangium simplex; it is transferred into Genus Haploangium, and is tentatively thought to also include the Krzemieniewskys Polyangium ochraceum.

Type material of H. rugaseptum has been deposited in the University of Missouri herbarium. Paratype material will be placed in the Farlow Herbarium in the near future and probably in one or two other herbaria in the more distant future.

Harloangium simplex (Thaxter) n. comb.
Bot. Gaz., 18:29. 1893.

Myxobacter simplex Thaxter, as cited above.
Polyangium simplex Thaxter, Bot. Gaz., 37:414. 1904.

Neotype: Specimens labeled Polyangium simplex Thaxter; collected and determined by Thaxter in October, 1892, at Waverly, Massachusetts; bearing Thaxter's Accession No. 4507; on deposit in the Farlow Herbarium.

> Fruiting bodies solitary cysts; irregularly rounded or oval; dull red-orange to red-yellow with glistening spots of irridescence on the surface; ranging in size from 55 x 90μ for those on bark to 350-400μ for those described by Thaxter. In transmitted light, cyst wall yellow and definite; some cysts surrounded by a yellow slime envelope in which many entrapped rods can be seen, but other cysts possess no such envelope; spore mass clearly seen through the wall of those cysts which possess a slime envelope, flesh-colored; wall of those cysts which do not possess slime

envelope is thicker and more deeply pigmented, difficult to see spore mass within, difficult to break wall open. Spores straight or slightly curved with squarish ends; 0.6 x 2.5-4.0μ; strongly adhering together in sheaths or elongate groups; some quite resistant to aniline blue dye. Vegetative cells cylindrical, rounded at either end; 0.7-0.9 x 4-7μ.

Material examined: One collection of Thaxter's material now on deposit in the Farlow Herbarium. Three occurrences during the current study.

Recorded collections: Thaxter, Maine, Massachusetts, 1893; Current study, Missouri.

H. simplex occurred three times during the course of this study. These occurrences were on bark collected from Ulmus americana, Quercus ellipsoidalis and Quercus alba. All three trees were growing in Missouri, two of them in dry, open habitats and the third in deep, mesic forest.

Attempts to culture this organism, using all seven of the substrates, were failures. Trials with all seven substrates were repeated, and again failed. The amount of material available did not allow further cultural trials.

Except for differences in size of both cysts and spores, the observations made on the specimens found on bark of living trees so well fit both P. simplex Thaxter and the organism

described as Polyangium ochraceum by the Krzemieniewskys (1926) that, at the present writing, it appears that the two species are the same organism. Both have been reported only by the original describer and neither description is particularly detailed or complete. The cysts of the Krzemieniewskys' P. ochraceum fall into the same size range as those found on bark; those of P. simplex are much larger. Some observations of the constricted membrane dividing the cyst content into two portions as described by the Krzemieniewskys for P. ochraceum have been made on the specimens from bark. Cysts both with and without the slime envelope which Thaxter described for P. simplex have been seen. The spores of both P. simplex and P. ochraceum are somewhat longer than those seen in the specimens found on bark. In the final analysis, the specimens found on bark have been identified as P. simplex because the slime envelope has been observed more constantly than has the constricted membrane. These appear to be the really distinctive differences between the descriptions given for the two species, if size of the fruiting body is disregarded as it probably should be.

One collection of P. simplex from the Farlow Herbarium was examined. It was not labeled "Type," but it was one of Thaxter's specimens and, therefore, can be considered valid. The collection consists of about one dozen fruiting bodies on a small piece of polypore. These specimens cannot be a part of Thaxter's original collection, because he describes them

as being on wet wood and bark in swamps. Therefore, this material in the Farlow Herbarium should be designated as the neotype material, but it cannot be assumed to be lectotype material.

There are some differences between the collection on deposit in the Farlow Herbarium and those specimens found on bark of living trees. For example, the fruiting bodies are plumper and more rounded than those which were found on bark, but, as with Polyangium vitellinum, this may be a shortcoming of the moist chamber. Thaxter's specimens are completely opaque whereas those found on bark are crystalline-translucent, but this may be due to aging since some observations of increasing opacity and dullness have been made. Finally, Thaxter's specimens tend to be yellow in color as opposed to the more orange and red casts of those found in the current study, although Thaxter described his specimens as reddish-yellow in the original description. In spite of the above differences, examination of Thaxter's specimens has given credibility to the identification.

Genus Podangium Jahn

Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Key to the species on the bark of living trees

1. Cystophore hyaline or yellowish; short, stout
    2. Cysts cylindrical ..... P. cylindricum
    2. Cysts globose or oval

3. Cystophores produced in clustered aggregates .. P. erectum

3. Cystophores solitary

4. Cystophore hyaline; rounded at apex ... P. gracilipes

4. Cystophore yellowish; poorly formed, often lacking ..... P. lichenicolum

1. Cystophore snowy-white; long; corkscrewed.. P. alboracemum

Podangium erectum (Schroeter) Jahn

Cohn, Kryptogamenflora v. Schlesien, 3:170. 1886

Cystobacter erectus Schroeter, as cited above.

Chondromyces erectus Thaxter, Bot. Gaz., 23:407. 1897.

Podangium erectum (Schroeter) Jahn, Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Neotype: Specimens on decaying leaf; collected and determined by Thaxter; dated May, 1893; bearing Thaxter's Accession No. 4559; on deposit in the Farlow Herbarium.

Fruiting bodies solitary cysts on single cystophores, but occurring in caespitose aggregates of a few to hundreds, with cystophores all radiating out from a central area; aggregates average 200-300μ in diameter by 100-125μ high, but both larger and smaller clusters occur; orange-red in color, cystophores not discernible when fresh; chestnut-brown, cystophores apparent when aggregate is dry. Fresh cysts plump, globose,

or oval, averaging 40 x 55μ, stippled or pitted in reflected light; more elongated, longitudinally shriveled, averaging 22 x 65μ when dried. Cystophores indefinite and variable; yellowish-white in color; variable in length from those which are indiscernible to those twice the length of the cysts (about 100μ); mostly 10-15μ wide; striated and twisted in appearance; not tough and persistent, breaking into an amorphous mass containing dried slime, some rods and occasional irregular globose inclusions when mounted. Spores extremely uniform in size and shape; 0.6 x 2.5-4.0μ; almost straight, slightly curved and slightly tapering toward the ends; stain uniformly with aniline blue. Vegetative cells 2-5μ long, about 0.8μ wide.

Material examined: Three collections of Thaxter's material borrowed from the Farlow Herbarium. Fifteen occurrences during the course of the current study.

Recorded collections: Schroeter, Germany, 1886; Thaxter, Massachusetts, 1897; Kofler, Germany, 1913; Jahn, Germany, 1924; Krzemieniewski and Krzemieniewska, Poland, 1928; Current study, Missouri.

P. erectum occurred a total of 15 times during the course of this study and is, therefore, one of the more commonly

found species of myxobacteria on bark of living trees. It occurred twice on the bark of an Ulmus americana growing in an open, dry, old-field type of habitat at the Pinnacles, Missouri. The collections were made in April, 1955, and the occurrences consisted of several dozen fruiting bodies in each. P. erectum was again found on two different pieces of bark collected in March, 1955, from a Juniperus virginiana growing at the very end and top of a bluff at Providence, Missouri, in an extremely difficult, windy, dry habitat. One of these occurrences consisted of profuse numbers of fruiting bodies and the other consisted of only four such structures. Two further occurrences were on bark of Quercus ellipsoidalis collected in April, 1955, at Duly Mill, Missouri. This tree, as was the previous one, was growing on the very top of a rocky ridge in a barren, windy, dry, difficult habitat. Each occurrence was represented by less than a half-dozen fruiting bodies. Six occurrences were on six different pieces of bark collected in May, 1955, from a Quercus alba which was growing high on a bluff in a dry, open-woods type of habitat. Two of the occurrences consisted of dozens of fruiting bodies, but the other four were represented by only about a half-dozen per occurrence. In later collections, a small amount of P. erectum was found on bark of Juglans nigra collected in the "Bootheel" of Missouri, and two other poor occurrences were found on bark from two different Acer saccharum trees. One of these trees was grow-

ing in a heavy, moist woods near Perryville, Missouri, and the other was in a deep, moist woods near Holstein, Missouri.

P. erectum was seeded onto all of the seven substrates used in the cultural portion of this study and pinkish-yellow colonies were produced on Homogenized Bark Agar, Rabbit Dung Decoction Agar and Rabbit Dung Pellet Plates. These colonies were composed of masses of vegetative cells averaging 0.8 x 4.0μ in size. True bacteria were present around the colonies, but were not actually mixed in with the myxobacterial cells as they were with the cultures of some of the other species. After a week, a few poorly formed fruiting bodies were produced on Rabbit Dung Pellet Plates and, after two weeks, a few fruiting bodies were produced on Sterilized Elm Bark. Transfers to fresh substrates were made with moderate success, but P. erectum is not easily grown on any of the substrates used in this study.

The Farlow Herbarium collection includes three packets of P. erectum, all originally in Thaxter's possession. The specimens on decaying leaf in one of these packets are magnificent and, fortunately, this one dates from 1893 and can be designated as neotype material. All three of these collections have been borrowed from the Farlow Herbarium and examined. There is no doubt about the accuracy of the identification in the case of P. erectum.

Podangium lichenicolum (Thaxter) Jahn

Bot. Gaz., 17:402. 1892.

Chondromyces lichenicolus Thaxter, as cited above.

Podangium lichenicolum (Thaxter) Jahn, Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Type: 602. Chondromyces lichenicolus Thaxter; on lichens on tree trunks; collected and determined in July, 1890, at New Haven, Connecticut, by Thaxter; on deposit in the Farlow Herbarium.

Fruiting bodies typically single, globose cysts on a solitary, short cystophore, deviating from the typical in one or more of the following respects: (1) irregular in shape in that two or three form together to appear as a lobed mass, or with two or three flat sides, or irregularly oval in shape; (2) cystophore lacking completely which, in fact, seems to be the rule, since the majority appear to fruit sessily on substrate or on fungus hyphae, lichens, etc. Fruiting bodies almost always solitary, but near many others appear as large clusters, probably all arising from the same vegetative mass. Cysts glistening orange, both when fresh and when dry; relatively uniform in size, ranging from globes 25-30μ in diameter to irregular shapes 35 x 55μ; dirty

yellow-orange in transmitted light, rods within easily discernible in definite packets. Cystophores hyaline with a slight milky tinge; often lacking and/or misshapen; ranging in length from unmeasurable shortness to 35-40μ; about 10μ wide regardless of length; very deciduous from the cyst, impossible to mount intact; very fragile, often breaking into indefinite pieces when mounted. Spores adhering in closely packed masses even when freed from the cyst; long and flexuous, 0.7 x 3.0-4.8μ, with the majority being about 4.5μ long; stain avidly and uniformly with aniline blue dye; squarish ends; anything but straight, since they appear to be curved and twisted around each other; when teased apart, all sorts of curves and S-shapes are apparent. Vegetative cells cylindrical, slightly tapered; 0.6 x 5-7μ.

Material examined: Type collection from Farlow Herbarium. One occurrence found during the current study.

Recorded collections: Thaxter, Connecticut, 1892; Thaxter, Indiana and Massachusetts, 1904; Quehl, Germany and Norway, 1906; Current study, Missouri.

P. lichenicolum occurred only once on a piece of bark of Acer rubrum collected in April, 1955. The tree was grow-

ing high on a slope above a ravine in a relatively dry situation at the Pinnacles, Missouri. This one occurrence consisted of literally hundreds of fruiting bodies scattered over an area of bark about one inch by one-half inch in size.

P. lichenicolum has not been reported for a great many years. It was originally described by Thaxter (1892) as parasitizing lichens and destroying them. The current observations tend to bear out this characterization, since a great mass of decomposed lichens was found on the bark substrate below the myxobacterial fructifications. However, observations on this particular piece of bark did not start soon enough to make any definite statements as to whether or not the myxobacteria had any responsibility for such decomposition. Thaxter later (1904) reported finding P. lichenicolum on species of algae on wet boards in a mill race and on lichens sent to him from Indiana. In the same paper, he stated that Zukal had reported the species from Austria. Quehl (1906) reported P. lichenicolum on rabbit and goat dung from Norway and on rotten leaves from Berlin. In spite of these several collections of this particular myxobacterium, the descriptions of it were extremely sketchy and the majority of the characteristics stated in the above diagnostic paragraph were contributed from the observations made on the specimens found on the bark of living trees during the course of the current study.

The arrangement of the spores within the cyst is worthy of special elaboration, since it has not been mentioned by any of the previous observers and since it is a striking characteristic. When the intact cysts are mounted on a slide and viewed in transmitted light, the spores within the cyst, easily discernible, give the effect of a roughly woven basket of several layers. Alternating packets of spores in end-view and in side-view appear across any one plane of focus. When the focus is changed, another layer of packets lying essentially opposite to the layer above (or below) it can be seen. Under pressure, the cysts break apart easily and free the spore mass within, but the rods still remain closely packed together in packets. Furthermore, several packets usually adhere together to produce squarish and rectangular masses of rods.

P. lichenicolum cysts were sown on all seven of the substrates in use with no results and this was repeated on all five of the agar substrates, again with no success. Since Thaxter has stated that cysts germinated readily when sown on moist lichens, four pieces of elm bark and two of oak, all of which had a heavy covering of lichens on them, were sterilized and sown with cysts. After three weeks, the pieces of bark were completely dry and no evidence of myxobacteria was found on any of them.

A collection of fine material, borrowed from the Farlow Herbarium, was examined and compared with the specimens

found on bark of living trees. This material was some of Thaxter's original collection and was designated as "Type." Thaxter has described the cysts of P. lichenicolum as being bright red, but 60 years of preservation in herbaria have taken their toll, since his specimens are now dirty gray-white with only the faintest trace of color apparent on very close examination. Although there had been some doubt as to the accuracy of designation of the organism found on bark before these specimens from the Farlow were seen, no such doubt existed after examination and comparison of the herbarium specimens.

Podangium gracilipes (Thaxter) Jahn

Bot. Gaz., 23:406. 1897.

Chondromyces gracilipes Thaxter, as cited above.

Podangium gracilipes (Thaxter) Jahn, Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Type: Specimens labeled Chondromyces gracilis; collected by H. H. Groves and determined by Thaxter in Lexington, Massachusetts, in April, 1895; bearing Thaxter's Accession No. 4514; on deposit in the Farlow Herbarium.

Fruiting bodies consisting of a solitary cyst on a definite, constant cystophore; small, totaling just under 50μ. Cysts globose to oval; 20-35μ in diameter when globose, those which are oval being 4-5μ longer than they are wide; mostly orange-red,

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but ranging to red on one extreme and to pale whitish-orange on the other; caducous; in transmitted light, almost hyaline in color with only a slight tinge of yellow; cyst wall not at all prominent; under magnifications of 1000X, fine hairs or spines can be seen on the wall; spores within easily discernible, arranged in constant and definite pattern. Cystophores whitish; 10-15μ long, 4-8μ wide; flattened on basal end, rounded on apical end; entrapped rods readily apparent in cystophores, lying perpendicular to the long axis. Spores average 5.0μ long, ranging from 0.5-0.8 x 3-6μ; stain well and uniformly with aniline blue dye; tapering toward the ends; curved once or twice. Vegetative cells with squarish ends, only slightly tapering; 1 x 5-10μ, averaging 7.5μ long.

Material examined: One type collection on deposit in the Farlow Herbarium. Twenty-six occurrences on bark of living trees during the current study.

Recorded collections: Thaxter, Massachusetts, 1897; Quehl, Germany, 1906; Kofler, Vienna, 1913; Jahn, Germany and Norway, 1924; Krzemieniewski and Krzemieniewska, Poland, 1928; Current study, Michigan, Illinois, Florida, Jamaica and Missouri.

This beautiful, minute species of myxobacteria had been reported from this country and from Europe on a half-dozen occasions over the past 60 years, but always on dung or from soil. During the course of the current study, it was found on bark of living trees from Michigan, Illinois, Florida, Jamaica and from five different locations in Missouri, for a total of 26 occurrences. In nearly all of the 26 occurrences, the fruiting bodies were found in tremendous profusion, each occurrence usually consisting of hundreds of solitary, tiny fruiting bodies.

The walls of the cysts of P. gracilipes are so thin and transparent that they are difficult to see in a microscopic mount. However, they are tough enough so that they persist fairly well during mounting. The spores within the cysts can readily be seen through the wall and are arranged in a constant, characteristic manner. When a cyst is seen from the side and when the focus is on the equator of the cyst, the rods within appear in end-view, but when a cyst is seen from either end, with the focus on the equatorial region, the spores appear in longitudinal view and radiate irregularly around the periphery of the cyst. However, as the focus is changed from the equatorial region in either instance, both longitudinal and end views of the rods appear.

Thaxter calls the cysts caducous and, indeed, they are fragile when disturbed. However, some pieces of bark with P. gracilipes on them have been kept and moved about by the

writer for five years without affecting the fruiting bodies in the least. Furthermore, Thaxter's type collection, which is 60 years old and which has been sent through the mail at least once, is still completely intact. When the fruiting bodies are touched with a needle, the cysts immediately fall off, leaving the whitish cystophores on the bark substrate. It has been impossible for the writer to mount a complete fruiting body, although, of course, cysts and cystophores have been readily mounted separately. The extreme deciduous nature of the cysts is probably explained by the rounded apical end of the cystophore. Thaxter has described the apical end of the cystophore as being "pointed," but the writer feels that "rounded" describes the cystophores of the specimens found on bark much better.

As has been noted in the descriptive discussion of Archangium primigenium, P. gracilipes and A. primigenium have often been found occurring in close association with one another. Whether or not there is any real association between the two is not indicated, but they do grow well together in the same culture. P. gracilipes produced pale pinkish-yellow colonies on Rabbit Dung Decoction Agar, Bark Decoction Agar and Rabbit Dung Pellet Plates in four days and fruiting bodies were produced on the surface of the agar and on the pellets in a week.

Podangium alboracemum n. sp.

Etymology: Latin, albus, white; Latin, racemus, stalk.

Fruiting body a single cyst on a long, white irregularly corkscrewed cystophore; 85-250μ tall, 125μ average. Cysts irregular globes; pale orange; crystalline; 35μ in diameter; bounded by an elastic, indiscernible membrane when fresh. Cystophore 4-6 times as long as cyst diameter; 20μ wide; snowy-white; sharply angled and irregularly corkscrewed; composed of amorphous material. Spores 0.8 x 2.5μ, slightly curved; difficult to separate from cyst and from each other. Vegetative cells 0.8-1.0 x 4.5-5.0μ; no tapering apparent; square ends.

Type: Peterson No. 282-3 (Slide).

Type locality: Round Spring, Missouri.

This organism is perhaps the most distinctive and striking of the 30 species found during the course of this study. It occurred on only two different pieces of bark, both Ulmus americana, but from quite different locations in Missouri. One tree was growing at Round Spring, Missouri, and the bark was collected in May, 1956. The other tree was growing near Perryville, Missouri, and the bark was collected in March, 1956. Both trees, however, were growing in moist, wooded river bottom areas. One occurrence consisted of from two to

three dozen fruiting bodies and a dozen fruiting bodies were counted on the other piece of bark.

The fruiting bodies of P. alboracemum consist of a single cyst on the end of a long, snowy-white, irregularly corkscrewed cystophore. The structure presents a very ungainly picture because the length of the cystophore is from four to six times the diameter of the cyst. The fruiting bodies are small, averaging about 125μ in total height, and barely discernible at 15X magnification under the stereoscopic microscope.

The cysts are irregular globes, pale orange and crystalline in reflected light. In transmitted light, they appear hyaline with only a trace of orange or yellow color. They are bounded by a wall which is distinctly gelatinous and elastic and quite indiscernible, but which is tough enough to hold the cyst together during rather harsh treatment. The spores within the cyst are clearly visible and show no particular orientation.

The cystophores of P. alboracemum are most striking and suggested the specific name which has been assigned to the organism. They are pure snowy-white by reflected light, but completely hyaline by transmitted light. Before mounting, they are sharply angled in irregular-corkscrew fashion in a striking, but undescribable, manner. The cystophores are composed of amorphous material which is very uniform in appearance and in which no vegetative cells or other structures

are found. This material has very little affinity for aniline blue and the cystophore stains only a faint blue.

When the first occurrence of this organism was found, some notations were made and the piece of bark was set aside for further study at a later date. Some time later, when the second occurrence presented itself in a moist, formative state, the first piece of bark was again observed. Absolutely no trace of the fruiting bodies on the first piece of bark could be found, although every millimeter of the bark was examined under 90X magnification. The first piece of bark was rewet in an effort to get the organism to complete its life cycle again, while photographs and critical notations were made of those fruiting bodies of the second occurrence. Vegetative cells were seen in mounts made from material taken directly from the bark as such material was rising into fruiting bodies. Before cysts of the second occurrence could be transferred to agar media, they too had deliquesced and disappeared. Both pieces of bark were rewet twice, but the fruiting bodies were never again seen.

In view of the above, neither specimens nor cultures of P. alboracemum are in existence. However, excellent photographs and microscope slides are documentary evidence of the existence of this will-o-the-wisp organism.

Podangium cylindricum n. sp.

Etymology: Greek, kylindrikos, cylindrical

Fruiting bodies consist of a cylindrical cyst on a short cystophore, many arising from a common hypothallus-like base to produce an aggregate of fruiting bodies; aggregates up to 350μ in size and containing 70-100 fruiting bodies. Cysts brownish-orange; up to 40 x 105μ; rounded at apex, square at base. Cystophores whitish at base, gradating to yellow at apex; irregular in size, usually 1/4 to 1/3 as long as cyst and 1/2 as wide; composed completely of rods in dried slime. Cyst contains oily globules and spores; oily globules sometimes large and prominent, sometimes very small. Spores 0.8 x 2.5-3.5μ; slightly curved; tapering toward both ends; mostly crescent-shaped. Vegetative cells 3.5-5.5μ long, occasionally up to 7.0μ; 1.0μ in center of cell in width, tapering toward both ends; straight. Vegetative colony yellowish in center, pink at periphery.

Type substratum: Bark of Cupressus sempervirens (Alexopoulos, GR-180)

Type locality: Olympia, Elis, Greece

P. cylindricum occurred only once on a piece of bark of Cupressus sempervirens gathered by Dr. C. J. Alexopoulos in April, 1955, at Olympia, Elis, Greece. This single occur-

rence, however, consisted of several hundred fruiting bodies scattered all over the piece of bark.

Although the fruiting bodies of this one occurrence were a little over a year old, profuse culture, in almost initially pure colonies, was readily accomplished. Vegetative masses and some fruiting bodies were produced four days after seeding on Rabbit Dung Pellet Plates and Bark Decoction Agar, and vegetative growth without fruiting bodies was found on Rabbit Dung Decoction Agar and Bacterial Suspension Agar. Growth was extremely good on Rabbit Dung Decoction Agar, but no fruiting bodies were formed on this medium. On the other hand, excellent and rapid fruiting occurred on the Rabbit Dung Pellet Plates. The other two agars were very inferior in supporting either growth or fruiting. After two weeks, many aggregates of fruiting bodies were observed on the Sterile Elm Bark, in spite of a heavy blanket of fungus contamination.

P. cylindricum has very definite similarities to P. erectum and even though the writer has strong tendencies toward being a "lumper," he believes that the two are different organisms. The reasons for this conclusion are: (1) the size and shape of the cysts differ in the two organisms; (2) the cystophores of P. cylindricum are composed of rods, whereas those of P. erectum are composed of slime without prominent rod inclusion; (3) the oily globules in the cyst contents of P. cylindricum have not been reported in the

literature for P. erectum and could not be found in any of the specimens of P. erectum from bark; and, (4) both the spores and the vegetative rods of P. cylindricum are somewhat larger than those of P. erectum, although they look much like their respective counterparts except for this difference in size.

The one piece of bark, on which the type material of P. cylindricum was found, has been deposited in the University of Missouri herbarium. Fruiting bodies which are the result of transfers and cultures will be distributed to other herbaria in the future.

Genus Chondromyces Berkeley & Curtis

Berkeley, Introduction to Cryptogamic Botany. London. 1857.

Key to the species on the bark of living trees

1. Cystophore branched
    2. Cysts borne in clusters at apex of branches ..... C. crocatus
    2. Cysts borne in chains ..... C. catenulatus
1. Cystophore essentially unbranched
    3. Cysts cylindrical ..... C. cylindricus
    3. Cysts globose or oval
        4. Cysts with apical appendage ... C. apiculatus
        4. Cysts without apical appendage; borne on thin stipe of dried slime
            5. Spores allantoid ..... C. minor
            5. Spores rod-shaped; ends square ..... C. medius

Chondromyces crocatus Berkeley & Curtis

Berkeley, Introduction to Cryptogamic Botany. 313. London. 1857.

Myxobotrys variabilis Zukal, Ber. Deutsch. Bot. Gesells., 14:340. 1896.

Neotype: A collection labeled "601. Chondromyces crocatus B. & C."; on horse dung in laboratory culture; Cambridge, Massachusetts; cultured and determined by Thaxter; the specimen box contains a note giving Thaxter's Accession No. 5168; undated; on deposit in the New York Botanical Garden.

Fruiting bodies consisting of a branched cystophore with spherical heads of straw-colored cysts at the apex of each branch; averaging 600μ over-all, occasionally 1 mm. Cysts conical, rounded at apex; 6-20 x 15-45μ, averaging 12 x 28μ; straw-yellow in both reflected and transmitted light. Cystophores orange to dark brown; slender, striated, often twisted and irregularly bent; typically branched several times. Spores uniformly 0.5μ wide, ranging in length from 1.2-4.5μ, averaging about 2.3μ; essentially straight with rounded ends; beaded upon staining with aniline blue, usually with three deeply-staining beads, but longest spores possess four such beads and the shortest show only two. Vegetative cells

cylindrical or slightly tapering; straight or slightly curved; 0.6-0.7 x 2.5-6.0μ. Vegetative colony pale orange-red.

Material examined: Thirteen collections, originally of Thaxter's, now on deposit in the Farlow Herbarium. Two collections, one of Thaxter's and one from the collection of George Massee, now on deposit in the New York Botanical Garden. Three occurrences found during the current study.

Recorded collections: Berkeley & Curtis, South Carolina, 1857; Berkeley, 1874; Thaxter, Massachusetts, 1892; Zukal, Vienna, 1896; Thaxter, Connecticut, 1904; Thaxter, 1904, also records C. crocatus as being found by Setchell in Iowa, Metcalf in Florida and Laubach in Java; Quehl, Germany, 1906; Jahn, Germany, 1924; Krzemieniewski and Krzemieniewska, Colombia, 1946; Hesseltine & Fennell, Iowa, 1955; Current study, Missouri.

C. crocatus was found a total of three times during the course of the current study, once each on Ulmus rubra, Acer saccharum and Quercus alba bark. The Ulmus rubra bark was collected from a tree growing at Providence, Missouri, high on a dry, southerly-exposed ridge, and both of the other two pieces of bark were gathered from trees growing in a heavy, mesic forest near Holstein, Missouri. All three occurrences consisted of only a few, small, atypical, malformed fruiting bodies.

When these specimens were first found on bark, detailed observations and data concerning them were recorded, but there was considerable question about their true identity. Some time later, a magnificent collection of C. crocatus was borrowed from the New York Botanical Garden and studied. In the face of these beautiful specimens, those found on bark shone as coal in a jeweled throne-room! Study of the New York Botanical Garden specimens, which had been contributed by Roland Thaxter, verified the identification of the bark specimens as C. crocatus. The specimens found on bark were so few and so atypical that they have contributed nothing to the above diagnostic paragraph of C. crocatus except the data concerning the spores, which were previously undescribed.

There are thirteen packets of C. crocatus on deposit in the Farlow Herbarium and two more on deposit in the New York Botanical Garden. All of these collections have been contributed by Thaxter, with the exception of one of the New York Botanical Garden collections, and all of them have been examined by the writer. A large number of these specimens are laboratory cultures, which Thaxter made, and several of them do not have any notation of date. Consequently, it was somewhat difficult to arrive at a definite conclusion as to which one should be designated as the neotype. After weighing all of the evidence, however, it is the writer's opinion that the collection described above is the proper neotype material.

Chondromyces cylindricus Krzemieniewski & Krzemieniewska

Acta Soc. Bot. Pol., 7:260. 1930.

Neotype: Specimens on a piece of bark of Ulmus americana (Peterson No. 217-e-2) on deposit in the University of Missouri herbarium.

Fruiting bodies are globose clusters of cylindrical cysts at the apex of a straight cystophore; bright yellow when moist, turning orange-brown with desiccation, cystophore darkening first and becoming browner than the cysts; usually solitary, but occasionally three or four fused together on a common hypothallus-like base; ranging from 100-300μ tall, averaging 200-225μ; globose cluster of cysts usually about 90-100μ in diameter. Cystophores usually unbranched, occasionally branched into a "Y" or into a few short branches near apex; 120-220μ long, averaging about 160μ; mean width 8-14μ; expanded into hypothallus-like base; slightly expanded into a globose club, with many irregular protuberances to which the cysts are attached, at the apex; bright yellow when mounted and seen in transmitted light; resistant to aniline blue dye; composed of bundles of cells according to the Krzemieniewskys, but the cystophores of those on bark are composed only of

dried slime, slightly striated and ridged. Cysts varying from irregularly rounded to cylindrical, with the majority definitely and uniformly cylindrical with rounded apical ends; 10-50 x 25-90μ in size; yellow in transmitted light, sometimes with a greenish tinge; cyst contents stain avidly with aniline blue, wall resistant, remaining yellow; according to Krzemieniewskys, borne on a slender stipe 20μ long which shrinks down with maturity so that cysts become sessile; rather commonly fused together at apical ends to form a reversed "Y" with two points of attachment. Spores 0.6-1.1 x 1.8-4.7μ; straight or slightly curved with squarish ends; stain well and usually uniformly with aniline blue, occasionally appearing somewhat irregularly stained and bumpy along length; adhere quite tightly together. Vegetative cells long rods, tapered at ends; 0.5-0.6 x 6.7-11.0μ. Vegetative colony thick, yellowish-green.

Material examined: Ten occurrences on bark during the current study.

Recorded collections: Krzemieniewski & Krzemieniewska, Poland, 1930; Current study, Missouri.

C. cylindricus has been reported previously only by the Krzemieniewskys (1930) who isolated it from Polish soil.

During this study, it was found on 10 different pieces of bark, the first two of which were collected from the same Ulmus americana. This tree was growing in a shady, moist habitat along a stream at Duly Mill, Missouri, and the bark from it was collected in April, 1955. In both instances, the occurrence consisted of several hundred fruiting bodies scattered over the entire piece of bark, which was about two inches long by three-quarters of an inch wide.

Some time later, in March, 1956, C. cylindricus was found on seven different pieces of bark from a Nyssa sylvatica growing near Perryville, Missouri, in a moist, heavily wooded bottom-land area. Many fruiting bodies made up these seven occurrences, but, in all cases, they were rather poorly formed, they were more orange in color, and they possessed a darker cystophore than the previous collections. The final occurrence of this species was found on a piece of bark collected in June, 1956, from a Fraxinus americana growing in a heavy forest habitat near Holstein, Missouri. This collection was meager, but typical and well formed.

The Krzemieniewskys designated C. cylindricus as a separate species from its closest relative Chondromyces aurantiacus (Berkeley & Curtis) Thaxter, on the basis of the differences in the cysts. The cysts of C. cylindricus, seen in this study, so beautifully fit the name of the species given by the Krzemieniewskys that there was no question of identification from the first time the species was observed.

The cysts of the specimens found on bark are quite definitely and uniformly cylindrical and, in fact, are apparently more uniform than were those described by the Krzemieniewskys.

Cysts of C. cylindricus were sown on all seven substrates and placed in all five Van Tieghem solutions. No growth was observed until, after three weeks, a few fruiting bodies were found on both Sterilized Elm Bark and Sterilized Oak Bark. Because of the dark substrate, no observations could be made on the vegetative colony, which the Krzemieniewskys say is greenish-yellow, but microscopic mounts were prepared from watery slime around these fruiting bodies and myxobacterial vegetative cells, the size of which fell adequately within the ranges given by the Krzemieniewskys, were found. Attempts were made to transfer both this watery slime and the newly formed fruiting bodies to agar substrates, but without results. All of the seven substrates were again seeded with the original cysts, but no further growth was attained.

Chondromyces apiculatus Thaxter

Bot. Gaz., 23:405. 1897.

Type: On Liberian deer dung; determined by R. Thaxter; from Africa; dated 1897; bearing Thaxter's Accession No. 4481; on deposit in the Farlow Herbarium.

Fruiting bodies consist of 1-4 dozen cysts in a spherical head on the terminus of a simple,

straight cystophore; from 200μ to 1 mm. tall, averaging about 400μ; spherical head of cysts about 200μ in diameter; pinkish-orange in color when immature, definite orange when dry and mature. Cystophores average about 300μ in length by 10-20μ in width; whitish-orange and glistening by reflected light, bright yellow by transmitted light; flared out at basal end, but not to the point of being a real hypothallus; slightly expanded, squarish at apical end, with ragged appearance due to numerous points of attachment of cysts; of dried slime without included cells, longitudinally striated, rigid, stiff, persistent. Cysts from cylindrical to turnip-shaped; 30-50μ, with only 4-5μ differences in length and width; bright orange, dull when mature in reflected light, bright yellow in transmitted light; wall yellow, tough, transparent enough to allow spores within to show, taperingly wrinkled toward both ends into apical appendage 70-80μ long, continuum of the cyst wall; stipe at base less than 50μ long, also a continuation of cyst wall; occasionally, two cysts fused together at base with only one cystophore attachment, but with two apical appendages. Spores uniform in size, measuring about 0.7 x 3.5μ;

usually straight with square ends; take aniline blue well, but with some lack of uniformity within individuals. Vegetative rods apparently very variable; Thaxter describes them as being 1 x 3-20μ, sometimes longer; Kofler (1913) states they are 3-5μ long; Kuhlwein (1952) describes them as being 9μ.

Material examined: Five packets, one of them a Type, of Thaxter's collections; all now on deposit in the Farlow Herbarium. Five occurrences on bark during the current study.

Recorded collections: Thaxter, Africa, 1897; Thaxter, Philippine Islands and Florida, 1904; Baur, Germany, 1905; Quehl, Germany, 1906; Kofler, Vienna, 1913; Kuhlwein, Germany, 1952; Current study, Missouri.

This beautiful and distinctive species of myxobacterium occurred a total of five times during the course of these observations. Four of these occurrences were on different pieces of bark collected from the same tree, a Juniperus virginiana, growing in a country churchyard in northeast Boone County, Missouri, in an open, dry situation, and collected in May, 1955. The fifth occurrence was on a piece of bark collected in March, 1955, from a Juglans nigra growing in a shady, moist, bottom-land habitat in the Ashland Wildlife Area at Ashland, Missouri. In all, about 200 fruiting

bodies were found on these five pieces of bark. Previous to the current report, this species had been observed only on dung.

Chondromyces medius Krzemieniewski & Krzemieniewska
Acta Soc. Bot. Pol., 7:263. 1930.

Neotype: Specimens on bark of Laguncularia racemosa (Alexopoulos, Fla-24c) on deposit in the University of Missouri herbarium.

> Fruiting bodies consist of a straight, whitish cystophore bearing a number of long, whitish stipes on each of which is an orange cyst; from 4-5 to 18-20 cysts per fruiting body; from 70-140μ in height, averaging about 120μ. Cystophores white in reflected light, yellow to pink in transmitted light, usually gradating from pink near the base to yellow at the apex; base rounded or square without any suggestion of a hypothallus, not closely appressed to the substrate; apex expanded or club-shaped, roughly irregular because of points of attachment of stipes; characteristically bulged in the center; 30-50 x 100-130μ in size, although smaller ones, and a few larger ones, may be found; cells included, giving a "bundle effect" according to the Krzemieniew-

skys, but producing a stippled effect in those found on bark; branching or straight. Cysts glistening yellow-orange in reflected light, bright yellow in transmitted light; variable in shape and size, slight oval to pear-shapes predominating; 20-80 x 25-95μ in size; wall definite, but thin, with the spore mass within easily seen as stipples; wall pinches down into stipe at basal end. Stipe composed of dried slime; white in transmitted light, yellow in reflected light; from as long as the cysts which they subtend to once-and-a-half as long as their cysts (from 20-45μ); about 5μ wide. Spores 0.8-1.0 x 2.2-3.5μ; mostly straight, but those which are slightly curved or slightly club-shaped are not uncommon; ends square; stain well and uniformly with aniline blue dye. Vegetative cells described only as rod-shaped. Vegetative colony colorless to pink.

Material examined: Four occurrences on bark during the current study.

Recorded collections: Krzemieniewski & Krzemieniewska, Poland, 1930; Current study, Florida, Jamaica, Greece.

This species, reported previously only by the Krzemieniewskys when they originally described it, occurred on two

different pieces of bark collected in August, 1951, by Dr. C. J. Alexopoulos from a Laguncularia racemosa growing at Hollywood, Florida. A third occurrence developed on a piece of bark collected from a Terminalia catalpa in July, 1952, at Runaway Bay, Jamaica, again by Dr. Alexopoulos. A final occurrence, again on bark collected by Dr. Alexopoulos, was found on a piece of Quercus sp. bark collected in April, 1955, from a tree growing at Olympia, Greece. In all four cases, the occurrences consisted of two or three dozen fruiting bodies over an area of about 10 mm. square.

Cultural attempts were made on all seven substrates without success. Further attempts were not made because of the meager amount of material available.

There does not seem to be much doubt that the specimens found on bark are correctly identified as C. medius. Those found on the bark from Greece were originally identified tentatively as Chondromyces pediculatus Thaxter, but further study and reflection proved them to be the same as the specimens making up the other occurrences. The final conclusion is that all four occurrences found in this study are the same organism and that this organism is Chondromyces medius Krzemieniewski & Krzemieniewska. The most striking characteristic of the specimens found on bark and of the specimens which the Krzemieniewskys described as C. medius is the long stipe on which the cysts are borne. This was also the outstanding character of Thaxter's C. pediculatus, a species

which has never been reported since the original description. Thaxter's specimens were larger and produced cysts of different shape than does C. medius, but it seems possible, in view of Thaxter's meager description of C. pediculatus, that the two could be the same.

Chondromyces minor Krzemieniewski & Krzemieniewska
Acta Soc. Bot. Pol., 7:265. 1930.

Neotype: Specimens on a piece of bark of Ulmus rubra (Peterson No. 205-a) on deposit in the University of Missouri herbarium.

Fruiting bodies consist of clusters of cysts on the apices of a sparsely-branching cystophore; about 100μ tall; cysts per cluster variable from only 2-3 to 20-24; cysts connected to cystophore on short, indefinite stipes which appear to be wrinkled, tapering extensions of the cyst walls. Cystophores 40-60μ long by 10-15μ wide, sometimes larger in both measurements; very light, dirty orange-brown to white in reflected light, light yellow in transmitted light; stippled in appearance, but such stippling not due to included cells; hypothallus sometimes present at basal end; no obvious points of attachment at apical end. Cysts 20-47 x 20-65μ, averaging about 28 x 38μ; variable in shape, short oval to pear-shaped;

rose-red when immature, becoming copper-red to orange when dry; wall yellow in transmitted light; no affinity for aniline blue; wrinkled and folded at basal end as it tapers into the stipe-like attachment, 10-25μ long; cysts very deciduous. Spores of specimens found on bark are 0.5 x 1.2-2.4μ, very uniform; ends rounded; curved to resemble tiny sausages; hyaline when unstained, but take aniline blue avidly; the Krzemieniewskys describe the spores only as being 0.6-0.8 x 2.9-4.3μ. Vegetative cells 0.6 x 3.8-7.2μ. Vegetative colony reddish-violet.

Material examined: One occurrence on bark during the current study.

Recorded collections: Krzemieniewski & Krzemieniewska, Poland, 1930; Current study, Missouri.

Only one occurrence of this species has been found during the course of this study. This occurrence consisted of some three dozen fructifications scattered over an area of bark about one centimeter square. The species developed on a piece of bark collected in March, 1955, from an Ulmus rubra growing on a southerly-exposed slope in a fairly dry, wooded situation near Providence, Missouri. Because of the meager amount of material available, no cultural attempts were made.

The only possible recognized species to which these specimens found on bark could be assigned is C. minor as described by the Krzemieniewskys (1930). The species has been reported by no other observer except the original describers and, therefore, some of the minor discrepancies between their descriptions and the current specimens cannot be considered too seriously.

Chondromyces catenulatus Thaxter

Bot. Gaz., 37:410. 1904.

Type: Four boxes in two packets, both of which are labeled "Type"; the material in all four boxes appears to be the same and both packets are labeled exactly alike, except for different accession numbers; labeled Chondromyces catenulatus Thaxter; on dead wood of Populus (on one packet), on poplar log (on the other packet); Hanover, New Hampshire, 1904; collected by G. R. Lyman, determined by R. Thaxter; bearing Accession No. 4518 on one packet, Accession No. 7258 on the other packet; all on the same herbarium sheet in company with three other collections of what appear to be the same material; on deposit in the Farlow Herbarium.

Fruiting bodies consist of cystophores which divide near apical end into several branches, from each of which arise a chain of cysts; appears to be a tiny, orange weeping willow; up to 400μ tall. Cystophores mostly ribbon-shaped, 80-100 x 10-15 x

3-5μ for those found on bark, but Thaxter's specimens often much larger, up to 360μ tall; sometimes broadened at base, but not usually hypothallus-like; of striated, yellow, dried slime, resistant to aniline blue dye; lower half of cystophore containing few imbedded cells, upper half packed with spore-like rods; branching at apex into branches up to 30μ long, branching portion almost white in color, apices pointed and slightly swollen; glistening in reflected light. Cysts 10-18 x 20-50μ; predominantly oval; yellow-orange in reflected light, yellow in transmitted light; dull; produced in chains up to 300μ long, sometimes branching once or twice; separated by short isthmuses of shriveled, dry slime; walls resistant to aniline blue, but spore mass within staining avidly and heavily. Spore mass contains rods, oil globules and tiny globose inclusions; spores slightly bean-shaped, 0.6 x 1.5-2.0μ; oil globules bright orange, variable in size from 1-25μ, no affinity for aniline blue; tiny globose inclusions take aniline blue, measure 1-3μ, perfectly spherical. Vegetative cells 1-1.3 x 4-6μ.

Material examined: Seven boxes, labeled as four collections, two of which are Types, all on the same herbarium

sheet; borrowed from the Farlow Herbarium. One collection from the New York Botanical Garden, contributed by Thaxter and, apparently, a portion of the same material as the Farlow material. One occurrence on bark during the current study.

Recorded collections: Thaxter, New Hampshire, 1904; Current study, Jamaica.

C. catenulatus was produced on a piece of bark from an unknown species of tree growing near Bath, Jamaica, and collected by Dr. C. J. Alexopoulos in July, 1952. There were an estimated 150 fruiting bodies scattered over the piece of bark, which was about two inches by one inch in size. In one area of about 30 square millimeters, the fruiting bodies were so profuse that a distinct orange powderiness could be seen with the unaided eye.

Thaxter described C. catenulatus in 1904 on rotten poplar wood from New Hampshire and he reports that, although the organism would renew itself readily on the original substrate, he could not culture it in any other fashion. This is the only record of this species in the literature. Current attempts to culture the organism have met with only slightly better success than those of Thaxter 50 years ago. On one occasion, success in getting a very heavy vegetative growth of C. catenulatus on Rabbit Dung Decoction Agar was attained, but attempts to subculture it on various other

media were unsuccessful. Eventually, the original culture was overgrown with contaminants and lost without ever producing fructifications. Foolishly, no slides or measurements of the vegetative cells were made, but Thaxter did provide measurements of the vegetative cells in his original paper.

Four years after this one cultural success, further efforts to grow C. catenulatus were made. The herbarium box containing the bark on which the species was found was borrowed from the Michigan State University herbarium and cysts were seeded onto all seven substrates and into all five Van Tieghem solutions. No germination or growth was found.

There are differences in size and a few differences in form between Thaxter's specimens and the specimens found on bark. Several details of which Thaxter makes no mention have been reported above. In spite of these differences and because of the very striking manner of production of the cysts in chains, there is no question that both collections have been of the same organism. This characteristic production of the cysts in chains is so striking, in fact, that it is difficult to understand why this lovely, little organism has not been seen by other observers in the past 50 years.

Family Myxococcaceae Jahn

Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Key to the genera on bark of living trees

1. Spores in masses; never in definite cysts

2. Slime of mature fruiting body deliquescent and indiscernible ... Myxococcus

2. Slime of mature fruiting body persistant and fully discernible ..... Chondrococcus

1. Spores contained in definite cysts ..... Angiococcus

Genus Myxococcus Thaxter

Bot. Gaz., 17:403. 1892.

Key to the species on bark of living trees

1. Vegetative colonies reddish; spores less than 1.5μ in diameter ..... M. fulvus

1. Vegetative colonies yellow-green; spores 1.75μ or larger in diameter .. M. virescens

Myxococcus virescens Thaxter

Bot. Gaz., 17:404. 1892.

Neotype: Specimens on a piece of bark of Ulmus americana (Peterson No. 212-h-1) on deposit in the University of Missouri herbarium.

Fruiting bodies rounded cushions or low pillars; directly on substrate, no suggestion of stipe or basal constriction; mostly about 100μ, ranging up to 500μ on occasion; dirty white, tan, yellow, greenish, or orangish in color; those which are white to greenish are dull and opaque in reflected light, those which are orangish are shiny and translucent; these two color phases

(whitish-greenish and orangish) are constant during culture of several weeks. In transmitted light, white-green phase fruiting bodies are colorless, the orange phase retain a strong orange color; no membrane, wall or slime discernible around fruiting body, but a sharp line of demarcation is apparent on the edges of some; a strong adhesive effect between the spores keeps the fruiting body intact during mounting. Spores perfectly spherical, perfectly uniform in any given fruiting body; 1.75μ in diameter in the white phase fructifications, 2.0-2.5μ in the orange phase; possessing an easily discernible wall, even when unstained; highly resistant to aniline blue dye. Vegetative cells slender, gently tapering, irregularly curved, squarish ends; 0.4-0.5 x 3-7μ, averaging about 0.5 x 5.0μ. Vegetative colony greenish-yellow.

Material examined: One strain obtained in culture from the American Type Culture Collection. Four occurrences on bark during the current study.

Recorded collections: Thaxter, New England, 1892; Jahn, Germany, 1924; Krzemieniewski & Krzemieniewska, Poland, 1926; Badian, Poland, 1930; Solntzeva, Russia, 1940; Sniesko, et al., Maine, 1943; Singh, England, 1947; Finck, Germany, 1950;

Noren, Sweden, 1950; Noren, England, 1951; Oetker, Germany, 1953; Current study, Michigan, Missouri.

M. virescens was first found on a piece of Ulmus americana bark collected on the campus at Michigan State University sometime in the early winter of 1950-51. The occurrence consisted of about five dozen fruiting bodies over an area about 10 mm. square. The second occurrence appeared, again, on Ulmus americana bark collected in April, 1955, from a tree growing in an open, dry old-field type of habitat at the Pinnacles, Missouri, and consisted of some 125 fruiting bodies scattered in an area about 10 x 20 mm. in size. The last two occurrences were on bark from Quercus rubra and Quercus alba growing near Perryville, Missouri, and Holstein, Missouri, respectively. Both of these occurrences consisted of a profusion of fruiting bodies and all of them were of an orange phase, as opposed to the whitish phase of the first two collections.

The wall surrounding the spores of M. virescens is worthy of special mention. None of the spores of the other four representatives of the Myxococcaceae observed during this study have walls as pronounced as those seen on the spores of M. virescens, yet no particular point has been made of this wall in the literature. Some of Badian's photomicrographs (1930) appear to show it, however. This wall is hardly thick enough to be measured, but it does show up very clearly, even in unstained preparations. In fact, the

spores of M. virescens do not take aniline blue dye at all well, presumably because of the presence of this wall. In mass, stained spores appear only a slight blue-gray in color and individual spores show no effect at all of staining.

M. virescens is an easy organism to grow in pure culture. It was grown during the course of this study on Rabbit Dung Decoction Agar, Bacterial Suspension Agar, Bark Decoction Agar and Rabbit Dung Pellet Plates. Both of the color phases described above were grown and transferred with no apparent differences in colony color or in vegetative cell morphology.

The strain of M. virescens in possession of the American Type Culture Collection is the only other specimen that could be located. Since living cultures cannot be designated as types after they have been transferred, the collections on bark have been designated as neotype material and will be retained in the University of Missouri herbarium.

Myxococcus fulvus (Cohn emend. Schroeter) Jahn
Beitrage z. Biol. d. Pflanzen, 1:181. 1875.

Micrococcus fulvus Cohn, as cited above.

Micrococcus fulvus Schroeter, Cohn, Kryptogam. v. Schlesien, 3:144. 1886.

Myxococcus rubescens Thaxter, Bot. Gaz., 17:403. 1892.

Myxococcus ruber Baur, Arch. f. Protistenkunde, 5:95. 1905.

Myxococcus pyriformis Smith, Jour. Bot., 39:71. 1901

Lyxococcus javanensis de Kruyff, Cent. f. Bakt., II Abt., 21:386. 1908.

Rhodococcus fulvus Winslow & Winslow, Systematic Relationships of the Coccaceae, 262. 1908.

Myxococcus fulvus Jahn, Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Neotype: Specimens on a piece of bark of Juniperus virginiana (Peterson No. 222-h-2) on deposit in the University of Missouri herbarium.

Fruiting bodies rounded masses of coccoid spores, varying in shape from spherical globes to elongated sausages; sometimes with rather pronounced constriction at base, resembling rudimentary stipe, sometimes with definite slimy stalk present; variable in size, from 35μ up to those 300μ in diameter; wet in appearance, dully glistening, salmon-pink to brownish-red when immature; shiny, transparent, appearing dry and hard, orange to brown when dry. In transmitted light, faint yellowish-pink in color, soon disappearing in lacto-phenol leaving the mass hyaline; no membrane or dried slime discernible around the spore mass. Spores 1.0-1.2μ in diameter; regular in size and shape; usually perfect spheres, but sometimes with flattened sides, presumably due to pressure in mass; stain avidly and uniformly with

aniline blue dye. Vegetative cells 0.4-0.7 x 4-10μ; slender, irregularly curved. Vegetative colony reddish to light flesh color.

Material examined: One culture obtained from the American Type Culture Collection. Three occurrences on bark during the current study.

Recorded collections: Cohn, Germany, 1875; Schroeter, Germany, 1886; Thaxter, New England, 1892; Smith, Wales, 1901; Baur, Germany, 1905; DeKruyff, Java, 1908; Kofler, Vienna, 1913; Jahn, Germany, 1924; Krzemieniewski and Krzemieniewska, Poland, 1928; Solntzeva, Russia, 1940; Sniesko, et al., Maine, 1943; Singh, England, 1947; Noren, Sweden, 1950; Finck, Germany, 1950; Noren, England, 1951; Oetker, Germany, 1953; Current study, Michigan, Missouri, Greece.

The first occurrence of M. fulvus found during the current study was on a piece of bark of an Ulmus americana growing in a parking lot on the Michigan State University campus and collected in July, 1951. It consisted of from three to four dozen well formed, almost completely globose fruiting bodies. The next occurrence was found on a piece of Juniperus virginiana bark, collected in May, 1955, from a tree growing in a country churchyard in Boone County, Missouri. This occurrence was composed of about six dozen fruiting bodies scattered over an area about 15 mm. square.

All of these fruiting bodies occurred individually, but, since they were confined to this small area of the piece of bark, they appeared to have all arisen from the same original mass of vegetative cells. The final occurrence of M. fulvus on bark was on a piece of bark of Juniperus phoenicia collected on the Island of Astypalaia, Greece, in 1955 and sent to Dr. C. J. Alexopoulos. The occurrence consisted of five to six dozen globular-shaped fruiting bodies.

M. fulvus fruiting bodies were seeded on only the five agar substrates. After four days, small, watery, pink colonies were found on all five substrates. Continued growth and fruiting was excellent on Rabbit Dung Decoction Agar and on Rabbit Dung Pellet Plates, but growth did not progress satisfactorily to fruiting bodies on the other three media. Transfers to fresh Rabbit Dung Docoction Agar and Rabbit Dung Pellet Plates were easily made and maintained.

One of the strains of M. fulvus in the possession of the American Type Culture Collection was obtained and compared with the material found on bark. M. fulvus has been reported frequently, but the American Type Culture Collection cultures are the only ones known to the writer. Since such living cultures cannot be named types, the specimens found on bark are designated neotype material and are on deposit in the University of Missouri herbarium.

The key in Bergey's Manual is misleading in stating that the "fruiting bodies are deliquescent" in Genus Myxococcus

and "firm, not deliquescent" in Genus Chondrococcus. Both of the species of Myxococcus seen during this study produce very persistent fruiting bodies. Sufficiently so, in fact, to last over a period of years. The slime which surrounds the spore mass during formation of the fruiting body, however, is deliquescent in Myxococcus as evidenced by the fact that no bounding structure of any type can be found in mature fruiting bodies of Myxococcus species, whereas such a structure is present in representatives of Chondrococcus. On the basis of the two species of each genus observed, this presence or lack of a bounding structure in mature fruiting bodies is the only morphological difference between the two genera.

Genus Chondrococcus Jahn

Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Key to the species on bark of living trees

1. Fruiting bodies simple or coralloid; never producing secondary fruiting bodies ..... C. coralloides

1. Fruiting bodies producing secondary fruiting bodies ..... C. blasticus

Chondrococcus coralloides (Thaxter) Jahn

Bot. Gaz., 17:404. 1892.

Myxococcus coralloides Thaxter, as cited above.

Myxococcus digitatus Quehl, Cent. f. Bakt., II Abt., 16:18. 1906.

Myxococcus clavatus Quehl, as cited above

Myxococcus polycystus Kofler, Sitzber. d. Kais. Akad. Wiss. Wein Math.-Nat. Klasse, 122:856. 1913.

Myxococcus exiguus Kofler, as cited above

Chondrococcus coralloides (Thaxter) Jahn, Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Chondrococcus polycystus (Kofler) Krzemieniewski and Krzemieniewska, Acta Soc. Bot. Pol., 4:46. 1926.

Neotype: Specimens on bark of Ulmus americana (Peterson No. 212-h-2) on deposit in the University of Missouri herbarium.

Fruiting bodies variable in shape, usually irregular pillars, sparsely branching or slightly globose-lobed, coral-like in a scanty fashion; glistening, pale yellow, orange, or rose; usually under 100μ, averaging 25-35μ in width by 50-90μ in height. When mounted and seen in transmitted light, pale yellow; bounded by a persistent, definite membrane of dried slime; membrane not tough, breaking open readily under pressure; wall slightly stained with aniline blue. Spores slightly irregular spheres; 1.0-1.3μ in diameter; strong tendency to adhere together in irregular masses when fruiting body is broken up. Vegetative cells slender, slightly tapering toward both

ends, usually curved once or twice; 0.4-0.5 x 4-7μ. Vegetative colonies pale pink to pinkish-red; watery, rather than slimy.

Material examined: Fifty-seven occurrences on bark during course of the current study.

Recorded collections: Thaxter, Massachusetts, 1892; Kofler, Vienna, 1913; Jahn, Germany, Lapland, Italy, 1924; Krzemieniewski & Krzemieniewska, Poland, 1928; Noren, Sweden, 1950; Finck, Germany, 1950; Noren, England, 1951; Oetker, Germany, 1953; Current study, Missouri, Michigan, Florida, Illinois, Greece.

C. coralloides occurred a total of 57 times on various barks and was the most common organism found during the course of this study. It was found on bark collected from trees growing in Missouri, Michigan, Illinois, Florida and Greece, from trees growing in all sorts of habitats, and on bark collected in different months of the year over a five year period. No purpose would be served in elaborating on the individual species of trees, tree habitats, or dates of collection, as concerns this particular organism. C. coralloides appears to be quite cosmopolitan, since it has previously been recorded on several occasions from various parts of the world. Most of the occurrences referred to above consisted of dozens, and even hundreds, of fruiting bodies in each case.

The specific name of the organism, as affixed by Thaxter (1892), is very descriptive of the form of the fruiting bodies encountered in the great majority of cases during this study. However, there are other forms of this species which do not always appear to be C. coralloides on superficial examination. Two varieties, C. coralloides var. clavatus (Quehl, 1906) and C. coralloides var. polycystus (Kofler, 1913, and Krzemieniewski & Krzemieniewska, 1926) have been reported in the literature and both have been found on bark during the current study. Neither of these varieties is coralloid in form. In addition, various other morphological variations of C. coralloides have been observed occasionally. It must be stressed, then, that this species takes many forms in its fruiting body production and that no description can adequately fit this entire variety of forms.

Several occurrences of what are apparently C. coralloides var. clavatus as described by Quehl (1906) were found during the course of this study. These fruiting bodies were larger than the typical C. coralloides, deeper orange in color, and simpler in structure, since most of them were unbranched pillars. The writer sees no reason why this should be considered as a variety. One point of interest concerning these collections, however, is that they closely resemble Myxococcus fulvus (Cohn emend. Schroeter) Jahn. So closely so, in fact, that until specimens are mounted and

the fruiting body wall of dried slime is either found to be present or absent, they cannot be distinguished each from the other. Since the wall is the only detectable difference between the two organisms, how constant a character its formation would be, or would not be, over a long period of culture is a question of future interest.

In 1913, Kofler described an organism as Myxococcus polycystus. Jahn (1924) considered Kofler's M. polycystus to be only a variety of C. coralloides. The Krzemieniewskys (1926) isolated from Polish soil a myxobacterium which they identified as identical with Kofler's organism, which they felt should be elevated to species rank, and which they named Chondrococcus polycystus. The compilers of the treatment of the Order Myxobacteriales in Bergey's Manual (1948) consider this organism to be a variety, polycystus, of C. coralloides.

One occurrence of what the writer considers to be C. coralloides var. polycystus, after Bergey's Manual, was found on a piece of bark collected in June, 1955, from a Carya ovata growing at Ashland, Missouri. This occurrence consisted of about three dozen fruiting bodies in the company of many hundreds of typical C. coralloides. Attempts to culture this variant were unsuccessful. Microscopic examination immediately made obvious the reasons for the above diversity of opinion concerning this organism.

The fruiting bodies of C. coralloides var. polycystus

are recumbent, irregular cushions, rather wrinkled, brownish-orange and somewhat glistening. They are extremely variable in size and shape, ranging from rounded masses about 50 x 50 x 20μ to irregular masses 40 x 30 x 200-300μ. In magnifications up to 90X in reflected light, no definite structure other than a slightly knobby appearance to the mass is discernible. However, in transmitted light, it can be seen readily that the fruiting bodies are composed of many, essentially globose or rounded-elongated divisions, measuring between 20μ and 35μ in their dimensions. These are the cysts to which the specific name given by Kofler applies. The writer cannot consider them cysts, since they do not have a definite membraneous wall around them, and, therefore, he has used the term "divisions" to describe them. They are separated from one another by a completely hyaline slime sheath, which, as far as can be determined, never becomes a membraneous slime wall. This sheath is usually just thick enough to be discernible, but, in some instances, it is 4-5μ thick. When the fruiting body is broken up, the divisions retain their identity very well and, then, resemble typical C. coralloides fruiting bodies.

In view of the single occurrence of this organism, and in view of the failure to grow the organism in culture, the writer does not feel qualified to offer an opinion as to the systematic status of this organism at this time. On the basis of the limited observations made, the writer tentatively

feels that the Krzemieniewskys may well be correct in calling the organism in question Chondrococcus polycystus. However, he does not believe that he can state such an opinion in good conscience in the present paper.

C. coralloides was seeded onto all seven of the substrates used in this study with excellent results. Colonies were formed on Rabbit Dung Decoction Agar, Bacterial Suspension Agar, Rabbit Dung Pellet Plates, Homogenized Bark Agar and Bark Decoction Agar after only four days. After three weeks, fruiting bodies were also found on Sterilized Elm Bark. Fruiting also took place in profusion on Rabbit Dung Pellets, but only scantily on the agar media. Transfers to new substrates were readily accomplished.

C. coralloides has not been infrequently reported in the literature and, of course, was the most frequently found species in the current study. In spite of this, there are no known specimens in existence. In order to fill this void, material from bark collections has been designated as neotype material and has been deposited in the University of Missouri herbarium. Other material from bark collections will be deposited in the Farlow Herbarium and, probably, in other herbaria in the future.

Chondrococcus blasticus Beebe

Iowa State Coll. Jour. Science, 15:310. 1941.

Type: None in existence.

Fruiting Body. Primary: Spherical to subspherical, usually sessile but occasionally with a short stalk or foot, pale to bright pink; 300 to 600μ in diameter. No outer wall or limiting membrane evident. Develops on sterilized rabbit dung in from 3 to 5 days at room temperature. Secondary: Arising as a budlike growth from the primary fruiting body. Develops into irregularly shaped, finger, coral, or budlike protuberances. Seldom branched, occasionally stalked but usually sessile on primary fruiting body. Deep pink to salmon pink in color. Quite variable in size and shape: 50-150 x 175-425μ. No outer wall or limiting membrane evident.

Spores. Spherical, thick-walled, highly refractile; 1.2-1.4μ in diameter. Held together in the fruiting body by the mass of slime.

Vegetative Colony. Thin, colorless, transparent at margin; surface broken by many small ridges, or veins. Center smoother, slightly thicker, often showing pale pink pigmentation.

Vegetative Cells. Long, slender, flexible rods, straight or curved to bent, ends rounded to tapered, gram negative. Often show one or two deep-staining bodies within, at or near center, while ends of cell stain lightly. 0.5-0.6 x

3.0-5.0μ. Usually found in groups of from 2 to 12, lying parallel, the group moving as a unit. Motile by a crawling or creeping motion; no flagella.

Material examined: One occurrence on a piece of bark during current study.

Recorded collections: Beebe, Iowa, 1941; Current study, Missouri.

The above description has been reproduced exactly as it appeared in Beebe's original paper describing C. blasticus. Of the 30 species of myxobacteria discussed in this paper, this is the only one to which nothing has been added in the direction of extended data, other than to record it as having been found on the bark of living trees.

One occurrence of C. blasticus was found on bark collected in May, 1955, from a Juniperus virginiana growing in a churchyard near the location known as Sandstone Bluffs, Missouri. The occurrence consisted of only four fruiting bodies lying within an area about 1 mm. square. Although only four fruiting bodies were seen, all of which were mounted, there is no doubt about the identification because of the characteristic production of secondary fruiting bodies described by Beebe. These specimens from bark show this very clearly.

Inquiries to Beebe have not indicated any specimens of C. blasticus to be in existence. As stated above, the current find on bark consists of only four fruiting bodies and all of these were mounted. These mounted specimens are hardly worthy of designation as neotype material and such action will not be taken. However, it is noted that the mounted specimens will be retained in the possession of the University of Missouri herbarium.

Genus Angiococcus Jahn

Beit. z. botan. Protist. I. Die Polyangiden. Leipzig. 1924.

Angiococcus moliroseus n. sp.

Etymology: Latin, moles, mass; Latin, roseum, rose

Fruiting bodies irregularly shaped, pink cushions of tiny cysts, resembling a pile of pink sand grains; less than 100μ in size, 50-60μ high. Cysts pink in mass, hyaline individually; 6-15u in diameter, averaging 10μ; cyst wall thin, tough, smooth, often with black, refractile granules on surface; no discernible connection between cysts; no discernible slime holding in mass. Spores of two types; one type, spherical, measuring 0.8-1.0μ in diameter, difficult to free from cyst, stain avidly with aniline blue; other type, spherical (1.2μ in diameter) to shortened rods (1.0 x

1.5μ) with gradients between, the predominant being oval, 0.8 x 1.3μ, somewhat separable from cyst; no avidity for aniline blue. Vegetative cells not described.

Type substratum: Bark of Ulmus americana (Peterson No. 212-h-2)

Type locality: Pinnacles, Missouri

Some 40 to 50 fruiting bodies of this organism were found scattered over a piece of Ulmus americana bark collected in April, 1955. The tree from which the bark was collected was growing in an open, dry situation at the Pinnacles, Missouri.

The fruiting bodies of A. moliroseus are irregularly shaped piles of very tiny cysts. The shape of the pile is predominantly a cushion, but may be irregularly elongate and not necessarily smooth on the surface. In fact, it can be nicely described as appearing to be a pile of sand grains stuck together. By reflected light, the fruiting bodies are a lovely, delicate pink in color and the specific name assigned to the organism was selected to describe this "pink mass." There is no suggestion of a stipe or cystophore and the mass simply lies on the substrate which, in this case, is the bare bark. The fruiting bodies are extremely variable in shape and size.

In transmitted light, the cysts are faintly pink in mass.

Observed individually, they are quite hyaline. Many of the cysts are covered with masses of tiny, black, refractile granules, which are almost the same size as the spores inside the cysts, often to the extent of making the entire cyst appear black. The black granules disappear when heated in lactophenol, leaving the cysts clear and hyaline. Such heating also destroys some of the faint pink coloration. The granules appear to be trapped in the dried slime composing the cyst wall, but no opinion is presented as to what they are, whether they actually belong to the myxobacterial organism, or whether they are extraneous material.

The spores are not completely understood at this writing. All of them are difficult to get free of the cyst walls and, when this is accomplished, the spores still adhere together in irregular masses. It is, therefore, difficult to find individuals for study and measurement. However, there appear to be two different types of spores present in the cysts. One type is essentially spherical in shape, with some irregularities due to pressure in mass, and measure about 0.8-1.0μ in diameter. They take aniline blue well and are extremely difficult to remove from the cyst. The second type ranges from spherical to shortened rods in shape with the majority of them being oval-shaped and measuring 0.8 x 1.3μ. The more spherical spores of this second type measure 1.2μ in diameter and the rod-shaped ones measure about 1.0 x 1.5μ in size. There are, of course, gradients between these extremes with

the oval-shaped spores described above representing the mean. These various spores of the second type show a lack of affinity for aniline blue and appear hyaline in stained preparations. They are also somewhat easier to separate from the cyst wall than are the first type.

The specimens of A. moliroseus available are somewhat limited and, originally, it was decided that no cultural attempts would be made. Further reflection concerning this organism dictated that a clearer understanding and verification of interpretations could be made if the organism could be cultured. Fruiting bodies were seeded, without success, on the five agar media used during this study. It is unfortunate, however, that nothing is known of the vegetative phase of A. moliroseus and that the above interpretations are unverified at this writing.

The Genus Angiococcus contains two other species in addition to the one now being added to it. Neither of these two species have been seen by the writer and, consequently, they are known to him only by descriptions and sketches. The first of these, A. disciformis, described by Thaxter (1904) and later reported by the Krzemieniewskys (1926), produces fruiting bodies composed of orange, disc-shaped cysts and does not appear to have any close affinities to A. moliroseus.

The second species of the genus, A. cellulosum Mishustin (1938), does have some characteristics in common with A. moliroseus. A. cellulosum produces yellow or pink, regularly

rounded (less frequently extended or angular) fruiting bodies. This description could pretty well fit A. moliroseus, also. The cysts of both species appear to be of the same general shape and size. Mishustin has described the spores of A. cellulosum as being shortened rods in globular masses which are easily broken up, but he has indicated no size for the spores. The description of "shortened rods" could easily enough fit some of the spores found in A. moliroseus, but the spores of A. moliroseus are anything but easily broken up from the cysts. The cysts of A. cellulosum are surrounded by an outer wall or envelope which is supported on from one to three short stalks or cystophores. No such structures are found in A. moliroseus and this is the prime difference--and a substantial one--between the two species in question.

The specimens of A. moliroseus, found during the course of the current study on the single piece of bark, are designated as type material. This piece of bark is on deposit in the University of Missouri herbarium.

Comprehensive Review of the Habitats of the Order Myxobacteriales, Including the Findings of the Current Study

Bergey's Manual recognizes 72 species of myxobacteria. Seven additional species have been described in the literature since publication of the 1948 Edition of the Manual and six new species are described in the current study. It is possible to categorize these 85 representatives of the Order Myxobacteriales into eight reasonably well defined habitat groups. These, in arbitrary order, may be descriptively named in the following fashion: (1) Marine; (2) Soil; (3) Dung; (4) Both Soil and Dung; (5) Dung and/or Soil and Some Other Habitat; (6) Decaying Plant Materials; (7) Parasitic on Other Organisms; and (8) Bark of Living Trees. The present, rather inadequate, state of knowledge regarding the Order Myxobacteriales dictates that such categorization will not stand up long. Further collections and studies will tend to establish some of these organisms as less fastidious in habitat requirements than they appear to be at this writing. Nevertheless, these eight habitat categories provide a reasonable basis for discussion at this time.

The Marine habitat group includes only three species. Two of these were isolated from seawater and reported by Stanier (1940) and the third was reported from seaweed by Humm (1946). The second habitat group, Soil, includes those

25 organisms which have been isolated only from soil. Winogradsky (1929), Fuller and Norman (1943), the Krzemieniewskys (1926, 1928, 1930, 1933, 1937), Hutchinson and Clayton (1919) and Noren (1950, 1951), in addition to others, were all primarily interested in soil microflora at certain stages of their careers and reported isolations of various species of the Order Myxobacteriales from soil during the course of such work.

The third habitat group includes those myxobacteria which have been found only on dung habitats. Nine such organisms fall into this category as described by Kofler (1913), Jahn (1911, 1924), Thaxter (1897, 1904), Faull (1916) and Finck (1950).

The fourth category consists of 11 organisms which have been described from both soil and dung substrates, but from no other substrate. In most of these instances, two or more different workers isolated the organisms in question from the two different substrates, but on different occasions, often in different parts of the world and often separated by many years of time. Therefore, it would not only be tedious to attempt to review the literature citations in which these isolations were reported, but valueless and repetitious as well. This will be done in tabular form in Table No. 7. This same general statement applies also to the following two habitat categories.

The fifth habitat category contains those species of

myxobacteria which have been reported on dung and/or soil and some additional substrate. In practically all cases, the "additional substrate" is some type of decaying plant material. Twenty-two species are included in this category. There is no inference made at the present time that these particular 22 species are less fastidious in habitat requirements than any other species of myxobacteria, although this may prove to be true. In each instance, these 22 species have been reported by two or more workers on different occasions, as is shown in Table No. 8. Rather than being less fastidious in habitat requirements, these nine organisms simply may be more common and, thus, have been more frequently reported and on a greater variety of substrates. Because some of these additional isolation substrates are bark and wood, or lichens, which may be on bark or wood, this category approximates the bark of living trees as a habitat and is of special interest to this study.

The sixth category of habitats includes only five species of myxobacteria and these species are those which have been reported only on decaying plant materials. Since all of these decaying plant materials are bark and/or wood, this category comes very close to the habitat type on which the present paper is reporting and these five species are also of special interest to the present study, since they might logically be expected to turn up on the bark of living trees, as, indeed, four of them did.

The seventh habitat category includes only two species which have been isolated from substrates which cannot be classified with any of the preceding six groupings, primarily because of the apparent parasitism of the organisms. These two organisms are Polyangium parasiticum Geitler, which was described by Geitler (1924) on a species of Cladophora in a pool in Vienna, and Chondrococcus columnaris (Davis) Ordal and Rucker, which was first described by Davis (1922) as the cause of a dermal disease of fresh-water fishes, by Fish and Ordal (1944) on salt-water fishes, by Ordal and Rucker (1944) on salt-water fishes, and by Nigrelli and Hutner (1945) on Killifish.

The current study has necessitated the erection of the eighth habitat category, the bark of living trees. The six organisms which are described as new in this paper, of course, constitute this category. These organisms are probably not restricted to bark, although it is quite possible that they may not be soil inhabitants, and further studies may find them on other substrates. They are predominantly small organisms. Consequently, they could easily have been overlooked in the past.

The 30 organisms observed in the study currently being reported change considerably the habitat picture for the Order Myxobacteriales as it appears in Bergey's Manual. The new habitat category, Bark of Living Trees, is the first of these changes. Four organisms, Polyangium cellulosum

Imsenecki and Solntzeva, Chondromyces cylindricus Krzemieniewski and Krzemieniewska, Polyangium luteum Krzemieniewski and Krzemieniewska, and Chondromyces minor Krzemieniewski and Krzemieniewska, which had previously been known only from soil, must be moved from the "Soil" habitat to the one which encompasses soil, dung and some other substrate. Therefore, the total number of organisms known only from soil is reduced from 29 to 25 by the findings of this study.

The list of myxobacteria which are known only from dung has been reduced from eleven to nine, since Archangium thaxteri Jahn and Chondromyces apiculatus Thaxter were both found on bark and now must be placed in a broader category. The habitat range of six organisms, Archangium primigenium (Quehl) Jahn, Archangium flavum (Kofler) Jahn, Sorangium sorediatum (Thaxter) Jahn, Podangium gracilipes (Thaxter) Jahn, Myxococcus virescens Thaxter and Chondrococcus blasticus Beebe, now has been extended from only soil and dung isolations to include bark.

Eight of the 30 organisms included in this study had previously been isolated from either soil or dung and some sort of decaying plant material. For these eight organisms, then, a bark of living trees substrate is added, although most of them had previously been reported on decaying wood or bark, which, of course, is closely akin to the habitat under consideration in the current study. These organisms are Polyangium vitellinum Link, Polyangium fuscum (Schroeter)

Thaxter, Podangium erectum (Schroeter) Jahn, Podangium lichenicolum (Thaxter) Jahn, Chondromyces crocatus Berkeley and Curtis, Chondromyces medius Krzemieniewski and Krzemieniewska, Myxococcus fulvus (Cohn emend. Schroeter) Jahn and Chondrococcus coralloides (Thaxter) Jahn.

Four organisms, Archangium serpens (Thaxter) Jahn, Stelangium muscorum (Thaxter) Jahn, Polyangium simplex Thaxter and Chondromyces catenulatus Thaxter, which are now reported on the bark of living trees, had previously been found only on decaying plant materials. Archangium serpens had been reported on decaying lichens, Stelangium muscorum on liverworts on living beech trees, and the other two on decaying wood. Consequently, adding bark of living trees to the habitat range of these four organisms is not much of an extension of the previously recorded substrate types.

In summation, the present study has expanded the known habitat ranges of 12 species of myxobacteria from soil and/or dung to include a plant material substrate, the bark of living trees. Twelve more species, which had previously been observed on plant materials, were found on the bark of living trees in varying degrees of profusion. A final six organisms, described as new species in this paper, are known only from bark of living trees. A compilation of the present status of habitat ranges and isolation substrates of all recorded members of the Order Myxobacteriales is given in Tables Nos. 4, 5, 6, 7, 8, 9, 10 and 11.

Table No. 4. Substrates of Order Myxobacteriales: Marine isolations only.

Organism	Reported by	Substrate and Location
Family Cytophagaceae		
Cytophaga krzemieniewskae Stanier	Stanier (1941)	seawater, California
Cytophaga diffluens Stanier	Stanier (1941)	seawater, California
Cytophaga sensitiva Humm	Humm (1946)	seaweed, North Carolina
No other families represented		

Table No. 5. Substrates of Order Myxobacteriales: Soil isolations only.

Organism	Reported by	Substrate and Location
Family Cytophagaceae		
Cytophaga hutchinsonii Winogradsky	Win. (1929)	soil, middle Europe
	Krzska. (1933)	soil, Poland
	Jensen (1940)	soil, Australia
Cytophaga lutea Winogradsky	Win. (1929)	soil, middle Europe
Cytophaga aurantiaca Winogradsky	Win. (1929)	soil, middle Europe
Cytophaga tenuissima Winogradsky	Win. (1929)	soil, middle Europe
Cytophaga rubra Winogradsky	Win. (1929)	soil, middle Europe
Cytophaga deprimata Fuller & Norman	F. & N. (1943)	soil, Iowa
Cytophaga albogilva Fuller & Norman	F. & N. (1943)	soil, Iowa
Family Archangiaceae -- No representatives		
Family Sorangiaceae		
Sorangium cellulosum Imsenecki & Solntzeva	I. & S. (1936)	soil, Russia
Sorangium spumosum Krzski & Krzska.	K. & K. (1928)	soil, Poland
Sorangium nigrum Krzski. & Krzska.	K. & K. (1937)	soil, Poland
Sorangium nigrescens Krzski. & Krzska.	K. & K. (1937)	soil, Poland

Table No. 5 (Cont.). Substrates of Order Myxobacteriales: Soil isolations only.

Organism	Reported by	Substrate and Location
Family Polyangiaceae		
Polyangium minus Krzski. & Krzska.	K. & K. (1926)	soil, Poland
Polyangium ochraceum Krzski. & Krzska.	K. & K. (1926)	soil, Poland
Polyangium aureum Krzski. & Krzska.	K. & K. (1930)	soil, Poland
Polyangium indivisum Krzski. & Krzska.	K. & K. (1928)	soil, Poland
Polyangium spumosum Krzski. & Krzska.	K. & K. (1930)	soil, Poland
Polyangium fumosum Krzski. & Krzska.	K. & K. (1930)	soil, Poland
Chondromyces brunneus Krzski. & Krzska.	K. & K. (1946)	soil, Poland
Family Myxococcaceae		
Myxococcus ovalisporus Krzski. & Krzska.	K. & K. (1926)	soil, Poland
Myxococcus albus Finck	Finck (1950)	soil, Germany
Myxococcus viperus Finck	Finck (1950)	vineyard soil, Germany
Myxococcus filiformis Solntzeva	Solntzeva (1940)	soil, Russia
Chondrococcus exiguus Singh	Singh (1947)	soil, Great Britain
Angiococcus cellulosum Mishustin	Mishustin (1938)	soil, Russia
Sporocytophaga myxococcoides (Krzska.) Stanier	Hutch. & Clay. (1919)	soil, Iowa
	Krzska. (1933)	soil, Poland
	Stapp & Bortels (1934)	soil, central Europe
	Ims. & Sol. (1936)	soil, Russia
	Speyer (1953)	soil, Germany

Table No. 6. Substrates of Order Myxobacteriales: Dung isolations only

Organism	Reported by	Substrate and Location
Family Cytophagaceae -- No representatives		
Family Archangiaceae -- No representatives		
Family Sorangiaceae		
Sorangium schroeteri Jahn	Jahn (1924)	rabbit dung, Berlin
Family Polyangiaceae		
Polyangium morula Jahn	Jahn (1911)	rabbit dung, Germany
Polyangium stellatum Kofler	Kofler (1913)	hare dung, Vienna
Synangium lanuginosum (Kofler) Jahn	Kofler (1913)	rabbit dung, Vienna
Synangium thaxteri (Faull) Jahn	Faull (1916)	deer dung, Canada
Chondromyces pediculatus Thaxter	Thaxter (1904)	goose dung, South Carolina
Family Myxococcaceae		
Myxococcus brevipes Finck	Finck (1950)	wild rabbit dung, Germany
Chondrococcus cirrhosus (Thaxter) Jahn	Thaxter (1897)	goose dung, Mass.
Chondrococcus megalosporus Jahn	Jahn (1924)	stag dung, Berlin

Table No. 7. Substrates of Order Myxobacteriales: Both soil and dung isolations, but no other.

Organism	Reported by	Substrate and Location
Family Cytophagaceae		
Cytophaga johnsonae Stanier	Stanier (1947)	soil, England
		compost, England
Family Archangiaceae		
Archangium gephyra Jahn	Jahn (1924)	deer, rabbit and hare dung, Berlin
	K. & K. (1926)	soil, Poland
	Noren (1950)	soil, Sweden
Family Sorangiaceae		
Sorangium septatum (Thaxter) Jahn	Thaxter (1904)	horse dung, Mass.
	K. & K. (1928)	soil, Poland
Sorangium compositum (Thaxter) Jahn	Thaxter (1904)	rabbit dung, S.Carolina
	Jahn (1924)	rabbit dung, Berlin
		hare dung, Oberharg
	K. & K. (1928)	soil, Poland
Family Polyangiaceae		
Polyangium ferrugineum Krzski. & Krzska.	K. & K. (1928)	soil, Poland
		rabbit dung, Poland
Melittangium boletus Jahn	Jahn (1924)	rabbit and deer dung, Berlin
	K. & K. (1928)	soil, Poland
	Solntzeva (1941)	manure, Russia
	Noren (1950)	soil, Sweden

Table No. 7 (Cont.). Substrates of Order Myxobacteriales: Both soil and dung isolations, but no other.

Organism	Reported by	Substrate and Location
Family Myxococcaceae		
Myxococcus cruentus Thaxter	Thaxter (1897)	cow dung, Tennessee
	K. & K. (1928)	soil, Poland
Myxococcus xanthus Beebe	Beebe (1941a)	cow dung, Iowa
	Noren (1950)	soil, Sweden
Myxococcus stipitatus Thaxter	Thaxter (1897)	dung, Mass., Maine, Tenn.
	K. & K. (1928)	soil, Poland
	Oetker (1953)	soil, Germany
Chondrococcus cerebriformis (Kofler) Jahn	Kofler (1913)	hare dung, Berlin
	Finck (1950)	soil, Germany
Angiococcus disciformis (Thaxter) Jahn	Thaxter (1904)	muskrat dung, Mass.
		deer dung, New Hampshire
	K. & K. (1928)	soil, Poland

Table No. 8. Substrates of Order Myxobacteriales: Soil and/or dung, and some other substrate

Organism	Reported by	Substrate and Location
Family Cytophagaceae -- No representatives		
Family Archangiaceae		
Archangium primigenium (Quehl) Jahn	Quehl (1906)	rabbit dung, Berlin
	Jahn (1924)	rabbit dung, Berlin
	Kofler (1913)	rabbit dung, Vienna
	K. & K. (1926)	soil, Poland
	Noren (1950)	soil, Sweden
	Current study	bark of living trees, Mich., Mo., Fla., Ill., Greece
Archangium flavum (Kofler) Jahn	Kofler (1913)	hare dung, Danube meadows
	K. & K. (1926,1928)	soil, Poland
	Current study	bark, Missouri
Archangium thaxteri Jahn	Jahn (1924)	rabbit dung, Germany
	Current study	bark, Missouri
Family Sorangiaceae		
Sorangium sorediatum (Thaxter) Jahn	Thaxter (1904)	rabbit dung, S. Carolina
	K. & K. (1928)	soil, Poland
	Current study	bark, Missouri

Table No. 8 (Cont.). Substrates of Order Myxobacteriales: Soil and/or dung, and some other substrate

Organism	Reported by	Substrate and Location
Family Polyangiaceae		
Polyangium vitellinum Link	Thaxter (1892)	wet wood & bark, Maine
	Jahn (1924)	old wood, Germany
		poplar bark, Germany
		rabbit dung, Germany
	Current study	bark, Missouri
Polyangium luteum Krzski. & Krzska.	K. & K. (1928)	soil, Poland
	Current study	bark, Missouri
Polyangium cellulosum Imsenecki & Solntzeva	I. & S. (1936)	soil, Russia
	Mishustin (1938)	soil, Russia
	Current study	bark, Missouri, Greece
Polyangium fuscum (Schroeter) Thaxter	Thaxter (1897)	rabbit dung, Calif.
	Kofler (1913)	rabbit dung, Vienna
	Jahn (1924)	dung, Germany
		poplar bark, Germany
		decaying lichens, Ger.
	K. & K. (1928)	soil, Poland
	Noren (1951) ?	soil, Great Britain
	Oetker (1953)	soil, Germany
	Current study	bark, Missouri

Table No. 8 (Cont.). Substrates of Order Myxobacteriales: Soil and/or dung, and some other substrate

Organism	Reported by	Substrate and Location
Podangium erectum (Schroeter) Jahn	Thaxter (1897)	horse dung, Mass.
	Kofler (1913)	mouse dung, Germany
	Jahn (1924)	manure, Germany
		bark, Germany
	K. & K. (1928)	soil, Poland
	Noren (1950)	soil, Sweden
	Oetker (1953)	soil, Germany
	Current study	bark, Missouri
Podangium gracilipes (Thaxter) Jahn	Thaxter (1892)	rabbit dung, Mass.
	Kofler (1913)	dung, Vienna
	Jahn (1924)	rabbit dung, Berlin
		goose dung, Norway
	K. & K. (1928)	soil, Poland
	Current study	bark, Mich., Fla., Ill., Mo.
Podangium lichenicolum (Thaxter) Jahn	Thaxter (1892)	parasitic on lichens, Conn.
	Thaxter (1904)	lichens, Indiana
		algae on wet boards, Mass.
	Quehl (1906)	rabbit & goat manure, Norway
		rotten leaves, Berlin
	Current study	bark, Missouri

Table No. 8 (Cont.). Substrates of Order Myxobacteriales: Soil and/or dung, and some other substrate

Organism	Reported by	Substrate and Location
Chondromyces crocatus Berkeley & Curtis	Thaxter (1892)	melon rind, S. Carolina
		old straw, Ceylon, Mass.
	Quehl (1906)	dung, Java
		deer dung, Berlin
	Zukal (1896)	Vienna
	Thaxter (1904)	Conn., Iowa, Fla., Java
	K. & K. (1946)	bark, Colombia
	Hessel. & Fenn. (1955)	soil, Iowa
	Current study	bark, Missouri
Chondromyces aurantiacus (Berkeley & Curtis) Thaxter	Berkeley (1857)	lichens
	Berkeley & Broome (1873)	rotten wood, Ceylon
	Thaxter (1892)	old wood & fungi, N. America
	Zukal (1896)	Vienna
	Thaxter (1897)	antelope dung, Africa
	Thaxter (1904)	Florida, Philippines
	Quehl (1906)	dung, Java
	K. & K. (1926)	soil, Poland
	Solntzeva (1940)	wood, Russia
Chondromyces cylindricus Krzski & Krzska.	K. & K. (1930)	soil, Poland
	Current study	bark, Missouri

Table No. 8 (Cont.). Substrates of Order Myxobacteriales: Soil and/or dung, and some other substrate

Organism	Reported by	Substrate and Location
Chondromyces apiculatus Thaxter	Thaxter (1897)	antelope dung, Africa
	Thaxter (1904)	deer dung, Philippines, Florida
	Baur (1905)	rabbit dung, Berlin
	Kofler (1913)	rabbit dung, Vienna
	Kuhlwein (1952)	goat dung, NE Liberia
	Current study	bark, Missouri
Chondromyces medius Krzski & Krzska.	K. & K. (1930)	soil, Poland
	K. & K. (1946)	bark, Panama
	Current study	bark, Florida, Jamaica, Greece
Chondromyces minor Krzski. & Krzska.	K. & K. (1930)	soil, Poland
	Current study	bark, Missouri
Family Myxococcaceae		
Myxococcus fulvus (Cohn emend. Schroeter) Jahn	Thaxter (1892)	lichens, paper, dung, etc.
	Smith (1901)	rabbit dung, Wales
	Baur (1905)	cow and dog dung
	DeKruyff (1908)	stable manure, Java
	Jahn (1924)	dung, bark, wood and lichens, Germany
	K. & K. (1928)	soil, Poland

Table No. 8 (Cont.). Substrates of Order Myxobacteriales: Soil and/or dung, and some other substrate

Organism	Reported by	Substrate and Location
	Kofler (1913)	rabbit, horse, goat, mouse, roe and deer dung, Vienna
		stem of clematis, decaying leaves, bird's nest, Vienna
	Cohn (1875) (?)	horse and rabbit dung
	Solntzeva (1940)	soil, Russia
	Noren (1950)	soil, Sweden
	Noren (1951)	soil, Great Britain
	Oetker (1953)	soil, Germany
	Finck (1950)	garden soil, Germany
	Sniesko, et al. (1943)	soil, Maine
	Singh (1947)	soil, Great Britain
Myxococcus virescens Thaxter	Thaxter (1892)	hen and dog dung, New England
	Jahn (1924)	rabbit, horse, stag and black cock dung, Germany
	K. & K. (1926)	soil, Poland
	Badian (1930)	Poland
	Sniesko, et al. (1943)	soil, Maine
	Solntzeva (1940)	soil, Russia

Table No. 8 (Cont.). Substrates of Order Myxobacteriales: Soil and/or dung, and some other substrate

Organism	Reported by	Substrate and Location
	Singh (1947)	soil, Great Britain
	Finck (1950)	sheep dung, Germany
	Noren (1950)	soil, Sweden
	Noren (1951)	soil, Great Britain
	Oetker (1953)	soil, Germany
	Current study	bark, Missouri, Michigan
Chondrococcus coralloides (Thaxter) Jahn	Thaxter (1892)	lichens, Massachusetts
	Jahn (1924)	rabbit, hare, horse, deer dung, Germany
		old bark and lichens, Germany
		goat dung, Lapland, Italy
	Kofler (1913)	field mouse, horse, hare, goat, roe and deer dung, Vienna
	K. & K. (1928)	soil, Poland
	Finck (1950)	deer dung, Germany
	Noren (1950)	soil, Sweden
	Noren (1951)	soil, Great Britain
	Oetker (1953)	soil, Germany
	Current study	bark, Missouri, Michigan, Florida, Illinois, Greece

Table No. 8 (Cont.). Substrates of Order Myxobacteriales: Soil and/or dung, and some other substrate

Organism	Reported by	Substrate and Location
Chondrococcus macrosporous Krzski. & Krzska.	K. & K. (1926)	leaves, Poland soil, Poland
Chondrococcus blasticus Beebe	Beebe (1941b)	goat dung, Iowa soil, Iowa
	Current study	bark, Missouri

Table No. 9. Substrates of Order Myxobacteriales: Plant materials only

Organism	Reported by	Substrate and Location
Family Cytophagaceae -- No representatives		
Family Archangiaceae		
Archangium serpens (Thaxter) Jahn	Thaxter (1892)	decaying lichens, Mass.
	Current study	bark, Missouri
Stelangium muscorum (Thaxter) Jahn	Thaxter (1904)	on liverworts on living beech trunks, Indiana
	Current study	bark of living trees, Missouri
Family Sorangiaceae -- No representatives		
Family Polyangiaceae		
Harloangium simplex Thaxter) n. comb.	Thaxter (1893)	wet wood and bark in swamps, U. S.
	Current study	bark, Missouri
Synangium sessile (Thaxter) Jahn	Thaxter (1904)	decaying wood, Florida
Chondromyces catenulatus Thaxter	Thaxter (1904)	decaying poplar wood, New Hampshire
	Current study	bark, Jamaica
Family Myxococcaceae -- No representatives		

Table No. 10. Substrates of Order Myxobacteriales: Parasitic organisms

Organism	Reported by	Substrate and Location
Family Cytophagaceae -- No representatives		
Family Archangiaceae -- No representatives		
Family Sorangiaceae -- No representatives		
Family Polyangiaceae		
Polyangium parasiticum Geitler	Geitler (1924)	on *Cladophora* sp., Vienna
Family Myxococcaceae		
Chondrococcus columnaris (Davis) Ordal & Rucker	Davis (1923)	parasitic on fresh-water fish, Mississippi Valley and St. Lawrence area
	Fish & Rucker (1944)	parasitic on cold-water fish, Washington
	Ordal & Rucker (1944)	parasitic on cold-water fish, Washington
	Nigrelli & Hutner (1945)	parasitic on Killifish, New York

Table No. 11. Substrates of Order Myxobacteriales: Bark of living trees only

Organism	Reported by	Substrate and Location
Family Cytophagaceae -- No representatives		
Family Archangiaceae		
Stelangium vitreum n. sp.	Current study	bark, Missouri
Family Sorangiaceae -- No representatives		
Family Polyangiaceae		
Haploangium rugaseptum n. sp.	Current study	bark, Missouri
Haploangium minor n. sp.	Current study	bark, Missouri
Podangium alboracemum n. sp.	Current study	bark, Missouri
Podangium cylindricum n. sp.	Current study	bark, Greece
Family Myxococcaceae		
Angiococcus moliroseus n. sp.	Current study	bark, Missouri

SUMMARY AND CONCLUSIONS

Representatives of the Order Myxobacteriales Jahn of the Schizomycetes were found to be produced frequently on pieces of bark collected from living trees and placed in moist chambers for a period of time. Study of 1081 random bark collections from 95 different trees, representing 32 different species, growing in various habitats in Missouri, yielded 267 pieces of bark on which myxobacteria were found, or 24.7% occurrence.

In addition to the above 1081 pieces, approximately 100 pieces of bark of various species of trees from Michigan, Illinois, Florida, Jamaica and Greece, on all of which myxobacteria had been found, were examined. A total of 30 species of myxobacteria were observed and studied. Twenty-four of these organisms are assigned to existing species and six are previously undescribed forms.

It is concluded that the bark of living trees is a natural habitat for members of the Order Myxobacteriales equally as important as any of those substrates of isolation previously known. This conclusion is based on (1) the frequency of occurrence on bark of living trees, and (2) the number of organisms found on this substrate in proportion to the total number currently known; i.e., over one-third of the 85 described species. Because of the scope of this habi-

tat, all of the habitats of the members of the Order Myxobacteriales are reviewed and tabulated, with the bark of living trees, as a habitat, included in the review.

The descriptive literature concerning those organisms reported previous to the current study was meager in many instances. The current study has extended character ranges and filled gaps in the knowledge of several of these organisms. In a number of cases, this is due to the fact that the organism in question is being reported in the current study for only the second or third time. Considerable further study to fill other such gaps, both descriptive and physiological, in the knowledge of organisms comprising the Order Myxobacteriales is necessary, and is planned, for the immediate future.

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