Studies on Genera of Clathraceous Fungi

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STUDIES ON GENERA OF CLATHRACEOUS FUNGI

A THESIS
SUBMITTED TO THE FACULTY OF ATLANTA UNIVERSITY
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FOR THE DEGREE OF MASTER OF SCIENCE

BY
CONSTANCE MARION WILLIAMS

DEPARTMENT OF BIOLOGY

ATLANTA, GEORGIA
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CHAPTER I

INTRODUCTION

Several collections of a clathraceous fungus were made during the summer of 1963 in a wooded area off Boulder Park Drive just outside the city limits of Atlanta, Georgia. Attempts to identify the fungus revealed the existence of confusion regarding the taxonomic position of certain clathraceous genera. After a more critical survey of the literature, it was evident that diverse opinions prevail relative to the nomenclatorial status of certain generic names and taxonomic delimitations of these genera.

The clathraceous fungi belong to the class Basidiomycetes, the subclass Homobasidiomycetes, the order Phallales, and the family Clathraceae. Opinions vary concerning the recognition of orders in the Homobasidiomycetes and this affects the number of families recognized. The order Phallales, however, and the families Phallaceae and Clathraceae are recognized by most mycologists. Fungi belonging to Phallales are commonly known as phalloids, so called because of the excessively fetid odor of the exposed gleba present on a horn-like receptacle. The term "phalloid", however, has a more valid reference to the family Phallaceae, to which Phallus belongs and upon which the family was established. The family Clathraceae, on the other hand, is based on the genus Clathrus and those related stinkhorns that have a receptacle composed of obliquely anastomosing branches or a columnar receptacle. The lattice-work pattern of branching is more characteristic of the group. This pattern may be confined to an apical
position or it may be completely lacking, with the receptacle consisting of simple vertical branches.

Uncertainty regarding generic limits and status prevail especially among those clathraceous members with the receptacle consisting of columnar branches. The problem still appears to be unresolved although several studies of fresh and preserved collections of clathraceous fungi assigned to different genera are reported in the literature. When an attempt was made to identify the locally collected specimens, five generic names were encountered. These included *Colonnaria*, *Colus*, *Clathrus*, *Laternea* and *Pseudocolus*. Three of these genera, *Laternea*, *Colonnaria* and *Pseudocolus*, were clearly based on the presence of columnar receptacles, and two, *Colus* and *Clathrus*, were based on a partial or full lattice-work receptacle pattern.

Since it was found that the status of *Colus* and *Clathrus* required no further clarification, it became the objective of these studies to attempt to clarify the status and relationship of the remaining three genera, namely, *Colonnaria*, *Laternea* and *Pseudocolus*. The principal delimiting features of the genera were found to involve variations in global position, the morphology of the receptacle, and the presence or absence of a stipe. The approach used in an attempt to resolve this problem was to critically study and evaluate the morphologic characteristics possessed by specimens assigned to these genera, in order to ascertain the limits of generic boundaries and the extent of species differences within these taxa.
CHAPTER II

REVIEW OF LITERATURE

Traditionally the clathraceous fungi have been placed in the Gasteromycetes, a subdivision of the subclass Homobasidiomycetes. Today, the term Gasteromycetes is not generally recognized as a taxonomic category. Martin (1961) has included Gasteromycetes as one of the two earlier series of the Homobasidiomycetes. At one time, all fungi in this series were grouped into the single order, Lycoperdales. Fischer (1890) recognized the order Lycoperdales and included as one of the families was Phallaceae, the taxon to which the genera Colus and Clathrus were assigned. Excluding Colus, he placed all columnar clathraceous fungi in the genus Clathrus. Clements and Shear (1931) followed Fischer’s treatment of the clathraceous fungi in their volume on known genera of fungi.

In the earlier work of Fries (1823), the Gasteromycetes were recognized as a valid class. He included in this class, the order Angiogastres and the suborder Phalloideae, to which four genera were assigned. Clathrus was among the included genera, Laternea being listed under it as a tribe.

Saccardo (1888) elevated Phalloideae to family status and designated Clathreae and Phalleae as subfamilies. The exact status of Laternea and Pseudocolus was not indicated.

In Coker and Couch’s (1928) study of the Gasteromycetes, the family Phallaceae, with subfamilies Clathreae and Phalleae, was recognized. Genera included in Clathreae were Clathrus and Colus;
Pseudocolus was only mentioned as a generic name and no further comment was made.

Fischer (1933) established Phallineae as a suborder and Clathraceae, including Clathrus and related forms, and Phallaceae, including Phallus and related forms, as subfamilies. Among the genera of Clathraceae recognized were Colonnaria, Laternea and Pseudocolus. Zeller (1949) published keys to the Gasteromycetes based on Fischer's treatment.

Differences extend beyond these categories to the genera. In Clathraceae, the morphology of the receptacle, variation in the gleba in relation to the receptacle, and the presence or absence of a stipe represent the features providing the taxonomic bases for generic delimitations.

The genus Clathrus established by Micheli (1729) was described as having a receptacle without a single distinct branch, forming an inflated hollow network. Colus, erected by Cavalier and Sechier (1835), was indicated as having 6 to 9 vertical branches of equal length, attached to an apical dome-shape lattice-work, to which the gleba adhered.

Clathraceous fungi with simple columns joined at the apex and free at the base have been placed in various taxa. Colonnaria, a genus erected by Rafinesque (1808), was described as having a receptacle divided "into four pillars united at the top which bear the seeds in the margin", Turpin (1822), apparently unaware of Rafinesque's Colonnaria, described the genus Laternea. The genus Laternea was described as having a receptacle consisting of slender,
smooth columns united at the apex with the gleba restricted to this apical region. Linder (1928), in his treatment of clathraceous genera, recognized the validity of Laternea. This genus was not recognized by Fischer (1890) in an earlier treatment, for he incorporated all columnar clathraceous fungi, except Colus, in the genus Clathrus. It was further suggested by Linder (1928), that Colonnaria, on the basis of priority, be recognized and include those clathraceous fungi with simple columnar receptacles having no "laterne" gleba. Linder suggested that Clathrus be reserved for those forms having anastomosed receptacles.

Cunningham (1931) separated the columnar species, previously included in Clathrus by Fischer (1890), and established for them the genus Linderia, differing from Laternea in having its gleba on the inner surface of the arms rather than in the "laterne" position. Linderia was later changed by Cunningham (1942) to Linderiella, since the name Linderia was similar in appearance to Lindera Thunberg, a member of Lauraceae. Cunningham indicated that investigators recognizing Colonnaria were operating on mere guess work in assuming that Rafinesque was dealing with a fungus. Lloyd (1907) described Rafinesque's report of a new fungus as being "Rafinesque raving". The opinions of both Lloyd and Cunningham were shared by Long and Stouffer (1948), who rejected Fischer's later treatment (1933) of Colonnaria and Laternea.

According to Santesson (1943), the rejection of Rafinesque's description of Colonnaria cannot be accepted in light of the present rules of nomenclature. Santesson expressed the opinion
that because of the wording of the description, the only fungus to which such a description could apply would be to a clathraceous fungus. Santesson therefore made *Linderia* a synonym of *Colonnaria*.

In 1933 Fischer recognized the genera *Laternea* and *Colonnaria*, and indicated the main difference delimiting these genera as being "fistutous columns" and "massive columns" respectively. Santesson (1943) reported that the receptacle of *Colonnaria* was not "massive" but was "lacunose"; the arms of *Laternea* were not "fistutous" but were "lacunose". Thus differing with the work of Fischer, he further indicated only a difference in the size of the cavities in the lacunose tissue, a difference deemed insufficient to warrant separation of the genera. Santesson considered *Laternea* to be a synonym of *Colonnaria*, recognizing the latter as the valid genus.

Linder (1928) indicated that the "laterne" gleba position was common to *Laternea*. For his studies, he only had comparative material preserved in alcohol of *Clathrus columnatus*, and therefore the gleba was misinterpreted, according to Santesson (1943), who did a detailed study of *Clathrus columnatus* and compared this to Linder's photographs of *Laternea triscapa*.

Lloyd (1907) erected *Pseudocolus* as a genus to contain those clathraceous fungi with arms branching from an extremely short or somewhat elongated stipe and clearly united at the apex. Cunningham (1931) reported *Anthurus* and *Pseudocolus* as synonyms, after amending the original generic description, and described *Anthus* as having a receptacle of 3 to 8 branches united apically, often
breaking free at maturity; the branches extending from the stipe.

His work was accepted by Paner (1960) of Czecho-slovakia. Zeller (1948, 1949) held that _Lysurus_ and _Anthurus_ were synonyms, disagreed with Cunningham's conclusions, and thereby accepted _Pseudoculus_. Zeller described _Lysurus_ as having a receptacle consisting of free vertical branches extending from the wall of the stipe, while _Pseudoculus_, also stipitate, had vertical branches attached apically.
CHAPTER III

MATERIALS AND METHODS

For this study, specimens of clathraceous fungi assigned to five genera, *Clathrus*, *Colonnaria*, *Laternea*, *Colus* and *Pseudococcus*, were obtained from the following herbaria: Farlow (FH), Indonesia (BO), New York Botanical Garden (NY), Paris (PC), Stockholm (S), the United States Department of Agriculture (USFS), and the University of North Carolina (NCU). The abbreviations used are those standardized for registered herbaria in Index Herbariorum (1954).

Photographs and drawings were obtained from Kew (K). Each specimen was labeled with such information as the scientific name, as determined by the collector or a later investigator, locality, date of collection, and, in some instances, the substratum was indicated. On several labels or on packets containing the specimens, annotations by various investigators who had previously examined the collection were present. Borrowed specimens were kept in herbaria cabinets, in which an ample amount of paradichlorobenzene had been placed as a preventative against insect deterioration.

To facilitate the comparison of morphologic features of genera and species, the relevant characteristics to be studied were listed. The morphologic features regarded as pertinent to the study were: the number and rugosity of the receptacles, internal structure of the receptacle, glebal position, volva color and size, presence or absence of a stipe, and size and color of the sporophore.

For several specimens, only external morphologic features were
studied, while other specimens were examined microscopically. The sporophores were soaked in 3% KOH just long enough for the receptacles to swell. Free-hand transverse sections were made of the arms. Both the sporophores and the transverse sections were observed under an American Optical Microstar binocular dissecting microscope, using the 10 and 15X objectives. Line drawings were made of several transverse sections.

Water mounts of the basidiospores, that had first been placed in a 3% KOH solution, were made. Spores were studied for morphologic details and measured under oil immersion at the magnification of 1000X. Between 25 and 50 spore measurements were taken for each specimen studied. The average range of the spore dimensions was recorded along with the extremes observed.

Permanent slides were made of the basidiospores by mounting them in CMC-10, a new non-resinous embedding material obtained from The General Biological Supply House. Dehydration of a specimen to be mounted is not necessary with this mounting medium. Various stains were used in an attempt to resolve critical spore detail. Phloxine, methylene blue, cresyl blue and violet, and cotton blue in lactophenol were employed as stains. Attempts to stain the spores were all unsuccessful, apparently due to the chemical nature of the thick spore wall. In order that the stain may penetrate the spore wall, several samples of the basidiospores from different genera were centrifuged for 20 minutes at 16,000g at 10°C. The spores remained unaltered after centrifugation.

Fresh specimens of sporophores and "eggs" of a clathraceous
fungus were found growing on rotten logs along a creek bank during the summer of 1963 in a mixed conifer and hardwood area, west of the Atlanta City limits, on Boulder Park Drive. Several collections were made throughout the summer. The specimens were photographed, placed in a liquid preservative, consisting of formalin, propionic, and acetic acid (FPA), or they were dried. Accession numbers were assigned each collection and they were stored in an herbarium cabinet. Several of the collected "eggs" were dried, others were placed in FPA and later sectioned serially with a razor blade, in order to make observations and sketches of the gross morphologic details. A few "eggs" were placed in a moisture chamber in an attempt to induce further development of the receptacle. These attempts were unsuccessful.

When a specimen is described in the text or on the charts, both the name of the herbarium and the accompanying herbarium number are given. When available, the date, substratum, and collector are indicated. As indicated earlier, standardized herbaria abbreviations, as approved by the International Association of Plant Taxonomy in Index Herbariorum, are employed, when reference is made to a herbarium from which a specimen or specimens were obtained. All local collections made are designated "AU", representing the Atlanta University Mycological Collection.
CHAPTER IV

OBSERVATIONS AND DISCUSSION

The Genus Clathrus

Since certain columnar clathraceous fungi have been described as being species of Clathrus, it was first necessary to review the original description and some salient morphologic features of the genus Clathrus. The genus was erected by Micheli (1729) and was described as having a receptacle forming a hollow network of which the inner surface are covered by the gleba. For this study specimens representing four species assigned to Clathrus were examined. Specimens labeled Clathrus columnatus were observed but a discussion of these specimens is included under Colonmarias, the genus to which this species has been transferred. Some other species, presently included in the genus Colonmarias, were previously placed in the genus Clathrus.

Clathrus is the largest genus of the clathraceous fungi, having a total of ten species, as reported by Ainsworth and Bisby (1961). Species of Clathrus are widely distributed and have been reported from many localities in the United States. The genus is easily recognized by the lattice-work pattern of the anastomosing branches of the receptacle (Fig. 1). The gleba is dispersed on the inner surface of the branches. External walls of the branches have a reticulate-pitted pattern. Transverse sections of the arms in some species revealed a hollow or lacunose condition. Basidiospores were found to be fusiform-ellipsoid to oblong-ellipsoid.
Fig. 1. Photograph of *Clathrus fischeri*.

Fig. 2. Photograph of *Colus hirudinosus*. 
ranging in size from (4–) 5–5.5 (–6) x (2–) 2.5–3 (–3.5)μ.

These additional features were noted in the spores of the specimens studied. Spores were nonamyloid; the walls were pale greenish, smooth and thick, measuring 0.5 to 1μ. In Clathrus treubei the spores were slightly larger with their measurement being (5–) 5.5–6 (–7) x 2–2.5μ.

Specimens examined: New Zealand: Brown (as Clathrus cibarius; USFS 23340); Laing (as Clathrus cibarius; USFS 23200, 150096); Baker (as Clathrus cibarius; USFS 50094).

Belgium Congo: Vanderyst (as Clathrus camerunensis; USFS 51981); Luja (as Clathrus fischeri; USFS 22600).

Australia: Paul (as Clathrus gracilis; USFS 50092).

The Genus Colus

In 1835 a clathraceous fungus with vertical columnar arms was described and placed in a new genus, Colus, by Cavalier and Sechier. The genus was described as having the following characteristics: receptacle consisting of 7–9 vertical arms attached to a apical lattice-work; arms and branches reddish, hollow, conical with transverse lines; gleba restricted to the apical region; stipe white.

Specimens representing Colus hirudinosus, the type species for the genus, were examined in this study (Fig. 2). C. hirudinosus is the only species listed for the genus by Ainsworth and Bisby (1961). The sporophore of the fungus consists of 4–10 vertical branches of equal length united apically to form a network, to which the gleba adheres. Arms of the receptacle are united at the base to form a
short, sometimes elongated, stipe. Arms of the receptacle have a reticulate-pitted outer surface and are hollow or lacunose in transverse section. Basidiospores greenish with thick, smooth walls, nonamyloid, oblong-ellipsoid or fusiform-ellipsoid, \((-3) 4-4.5 \text{ (-5.5)} \times 1.5-1.8 \text{ (_2)\mu.}\)

Specimens examined: Portugal: Torrend 1907, 1909 (USFS; S).
Intibes: Bornet 1862, 1871 (PC).
Corsica: 1844 (PC; NY).
Montgilboa: 1952 (PC).

The genus Colus has been variously treated by mycologists working with the clathraceous fungi. Species assigned to such genera as Anthurus and Pseudocolus have at times been included in the genus Colus.

The Genera Colonnaria and Pseudocolus

Confusion has arisen over the generic boundaries of those clathraceous fungi whose sporophores have two to several vertical arms simply united at the apex. Fungi with these characteristics have been assigned to different genera. Stipitate forms have been placed in the genera Colus, Pseudocolus and Anthurus. The nonstipitate forms have been placed in the genera Clathrus, Colonnaria, Laternea and Linderiella.

As mentioned previously, the generic boundaries of Colus are clear and the genus is fully recognized as being valid. Some questions regarding the generic limits of Anthurus have been raised. Anthurus was described by Kalchbrenner (1880) as having its vertical
arms free at the top. The stipe of the sporophore is greatly elongated and the arms are short. Since this study was primarily concerned with those clathraceous forms whose sporophore had arms united at the top, a critical review of Anthurus and its relationship to other genera has not been attempted. It is recognized, however, that the ultimate elucidation of taxonomic problems in this phalloid family must involve a study of Anthurus and certain related genera. In this study Pseudocolus is recognized as the valid genus for those stipitate forms with branches apically united.

Much of the confusion regarding the validity of generic names of clathraceous fungi has centered around the nonstipitate forms whose sporophores have apically united vertical branches. As mentioned earlier, Colonnaria was established by Rafinesque (1808) and was based on a fungus with nonstipitate sporophores. Turpin (1822) later established the genus Laternea on a similar kind of fungus. Much later Cunningham (1931, 1942) studied specimens of Colonnaria and Laternea, rejected Colonnaria and erected Linderia, changed later to Linderiella. The present study is in agreement with the conclusions of Santesson (1943) and recognizes Colonnaria as the genus to which these forms properly belong. A comparison of the salient morphologic features characterizing Colonnaria, Colus, Clathrus and Pseudocolus are included in Table I.

The Genus Colonnaria

Fischer (1890) placed all columnar clathraceous fungi, excluding Colus, in the genus Clathrus. Since Fischer's treatment,
TABLE I
TABULATED COMPARISON OF SALIENT MORPHOLOGIC FEATURES OF FOUR CLATHRACEOUS GENERA

<table>
<thead>
<tr>
<th>GENUS</th>
<th>Branch Pattern</th>
<th>External Profile</th>
<th>Internal Profile</th>
<th>STIPE</th>
<th>GLOBAL POSITION</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>CLATHRUS</strong></td>
<td>Anastomosed</td>
<td>Tubular,</td>
<td>Hollow or</td>
<td>Dispersed or</td>
<td></td>
</tr>
<tr>
<td></td>
<td>fully forming</td>
<td>reticulate-pitted</td>
<td>lacunose</td>
<td>inner surface</td>
<td></td>
</tr>
<tr>
<td></td>
<td>a lattice-work</td>
<td>furrows absent</td>
<td></td>
<td>of branches</td>
<td></td>
</tr>
<tr>
<td><strong>COLUS</strong></td>
<td>4-10 vertical</td>
<td>Tubular,</td>
<td>Hollow,</td>
<td>Inner of</td>
<td></td>
</tr>
<tr>
<td></td>
<td>branches united</td>
<td>reticulate-pitted</td>
<td>lacunose, or</td>
<td>apical</td>
<td></td>
</tr>
<tr>
<td></td>
<td>at apex to form</td>
<td>furrows present</td>
<td>lacunose near</td>
<td>lattice-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>network</td>
<td>or absent</td>
<td>edges</td>
<td>work</td>
<td></td>
</tr>
<tr>
<td><strong>COLONNARIA</strong></td>
<td>2-5 branches,</td>
<td>Smooth flattened</td>
<td>Hollow or</td>
<td>Underside of</td>
<td></td>
</tr>
<tr>
<td><strong>(LATERNEA)</strong></td>
<td>united at apex</td>
<td>outer surface to</td>
<td>lacunose</td>
<td>apical union,</td>
<td></td>
</tr>
<tr>
<td></td>
<td>or connected</td>
<td>tubular,</td>
<td></td>
<td>&quot;laterne&quot;</td>
<td></td>
</tr>
<tr>
<td></td>
<td>short apical</td>
<td>reticulate-pitted</td>
<td></td>
<td>position</td>
<td></td>
</tr>
<tr>
<td></td>
<td>band</td>
<td>furrows present</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>or absent</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>(LINDERIELLA)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>PSEUDOCOLUS</strong></td>
<td>3 vertical</td>
<td>Tubular,</td>
<td>Hollow or</td>
<td>Underside of</td>
<td></td>
</tr>
<tr>
<td></td>
<td>branches, some-</td>
<td>reticulate-pitted</td>
<td>lacunose</td>
<td>apical union</td>
<td></td>
</tr>
<tr>
<td></td>
<td>times 4, united</td>
<td>furrows present</td>
<td></td>
<td>and extending</td>
<td></td>
</tr>
<tr>
<td></td>
<td>at the apex</td>
<td>or absent</td>
<td></td>
<td>short distance</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>below</td>
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</table>
various mycologists have at times recognized Laternea, Linderiella, and Colonnaria as valid genera. Certain species that have been included in Clathrus have receptacles of simple columns instead of a lattice-work. It was found that these columnar forms do not conform with the original description of Clathrus by Micheli (1729). Colonnaria was described by Rafinesque (1808) as having a receptacle "divided into four pillars, united at the top, which bear the seeds in the margin". Turpin (1822), unaware of Colonnaria, erected Laternea. It is evident that both investigators made reference to the same fungus. The genus Colonnaria has been rejected by many who shared the opinion of Cunningham (1931) that Rafinesque's description was not adequate and those accepting this work were merely guessing that Rafinesque described a fungus. Cunningham (1931) established the genus Linderia, later changed by him to Linderiella, to include those nonstipitate clathraceous fungi placed in Clathrus by Fischer (1890). Linder (1928) recognized Laternea and reported a "laterne" global position as characteristic of this genus. He also suggested that Colonnaria be used to include all columnar forms other than species included in Laternea. Santesson (1943) made a careful study of fresh specimens and concluded that Laternea, Linderiella and Colonnaria were synonymous genera. He recognized Colonnaria as the valid genus.


Receptacle pale orange, orange, red or white, consisting of 2–5 columns united apically and free at the base; columns tubular or having a smooth flattened outer surface, reticulate-pitted, tapering apically, lacunose or hollow in transverse section; global position apical, "laterne", spores pale greenish, thick with smooth walls, oblong-ellipsoid to fusiform-ellipsoid.

No type species has been designated for this genus. On account of the widespread occurrence of Colonnaria columnata and its familiarity to mycologists in general, it could be selected as the type species.

Key to the species of Colonnaria

1. Reticulate-pitted, tubular, hollow, lacunose receptacle; arms united at the apex, free at the base. ........................ 2

2. Branches of the receptacle 4; receptacle white, with arms strongly tapered apically; hollow in transverse section. .................. (2) C. angolensis

3. Columns 2, laterally compressed; receptacle pale red to red, or pale orange to orange;
lacunose in transverse section...(3) C. bicolumnata

3. Columns 2-4; sporophore small, to 2.5 cm., columns slender, tubular......................... 4

4. Columns typically 2, rarely 3;
receptacle hollow in transverse
section....................... (4) C. pusilla

4. Columns typically 3, rarely 4;
receptacle lacunose in transverse
section....................... (5) C. triscapa

1. **Colonnaria columnata** (Bosc) Ed. Fischer, Engler and Prantl.

   II ed. 7a 1-122. 1933

   **Clathrus columnatus** Bosc, Magaz. der Gesellsch naturforscher Freunde Berlin V:85, tab. V,f.5. 1811.


   **Laternea columnata** Nees, Nees und Henry Sys. der Pilze.
   p. 96, tab. 23. 1856.


   **Lindereiella columnata** Cunningham, New Zealand Journ. Sci. & Tech. 23:171B-172B. 1942.

   Sporophore pale orange to orange; receptacle typically of 4 arms, 2-5 common; branches tubular, reticulate-pitted on inner surface, smooth and flattened on outer surface; arms united
Fig. 3. Mature sporophores of *Colonnaria columnata*.

(Specimens from National Fungus Collections)
apically, sometimes by a short band; globa a definite differentiated body attached at the apex to the under side of union of arms, in a "laterne" position; basidiospores greenish, thick with smooth walls, nonamyloid, oblong-ellipsoid or fusiform-ellipsoid, (3.5) 4-4.5 (-5) x 1.5-1.8 (-2) μ.

Several specimens representing this species were examined. The species is easily recognized by the 3 to 4 vertical arms, flattened and reticulate-pitted on their outer surfaces. A transverse section of the branches of all specimens examined revealed a lacunose structure. At the point of apical union, the branches were sometimes attached to a short band of tissue that resembled the columns; this condition was observed in specimen No. 23211 of the U. S. National Fungus Collection (USFS). C. columnata is widely distributed with species being reported from many localities in North and South America as well as from several other countries.

Specimens examined: Brazil: Rio Grande deSul, Rick (as Laterne columnata USFS 151326).

Florida: Loucks and West 1928 (as Clathrus columnatus USFS 1932); Chipley, Pleas (as Laterne columnata USFS 23175); Inverness, Noble (as Laterne columnata USFS 23174); Kelberx 1935 (as Clathrus columnatus NY); Burlingham 1938 (as Linderia columnata NY); Underwood (as Laterne columnata NY 1600); Shear 1946 (as Linderiella columnata USFS).

Georgia: Benson (as Laterne columnata USFS 23179); Brown 1923 (as Clathrus columnatus NY).

Louisiana: Lowy 1960 (as Clathrus columnatus USFS); Langlois
Mississippi: Oleson (as Clathrus columnatus USFS 23211).

North Carolina: Earle 1906 (as Colonnaria columnata NY);

Chapel Hill, Homer (as Clathrus columnatus NCU 10410).

South Carolina: Coker (as Clathrus columnatus NCU 6016, 8432); Ravenel 1885 (as Clathrus columnatus NY).

India: Foreau (as Laternea columnata USFS 56973).

As mentioned previously, this species was originally placed in the genus Clathrus and is commonly identified and deposited in herbaria as Clathrus columnatus. These studies support the contention of Santesson (1943), that the species properly belong in the genus Colonnaria. No evidence of a tendency toward a lattice-work pattern of branching was observed in any of the specimens examined; nor were any reports found in the literature that mentioned this tendency in any collection of sporophores representing this species.

The position of the gleba, as shown in Fig. 4, is of basic taxonomic importance as a feature distinguishing this genus. Santesson (1943) has made the most careful study of this feature and has provided the most detailed description. The well-differentiated gleba as described by Santesson, represents the so-called "laterne" glebal position characterizing the genus Laternea, as erected by Turpin (1822). Burt (1896) also referred to a "dome-like" gleba in his classical study of the development of sporophores in this species. Santesson (1934) has stated that the "laterne" gleba is often not observed by collectors for its form is quickly altered after receptacle expansion and is therefore commonly not
Fig. 4. Sketches of *Colonnaria columnata* showing the morphology of the sporophore and globular position (after Santesson 1943).
evident in mature specimens.

The absence of a stipe is not a distinguishing feature of the genus for there is no stipe in sporophores of *Clathrus*. The genus is similar to *Clathrus* also in the morphology, size and color, of its spores.

2. *Colonnaria angolensis* (Welwitsch et Currey) Ed. Fischer,

Engler und Prantl, II ed. 7a 1-122. 1933.

Laternea *angolensis* Welwitsch et Currey, Trans. of Linn. Soc. of London XXVI: 286, tab. 17, fig. 7. 1870.

Receptacle white, reticulate-pitted, 4 columns tubular, hollow in transverse section, united and strongly tapered apically.

Specimen examined: Mauritius: O'Connor (as Laternea *angolensis* USFS 23185).

A greatly fragmented specimen was examined; it was evident that four columns were present. No gleba was observed nor reported by the collector. The surfaces of the branches were reticulate-pitted, and a transverse section revealed the hollow pattern.

According to Lloyd (1907) the type material was found in Angola. The specimen observed was collected in Mauritius.

3. *Colonnaria bicolumnata* (Saccardo and Trotter) nov. comb.


Receptacle pale red to pale orange, 2 columns reticulate-pitted, tubular, broad, laterally compressed, lacunose in transverse section; basidiospores greenish, smooth with thick walls, oblong or fusiform-ellipsoid, (-3) 4-5 (-6) X 1.5 -2 (-2.5) μ.

Specimen examined: California: Chico Krieger (as Laternea bicolumnata USFS 23183).

The receptacle in this species consist of 2 laterally compressed tubular columns that taper apically. The arms are lacunose in transverse section and the outer surface reticulate-pitted. It was indicated by Krieger, who collected this specimen in California, that both arms were adhering before drying.

4. Columnaria pusilla (Berkeley & Curtis) nov. comb.


Sporophore extremely small 2.5 cm. tall (dried specimen); receptacle pale orange, reticulate-pitted; columns typically 2, rarely 4, hollow in transverse section, united at apex; basidiospores greenish, smooth with thick walls, oblong or fusiform-ellipsoid.

Specimen examined: Jamaica: (as Laternea pusilla USFS 23182).
In the description of the type specimen the sporophores were reported to be extremely small. The specimens were collected in Cuba and deposited in the Kew herbarium. A photograph of this species, obtained from Kew, was observed; the "laterne" global position was evident. A fragmented specimen assigned to *Laternea pusilla* was examined. The arms had the reticulate—pitted pattern and were hollow in transverse section. After studying the Kew photograph, and the original description of Berkeley and Curtis (1869) it appears doubtful that *C. pusilla* can be separated from the next species *C. triscapa*. For the present, however, both species are being recognized.


**Clathrus triscapus** (Turpin) E. Fries, Systema Mycologicum Vol. II: 287. 1823.

Receptacle pale orange, 3 arms typically, 4 rare, reticulate—pitted, slender, tubular with a flattened outer surface, 3 typical, 4 rare, lacunose in transverse section; basidiospores greenish, smooth with thick walls, oblong—ellipsoid to fusiform—ellipsoid, (3—) 4—4.5 (—5) X 1.5—2μ.

Specimens examined: Massachusetts: Piguet 1551 (as *Laternea triscapa* FH).

Brazil: Rick (as *Laternea triscapa* USFS 23180, 57842).
South Carolina: Underwood (as Laternea triscapa NY 325); Stevenson 1899 (as Laternea triscapa USFS 57843); Duss (as Clathrus triscapus USFS 1610).

The specimens examined appeared to be reticulate-pitted, rather than smooth as indicated by Linder (1928). A dried sporophore collected by Piguet from Massachusetts (FH) was 4.4 cm. in length with three columns. A specimen having four columns was reported by Berkeley and Curtis (1869). The size of the sporophore and the number of arms have been used as a taxonomic basis for this species; however, as mentioned above, this species is closely related to C. pusilla, the only reported difference being in sporophore size and number of the arms.

Excluded Species


Specimens assigned to these taxa have been placed by Santesson (1943) in Colomnaria columnata. No specimens representing these species were available. Santesson's disposition of these species appears reasonable and, as a result, until further studies can be made on newly collected material, it is suggested that these two species be regarded as synonyms of C. columnatus.

The Genus Pseudocolus

Doubt has been raised by several investigators concerning the validity of this genus. Species assigned to Pseudocolus have been
assigned to the genera *Colus* and *Anthurus*. The brief treatment of *Colus*, appearing earlier, clearly indicates the characteristics of this genus. In *Colus* the arms of the receptacle may be numerous and they terminate into a lattice-work type of structure. This pattern of apical union is clearly absent in *Pseudocolus*. The difference between *Pseudocolus* and *Anthurus*, however, may not be as clear cut. *Anthurus* is usually described as having free arms, not united apically. In *Pseudocolus* the arms are clearly joined.

Zeller (1949) indicated that *Lysurus* and *Anthurus* were synonyms, *Lysurus* being the valid genus. Massee (1911), having studied the type material of *Lysurus*, indicated that the arms are free, "but during the young stage are closely pressed together, and having been dried in that condition appear united". Cunningham (1931) amended the generic diagnosis of *Anthurus* to include stipitate forms with arms "organically" united at the apex, often breaking free at maturity. He therefore made *Pseudocolus* a synonym of *Anthurus*

According to the original description of *Anthurus* by Kalchbrenner (1880), the arms were free.

All specimens assigned to *Pseudocolus*, examined in this study, have had their arms clearly united and the length of the arms is always greater than that of the stipe. It is for these reasons that I am recognizing *Pseudocolus* as a valid genus distinct from *Anthurus*.

*Pseudocolus* Lloyd, Myc. Writings, Vol. II: 705. 1907. Fig. 5.

Sporophore white, pale orange to orange, consisting of three columns, rarely four; columns united apically and consolidated basally into a short or elongated stipe; arms reticulate-pitted on
Fig. 5. Mature sporophores of *Pseudocolus javanicus*.
all surfaces, lacunose or hollow in transverse section; basidiospores greenish, smooth with thick walls, oblong or fusiform ellipsoid, \((-3) 4-5 \((-7) \times (1.1-)\) 1.5-2 \((-3)\).

Lloyd did not designate a type species when he erected the genus. *P. javanicus*, a common widespread, but somewhat variable species, may serve as the type species for the genus.

Seven species have been indicated as members of the genus. Of the seven, six were originally assigned to the genus *Colus*. As far as can be ascertained, only one, *P. archeri*, was originally placed in *Anthurus*. The status of this species is in doubt for Lloyd (1909) referred to it, accompanied by what he indicated as a drawing of the original specimen, as *Anthurus archeri*. Lloyd also described *P. rugulosus*, however, I have seen Lloyd's specimen and the description of the species and it appears to be *P. javanicus*.

For the remaining five species, three have been reduced to synonymy, viz., *P. schellenbergiae*, *P. rothae* and *P. javanicus*, and are now considered as *P. javanicus*. A fourth species *Colus fusiformis*, was regarded by Fischer (1933) as being the same as *P. javanicus*. It was suggested by Lloyd (note in packet, USFS 30628) that the Australian specimen and the Japanese specimen determined as *P. rothae* were probably the same as *P. javanicus*. A study of the available specimens labelled *P. rothae*, and a careful review of the description and figures of *P. rothae*, leads me to the conclusion that what was described as *P. rothae* is in all likelihood a somewhat smaller form of the rather ubiquitous and variable *P. javanicus*. Recognition of *P. garciae* will remain thereby leaving
two species in the genus *Pseudocolus*.

Key to the species of *Pseudocolus*

1. Receptacle pale orange to orange, consisting of 3 to 4 columns united apically, and basally to form a short or elongate stipe; columns tubular, reticulate-pitted, hollow or lacunose......................... (2) *P. javanicus*

1. Receptacle white, consisting of 3 broad columns united apically, and basally to form broad elongate stipe; columns tubular, reticulate-pitted ............ (1) *P. garciae*


   *Colus schellenbergiae* Sumstine, Mycologia 8: 183. 1916.


Receptacle pale orange to orange, red, typically having 3 columns, sometimes 4, united apically; stipe short or elongate, not exceeding one-third the length of the sporophore; branches hollow or lacunose in transverse section; basidiospores, greenish, smooth with thick walls, oblong-ellipsoid or fusiform-ellipsoid, (3.5-) 4-5 (-7) X 1.4-1.8 (-3) μ.

Specimens examined: Japan: Seuda: Yasuda (as *Pseudocolus*
Pseudocolus javanicus is here recognized as the species to which most taxa included in the genus belong. It appears to be a highly variable species in terms of the length of the stipe, color of the volva, and size of the sporophore. Marked variability in these morphologic features may be observed among sporophores of a single collection of the species. As a result, it appears taxonomically unsound to separate species on the basis of stipe length or on the internal structure and the cross-sectional outline of the columns.

The specimens collected in the Atlanta vicinity are determined as *P. javanicus*. Detailed studies of the sporophores and "eggs" of these collections have been made. Findings concerning the differentiation of the "eggs" largely agree with the observations of Burt (1896) for *Colonnaria columnata* (*Clathrus columnatus*).

In young "eggs", the cortical layer and medullary layer are in contact. In the older stages, separation appears to begin along the cortical plate, the region where the columns become established.
The cortical plate extends from the base to the apex and connects the columns with the outer cortical layer, destined to form the volva. Hyphae from the cortical plate were found to penetrate and become adnate to the medullary surface, forming the lacunose tissue of the columns. The lacunose tissue was found to be filled with a gelatinous material which is absent in the mature sporophore. The gleba develops from the medullary layer. The gelatinous material forming the gleba and the gelatinous layer restricted to the inner surface of the volva are of independent origin, the former arising from the medullary layer and the latter from the cortical layer. This pattern of development was indicated by Burt (1896).

Three columns were typical (Fig. 6), sometimes four (Fig. 7), in the "eggs" studied. The cells of the central medullary layer were noted to give rise to the hymenial layer. In both the mature and immature sporophore, there was no evidence of a body of pseudo-parenchymatous tissue holding the glebal mass, as in the "laterne" type gleba (Fig. 4). Basidia in the "eggs" were elongate, irregular in shape and developed in clusters at the end of proliferating hyphae (Fig. 8). Each basidium was ornamented with eight short, blunt, sterigmata. The basidiospores were greenish with smooth thick walls. They were oblong-ellipsoid of fusiform-ellipsoid with rounded or truncate ends. In some instances portions of a sterigma were found adhering to the base of the spore.


Figs. 6-7. Transections of "Eggs" of Pseudocolus javanicus collected in wooded area west of Atlanta city limits. Fig. 6. Sections of "egg" showing three columns and global region; Fig. 7. Sections of "egg" showing four columns and global position.
Fig. 8. Basidia and basidiospores of *Pseudocolus javanicus*. 
Receptacle white, reticulate-pitted, lacunose; columns 3 united apically, transverse ridges on inner surface; stipe thick, elongate; basidiospores greenish, thick with smooth walls, oblong or fusiform-ellipsoid. The above description is based on Moller’s original description.

No specimens were available for examination, however, the photographs of Moller, as included in several references, were observed. *P. garciae* is here recognized as a species distinct from *P. javanicus*. This decision is based on the reported white color and broad arms of the receptacle. This recognition must be a tentative one, however, for newly collected specimens might reveal that these morphologic characters are not stable.

Doubtful and Excluded Species

   
The disposition taken concerning this species has been mentioned previously. Cunningham (1931) reported that Lloyd (1913 and 1914) indicated, in Letters 47 and 51 respectively, that he received stipitate sporophores with the arms united apically, which he determined to be *P. archeri*. I have not examined any specimens assigned to this species.

2. **Pseudocolus rugulosus** Lloyd, Myc. Writings 3: 52. 1909.
   
Santesson (1943) indicated that this species is probably *Pseudocolus javanicus*. However, no specimens assigned to this species were observed.

Fischer (1933) later reported that *C. fusiformis* was a synonym of what is now known as *Pseudocolus javanicus*. No specimens were available for examination.
CHAPTER V

SUMMARY

1. This study represents a critical review of those genera of clathraceous fungi whose sporophores have vertical arms united apically. The genera involved were Colonnaria, Laternea, Linderiella (Linderia), Colus and Pseudocolus. Some consideration was given to the genus Clathrus, because of those species with vertical arms that have been placed in the genus.

2. Specimens used in the study were obtained from several herbaria in the United States and in other countries. In addition, specimens collected from a wooded area west of the Atlanta city limits were studied. These specimens representing the clathraceous genera mentioned have been studied with the objective in mind of establishing their proper generic limits and taxonomic status.

3. These studies have revealed that the principal morphological features upon which this group of clathraceous genera should be based are: (1) anatomical features of the receptacle, (2) global position and (3) presence or absence of a stipe.

4. Sessile clathraceous fungi with simple columns united apically have been placed in Clathrus, Colonnaria, Laternea, and Linderiella (Linderia). I have transferred sessile columnar forms assigned to Clathrus to the genus Colonnaria. In concurrence with some other investigators I have regarded Laternea and Linderiella (Linderia) as synonyms of Colonnaria. On the basis of priority, Colonnaria is designated as the valid genus. I recognized five species in this genus.
5. Stipitate clathraceous fungi with simple columns united apically have been assigned to *Colus*, *Anthurus* and *Pseudocolus*. *Colus* is described as having a reduced apical lattice-work. *Anthurus* was first described as having free short arms and the length of the stipe was from two-thirds to three-fourths the total length of the sporophore. *Pseudocolus* is distinguished from the other two genera by the apical union of the simple columns whose length was from one-half to two-thirds the total length of the sporophore. I have recognized two species in this genus.
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