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Cytomorphological Studies of the Ascogenous Hyphae of Four Species in the Genus Chaetomium

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CYTOPHYSIOLOGICAL STUDIES OF THE ASCOGENOUS HYPHAE OF FOUR SPECIES IN THE GENUS CHAETOMIUM

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I. INTRODUCTION

The purpose of this study was to investigate the morphology and the cytology of the ascogenous hyphae of four species in the Ascomycete genus Chaetomium.

The genus Chaetomium was established by Kunz in 1817 in a monograph treating Chaetomium globosum and nine other species (Chivers, 1915). According to Chivers, Kunz described the genus as having perithecia that were membranaceous, clothed on all sides with opaque hairs, and pierced by an opening at the summit. The spores were described as pellucid and mingled in a gelatinous mass. In his six volume publication issued between 1837 and 1854, Corda improved the original description by the discovery of asci in the centrum of the perithecium (Chivers, 1915). Although Corda was not aware of the true function of the ascus, he recognized that it was in some way responsible for supporting the spores. In 1849 Fries (Chivers, 1915) recognized the true nature of the ascus as the container of the spores. In 1881, Zopf contributed a notable monograph with excellent illustrations and clear-sighted descriptions of ten species listed under two sub-genera: Chaetomium having an ostiolate perithecium, and Chaetomidium with a non-ostiolate perithecium. Chaetomidium was elevated to a genus by Saccardo (1882). Bainier (1910) described a number of Chaetomium species, many of which were reduced to synonyms at later dates. Bainier accepted Saccardo's treatment of Chaetomidium as a genus.

A. H. Chivers (1915) published an illustrated monograph of the genera Chaetomium and Ascotricha, recognizing twenty-eight distinct species of Chaetomium. The form of the perithecial hairs was used as the major separation character. Skolko and Groves (1948) suggested that the shape and the size of the perithecia, conspicious characters of the hairs, and the

shape and size of the spores provide a more practical basis for species classification. In their monograph (1948, 1953) fifty-three species of Chaetomium were recognized. In 1961 L. M. Ames recognized eighty-five species of Chaetomium and used such characters as the shape of the perithecium, the form of the perithecial hairs, the shape of the ascus and ascospores, for species separation.

Most investigators characterize the genus as having superficial perithecia that are ostiolate. The wall of the perithecium is membranous and modified hairs are produced from the cells of the wall. The hairs at the top of the perithecium are specialized and may be arched, spine-like, coiled, or branched. The ascus is gelatinous-walled and may be club shaped, linear, or cylindrical. Deliquescence takes place before the ascospores are mature and most asci contain eight spores, but at least one species contains four (Chaetomium tetrasporum Hughes). The single celled ascospores may be light or dark colored and are usually lemon shaped. The economic importance of Chaetomium lies in its ability to deteriorate cellulose materials such as military equipment and clothing. Certain species are thought to be responsible for plant diseases such as a spot rot of apple. Most species, however, are saprophytic. Isolates of the genus often occur on samples of soil, paper, cloth, dung, and similar materials.

The genus Chaetomium is generally assigned to the Chaetomiaceae, a family characterized by having non-stromatic perithecia, noticeable hairs, and evanescent asci with unicellular ascospores. Chaetomidium, Ascotricha, and Lophotrichus are three other genera usually placed in this family. The perithecium of Chaetomidium is approximately twice as large as the typical Chaetomium perithecium and lacks an ostiole. Ascotricha possesses a

definite conidial stage that distinguishes it from Chaetomium and Chaetomidium. Recently, however, Daniels (1961) described an imperfect stage of Chaetomium piluliferum Daniels that was found to be Botryotrichum piluliferum. Species of Lophotrichus characteristically possess submerged perithecia with long necks and prominent hairs surrounding the ostiole.

The family Chaetomiaceae is usually placed in the order Sphaeriales of the Pyrenomycete series of the Ascomycetes (Lindau, 1897; Gwynne-Vaughan, 1922; Miller, 1949; Bessey, 1950; Alexopoulos, 1952). Members of the Chaetomiaceae generally possess such characteristics of the order as ostiolate ascocarps, paraphyses, periphyses, and a definite hymenium. One of the major departures from this treatment was that of Nannfeldt (1932), who places the Chaetomiaceae in the Plectascales, an order that is characterized by early deliquescence of the ascus, irregular arrangement of the asci, and usually closed ascocarps. On the basis of centrum characteristics Lutrell (1951) places the Chaetomiaceae in his order Xylariales, an order similar in concept to the Sphaeriales. Recently, Martin (Ames, 1961) established the order Chaetomiales for the family Chaetomiaceae, the order Chaetomiales differing from the Sphaeriales by its possession of evanescent asci. Alexopoulos (1962) and Ames (1961) adhere to Martin's interpretation.

In most Ascomycetes, except the yeasts and a few similar forms, the asci arise from the ascogenous hyphae. The ascogenous hyphae are generally considered to be outgrowths of an ascogonium. In Pyronema omphalodes (Claussen, 1912), the Discomycete fungus on which discussions of ascogenous cells are often based, the terminal cell of each ascogenous hypha curves back upon itself to form a binucleate hook-shaped cell known as a crozier. The nuclei in the crozier divide simultaneously and septations are laid down, leaving two of the nuclei at the curve, one nucleus at the tip, and

the other one in the base cell. The uninucleate tip cell is known as the ultimate cell, the binucleate curved cell is the penultimate cell, and the base cell is called the antepenultimate cell. The two haploid nuclei in the penultimate cell fuse, and this cell elongates and becomes the young ascus. The ultimate and antepenultimate cells fuse and produce a new crozier, and this process of crozier formation may then be repeated many times. The diploid fusion nucleus of the young ascus undergoes three successive divisions. The first two are meiotic and the third a mitotic division resulting in eight haploid nuclei that mature into the ascospores.

Enough studies of ascogenous hyphae in various genera of Ascomycetes have been made, however, to indicate that variation among genera, and even among species within a genus, exist in the ascogenous cells. In 1937 Andrus and Harter (Gaumann, 1952) indicated that in certain species of Ophiostoma, as O. fimbriatum (E. & H.) Nannf., the diploid crozier is represented by a naked cytoplasmic ball that does not develop directly into an ascus. The true functional ascus lies within this cytoplasmic ball. Emmons (1932) in his morphological study of two species of Thielavia found asci originating from croziers in one species, Thielavia terricola, and asci originating from uninucleate cells in the other one, Theilavia Sepedonium. Seventeen strains of twelve species of Penicillium and one related species, Byssochlamys fulva Oliver & Smith, were studied by Emmons in 1935. The study revealed two lines of ascus development. One line was characterized by asci borne in chains. Penicillium Wortmanni Klocker and Penicillium spiculisporum Lehmann were considered to be representatives of this series. The second line of ascus development was represented by Penicillium luteum Zukal and Byssochlamys fulva. This series produced asci from typical croziers and the ascus was borne as a sessile side bud or on a stalk arising from the ascogenous hyphae. Benjamin (1955) supported

Emmons' study of Penicillium. He also reported variation in the ascogenous hyphae of Aspergillus.

An analysis of variation in the ascogenous hyphae in the genus Chaetomium is limited to the Discussion and Conclusion section of this paper.

II. LITERATURE REVIEW

Despite the large number of species in the genus Chaetomium and the fact that most species grow readily in culture and produce mature perithecia rapidly, few studies have been made of the ascogenous hyphae. Greis (1941) reported information pertaining to the ascogenous hyphae of Chaetomium globosum and Chaetomium bostrychodes in his study of the fertilization processes in the genus Chaetomium. Presumably his observations were all from sectioned material, since he makes no mention of the carmine smear technique. Greis described the ascogenous cells as binucleate and he considered the asci to arise without crozier formation. Under certain conditions, an additional ascus was reported to originate from the base of the original ascus, likewise, without croziers. Karyogamy was expressed as taking place in the young ascus.

Van der Weyen's (1954) investigation of the ascogenous hyphae of Chaetomium globosum was primarily cytological and he made extensive use of the carmine smear method. He explored the ascogenous hyphae of numerous perithecia and reported that the majority of the cells were uninucleate and a small minority were binucleate. The binucleate ones were frequently seen as the terminal cell of an ascogenous hypha and interpreted as representing a young ascus. Van der Weyen described crozier formation as occurring on occasion and the fusion of the dikaryotic nuclei was reported as taking place in a bud previously formed on the penultimate cell.

Likewise utilizing the carmine smear method, Whiteside (1959) studied two species of Chaetomium in his cytomorphological investigation of members of the family Chaetomiaceae. He reported that the ascogenous cells of Chaetomium globosum appeared predominantly uninucleate in both sectioned

material and carmine smear preparations. Whiteside observed no croziers in Chaetomium globosum, but abundant croziers were reported for Chaetomium brasiliense.

III. MATERIALS AND METHODS

Four species of Chaetomium were studied in this investigation. Two of them, Chaetomium dolichotrichum Ames (1044.7) and Chaetomium murorum Corda (1044.8), were obtained from the Mycological Culture Collection of the University of Illinois, these cultures being originally provided by L. M. Ames and bearing his culture numbers. The two other species of Chaetomium were isolated by Dr. Whiteside. An isolate that was obtained in 1955 from the leaves of Hemerocallis plants growing in the Botany Annex Greenhouse of the University of Illinois proved to be identical with a specimen revived from the Mycological Collection of the University of Illinois, originally provided by Ames as Chaetomium aureum (1043.9). The other species was isolated in Coles County in 1961 from a dung sample. It was identified with the aid of Ames' taxonomic monograph of the Chaetomiaceae (1961) as Chaetomium caprinum Bainier.

The medium used was sterile oatmeal flakes over which 1½% agar was poured, and the inoculated plates were incubated at 28° C. for seven to ten days. Small blocks of agar containing many mature perithecia were then cut from the plate and allowed to soak in Carnoy's killing solution (three parts of absolute alcohol and one part of glacial acetic acid) for six hours. The agar blocks were then immersed in propiono-carmine stain for a period of time ranging from twenty-four hours to seventy-five hours. The propiono-carmine stain was prepared by combining 90 cc of propionic acid in a flask with 110 cc of distilled water and one gram of carmine stain. The solution was boiled for at least two hours at a constant temperature.

After the agar blocks had been soaked in the stain, a few perithecia were then removed and put into a fresh drop of stain on a microscopic slide. The ascogenous cells were dissected from the perithecia and a rusty dissecting

needle was dabbed into the drop of stain containing the ascogenous cells to intensify the color of the nuclei. The ascogenous cells were then washed with fresh stain, carefully spread out, and examined. The better slides were sealed with a fluid prepared by combining, in the order mentioned, one part 45% glacial acetic acid, one part white Karo syrup, and one part saturated aqueous suspension of pectin. The sealed slides were then stored at a cool temperature for further examination.

All of the drawings were made from these slides with the aid of a camera lucida and their magnifications are indicated.

IV. OBSERVATIONS

The cytomorphology of the ascogenous hyphae of four species of Chaetomium were studied. The species were selected on the basis of their availability and such external features as the form of the terminal hairs and the size of the perithecium.

A. Chaetomium aureum

Chaetomium aureum was selected for study because it has essentially straight terminal perithecial hairs and a small perithecium measuring 100 to 140 microns in diameter. Under the cultural conditions employed, perithecia were abundant after an eight day growth period.

The ascogenous cells were small and appeared granular when stained with propiono-carmine. They measured 1 to 3 microns in width and were entangled in a gelatinous mass that made the preparation of adequate slides difficult. The nuclei were compact and stained a light red, their size about half the width of the ascogenous cell. The ascus appeared to originate from an ordinary ascogenous cell and no evidence of crozier formation was observed. Most cells of the ascogenous hyphae were uninucleate (Plate I), but an occasional binucleate terminal cell was seen (Plate I, fig. 4).

B. Chaetomium murorum

Chaetomium murorum was studied because its large perithecia, measuring 240 to 340 microns, are adorned with long slender terminal hairs with circinate tips. Perithecial growth was scattered and not abundant after an eight day growth period.

The ascogenous cells were large, measuring 3 to 5 microns in width, and separated easily. The cells were predominately uninucleate (Plate II) but a few binucleate cells were observed (Plate II, figs., 12, 17, and 18).

The nuclei were compact and stained a light red, their size about one-third to one-half the width of the mature ascogenous cell. The asci arose from the typical ascogenous cell and no evidence of croziers was seen.

C. Chaetomium caprinum

Chaetomium caprinum was selected for study because of its tall vase-shaped perithecium with spirally coiled terminal hairs. The base of the perithecium measured 200 to 240 microns. Perithecia were scattered and rather sparse after an eight day growth period.

The ascogenous cells were very granular when stained and measured 2 to 4 microns in width. They separated easily, making it possible to prepare excellent slides. The diffuse nuclear material stained vividly and most nuclei measured approximately 2 microns in diameter. Typical croziers were abundantly observed (Plate III) and the asci were seen to originate from the penultimate cells of the croziers. Often the ultimate and antepenultimate cells fused to form a new crozier (Plate III, fig. 20).

D. Chaetomium dolichotrichum

Chaetomium dolichotrichum was selected for study because it is representative of a group of species having dichotomously branched terminal hairs. Its perithecia are relatively small, measuring 110 to 150 microns in diameter. Perithecia were abundant after an eight day incubation period.

The ascogenous cells were small, measuring one to three microns in width, and separated easily. The nuclei usually stained light red and were compact, but in some instances, the nuclear material was diffuse and stained darker. Croziers were found to be abundant (Plate IV). The asci appeared to arise from the penultimate cells of the abundant croziers. The ultimate and penultimate cells regularly appeared to unite and form new croziers.

DISCUSSION AND CONCLUSION

The four species of Chaetomium that were studied illustrated two types of ascus development. In Chaetomium aureum and Chaetomium murorum the ascus arose from an ascogenous cell and no definite evidence of croziers was observed. On the other hand, in Chaetomium caprinum and Chaetomium dolichotrichum, croziers in the ascogenous hyphae were regularly observed and the ascus developed from the penultimate cell of a crozier.

Greis (1941) reported that the ascogenous cells of Chaetomium globosum were binucleate. Van der Weyen (1954) described the ascogenous cells of Chaetomium globosum as mostly uninucleate, although occasional binucleate cells were seen. Whiteside (1961) supported this part of Van der Weyen's observations on Chaetomium globosum. Van der Weyen regarded the binucleate cells as representing young asci originating from a crozier. It was Whiteside's opinion that this species lacked croziers and the binucleate cells might be young asci prior to nuclear fusion or more probably ascogenous cells in which the formation of septa had not yet occurred after a nuclear division. Similar nuclear characteristics for Thielavia Sepedonium Emmons were reported by Emmons (1932). He also considered that the asci developed from the uninucleate cells, while the binucleate ones were in a stage prior to septum formation. In this present study, a similar condition was observed in Chaetomium aureum and Chaetomium murorum. It is the opinion of this investigator that the asci of these two species of Chaetomium arose from the uninucleate ascogenous cells and that the binucleate cells represent a cell stage prior to septum formation.

In Whiteside's (1957) morphological studies of the genus Chaetomium, he suggested that the form of the terminal peritheceial hairs may not always

be an indication of a close relationship of species. In particular, on the basis of the ascogonium, mycelial hairs, and other perithecial characteristics, he felt that Chaetomium aureum and Chaetomium brasiliense were very closely related although they had distinctly different terminal hairs. He found that Chaetomium brasiliense had croziers but he did not study the ascogenous hyphae of Chaetomium aureum. In this present study it had been expected that croziers would very probably occur in Chaetomium aureum. Since no evidence of croziers in this species was observed, perhaps there is some question of how useful the characteristics of the ascogenous hyphae might prove to be in establishing taxonomic relationships in the genus.

Whiteside's description of the two species of Chaetomium, Chaetomium brasiliense possessing definite croziers and Chaetomium globosum devoid of croziers, parallels Emmons' investigation of Thielavia Sepedonium as producing uninucleate ascogenous hyphae lacking croziers and Thielavia terricola as producing asci by crozier formation. This present investigation reporting two Chaetomium species possessing croziers and two lacking them further extends Whiteside's findings in the genus Chaetomium. On the basis of these studies it is probable that in Ascomycetes much species variation in ascogenous hyphae within a genus might be expected, and this is an area of investigation that has been largely neglected.

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EXPLANATION OF PLATE I

Chaetomium aureum Chivers

Fig. 1. Uninucleate ascogenous hyphae and young asci. X 1750.

Fig. 2. Four uninucleate ascogenous cells in early stages of asci development. X 1750.

Fig. 3. A group of uninucleate ascogenous cells and young asci. The binucleate cell is in a stage prior to septum formation. X 1750.

Fig. 4. A cluster of young asci and ascogenous cells. The binucleate ascogenous cell represents a stage prior to septum formation. X 1750.

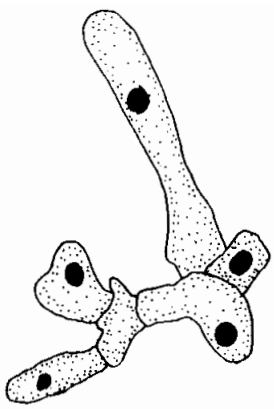
Fig. 5. A small cluster of young asci. X 1455.

Fig. 6. Uninucleate asci and ascogenous hyphae. Two ascogenous cells show asci buds. X 1750.

Fig. 7. A long strand of ascogenous hyphae and asci. X 1750.

Fig. 8. A cluster of asci just prior to reduction division. X 1750.

PLATE I



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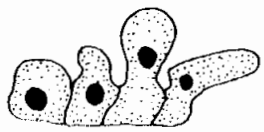

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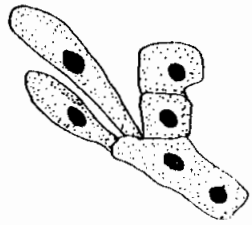

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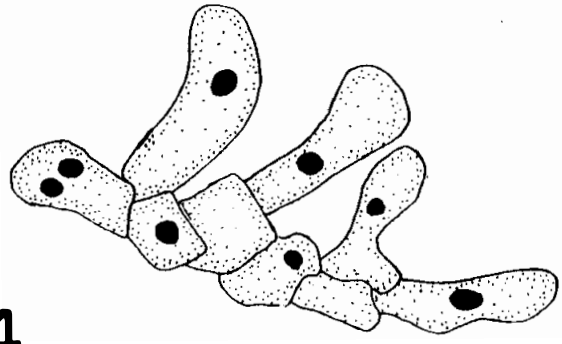

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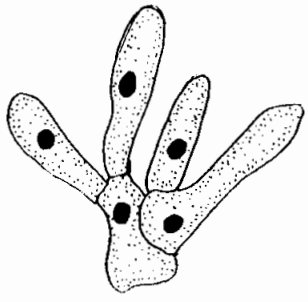

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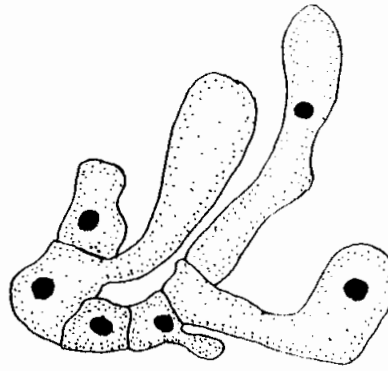

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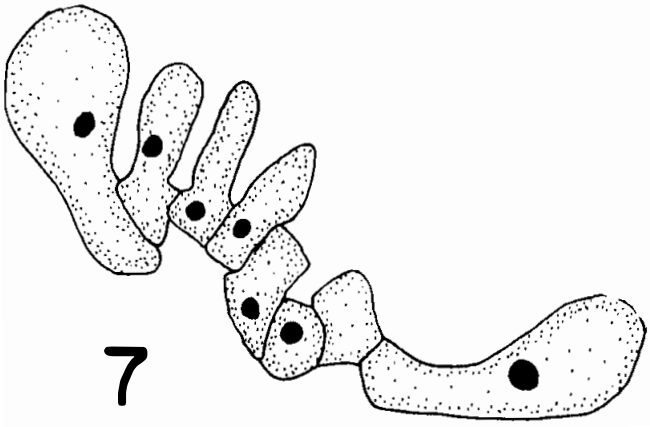

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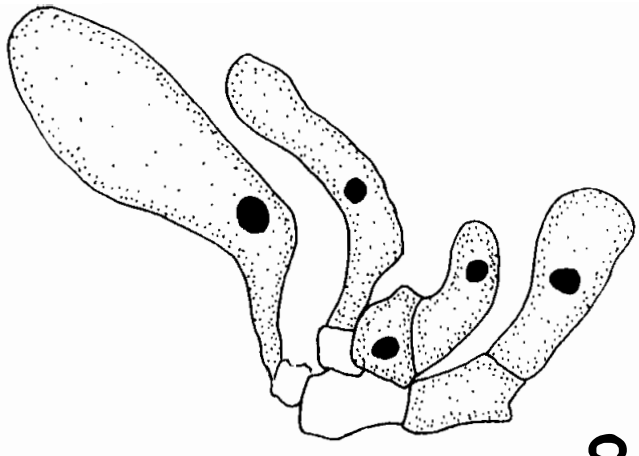

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Chaetomium aureum

EXPLANATION OF PLATE II

Chaetomium murorum Corda

Fig. 9. A strand of uninucleate ascogenous cells showing developing ascus buds. X 1750.

Fig. 10. A cluster of uninucleate ascogenous cells and asci. X 1750.

Fig. 11. A strand of uninucleate ascogenous cells showing ascus buds. X 1750.

Fig. 12. Two ascogenous cells. The binucleate cell is in a stage prior to septum formation. X 1750.

Fig. 13. Uninucleate ascogenous hyphae showing early stages of developing ascus buds. X 1750.

Fig. 14. Uninucleate ascogenous hyphae with developing ascus buds. X 1750.

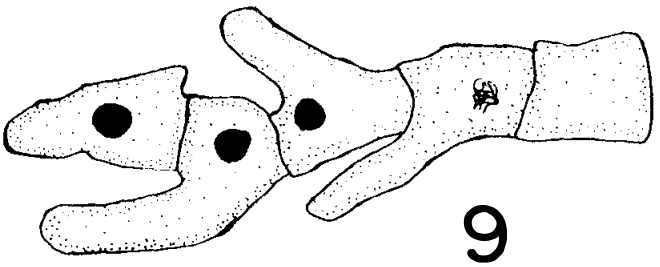
Fig. 15. Ascogenous hyphae with ascus buds. X 1750.

Fig. 16. Migration of nuclei into young asci. X 1750.

Fig. 17. Uninucleate ascogenous hyphae and asci with a binucleate cell. X 1750.

Fig. 18. Three ascogenous cells, one at a stage prior to septum formation. X 1750.

PLATE 11



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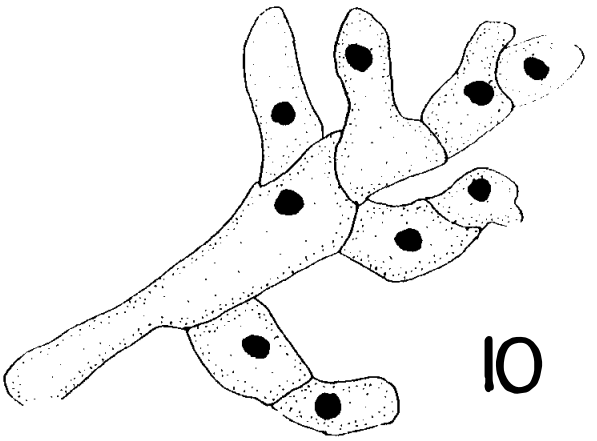

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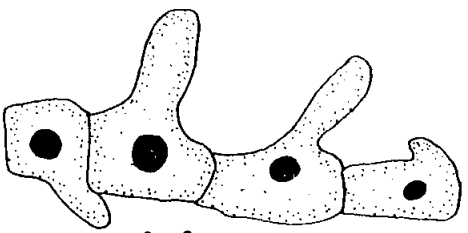

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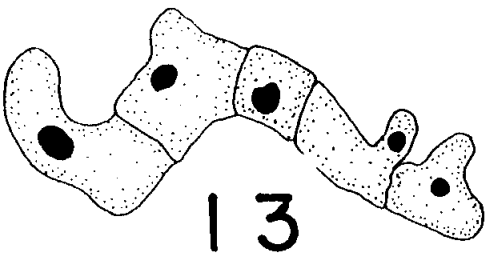

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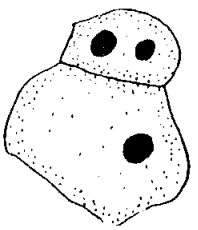

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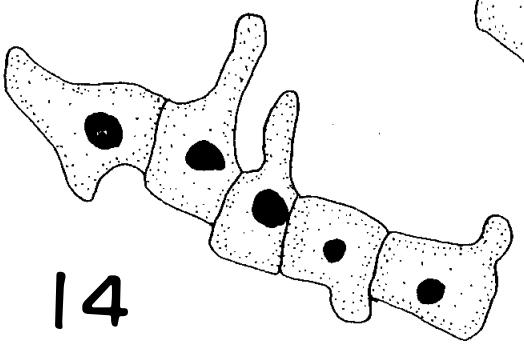

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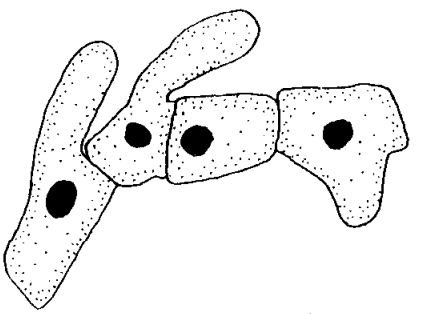

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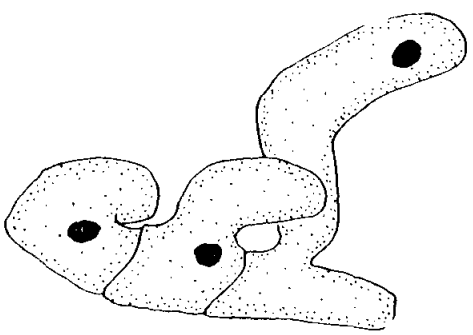

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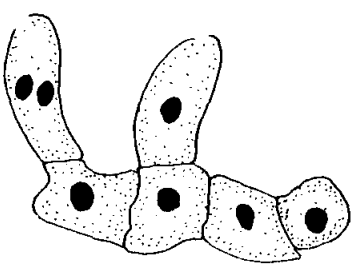

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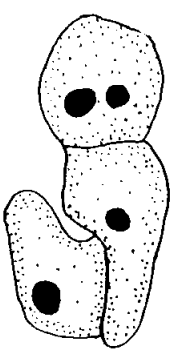


18

Chaetomium murorum

EXPLANATION OF PLATE III

Chaetomium caprinum Bainier

Fig. 19. A binucleate curved ascogenous cell. This cell is an early stage in the formation of a crozier. X 1750.

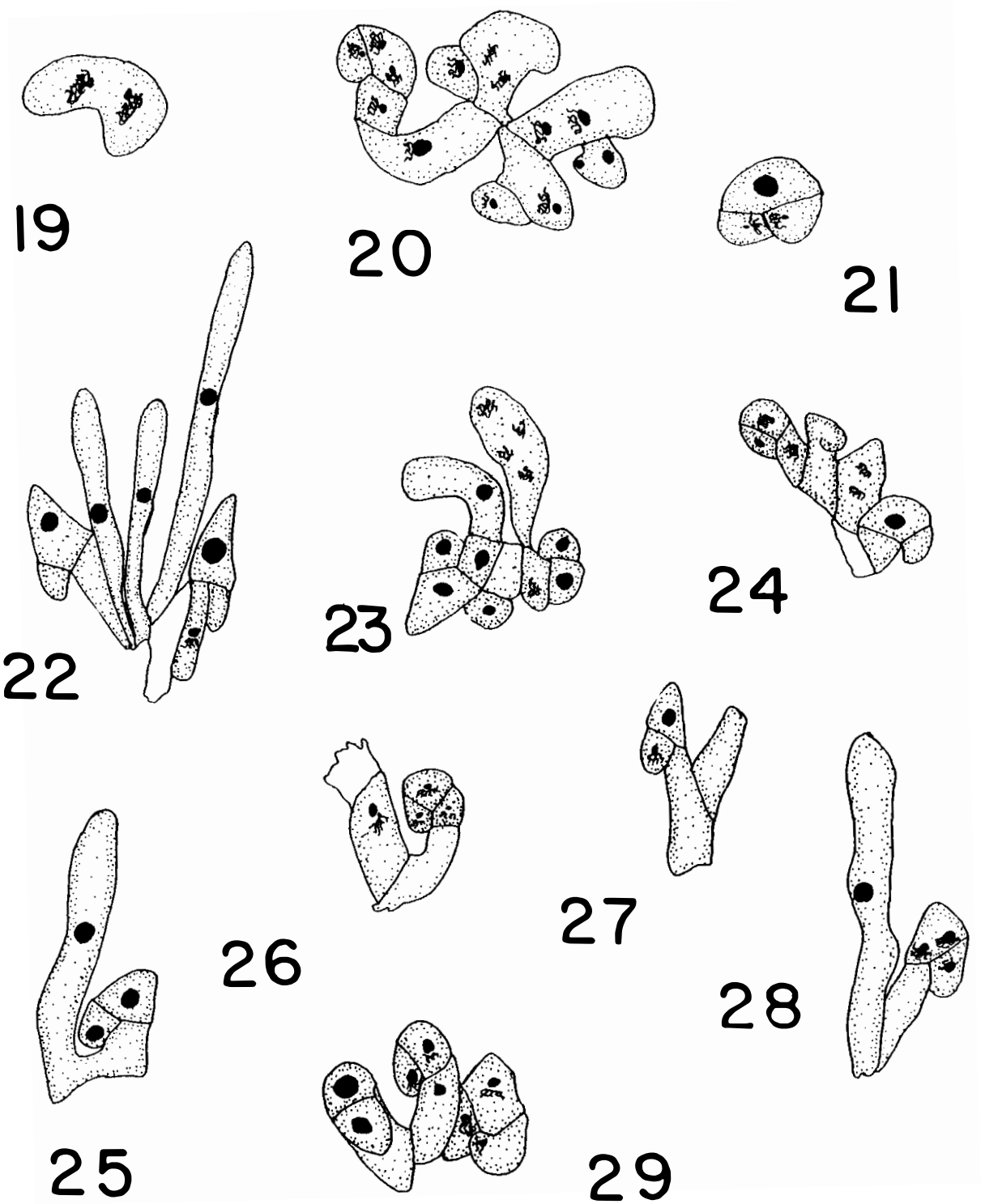
Fig. 20. A cluster of ascogenous cells showing a well developed crozier. A young crozier can be seen developing from the ante-penultimate cell of a previous crozier. X 1750.

Fig. 21. A well developed crozier. The two nuclei have fused in the penultimate cell and the ultimate and ante-penultimate cells are about to fuse. X 1750.

Fig. 22. A group of asci and associated crozier formations. X 1750.

Figs. 23-29. Clusters of ascogenous cells showing asci and crozier formations in various stages of development. X 1750.

PLATE III



Chaetomium caprinum

EXPLANATION OF PLATE IV

Chaetomium dolichotrichum Ames

Fig. 30. The binucleate curved cell in figure 30 is an early stage in the formation of a crozier. X 1750.

Fig. 31. A well developed crozier with the two nuclei in the penultimate cell and one nucleus each in the ultimate and ante-penultimate cells. X 1750.

Figs. 32-34. Clusters of ascogenous cells showing asci and well defined croziers. X 1750.

Fig. 35. A cluster of ascogenous cells showing a young crozier originating from the ante-penultimate cell of an earlier crozier. X 1750.

Figs. 36-38. Groups of ascogenous cells showing abundant croziers. X 1750.

EXPLANATION OF PLATE IV

Chaetomium dolichotrichum Ames

Fig. 30. The binucleate curved cell in figure 30 is an early stage in the formation of a crozier. X 1750.

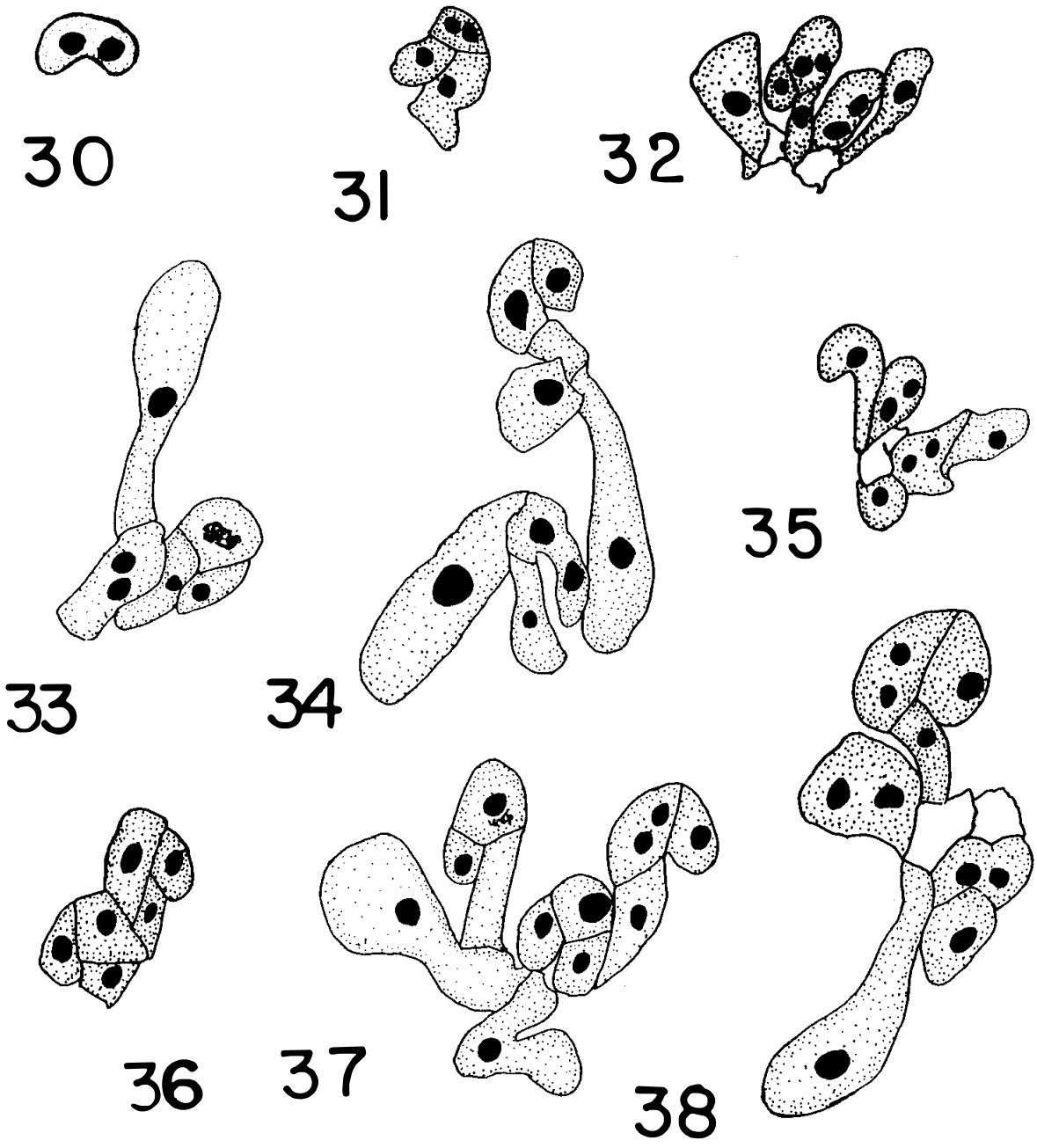
Fig. 31. A well developed crozier with the two nuclei in the penultimate cell and one nucleus each in the ultimate and ante-penultimate cells. X 1750.

Figs. 32-34. Clusters of ascogenous cells showing asci and well defined croziers. X 1750.

Fig. 35. A cluster of ascogenous cells showing a young crozier originating from the ante-penultimate cell of an earlier crozier. X 1750.

Figs. 36-38. Groups of ascogenous cells showing abundant croziers. X 1750.

PLATE IV



Chaetomium dolichotrichum