

Studies in Basidial Nuclear Behavior of Selected Species of Clavarioid and Cantharelloid Fungi

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Abstract. Basidial nuclear behavior was examined in several pivotal taxa of Homobasidiomycetes in order to help elucidate, in conjunction with known biochemical and morphological characters, their phylogenetic position. The taxa investigated were *Cantharellus minor*, *Clavulinopsis aurantio-cinnabarina*, *C. amoena*, *C. fusiformis*, *C. corniculata*, *C. laeticolor* and *Multiclavula mucida*. Meiotic figures in the basidium were stained using Cléménçon's technique.

Early attempts to delineate discrete taxa of the fleshy fungi drew on gross morphological characters (SCHAEFFER, 1774; PERSOON, 1801; FRIES, 1821), but later, microscopic examination of fruit bodies led to the inclusion of additional characters (i. e. PATOUILLARD, 1900). The use of certain staining and sectioning techniques (specifically, iron haemotoxylin-stained tissue embedded in paraffin) allowed analysis of intracellular phenomena, including nuclear behavior. Two distinct patterns of meiotic nuclear behavior were observed and described by JUEL (1898), based on the position and direction of meiotic spindles in the basidium. In one pattern (chiastic), the diploid nucleus was located in the extreme distal position of the immature basidium immediately prior to the onset of meiosis I. Spindle orientation during metaphase and anaphase I was perpendicular to the long axis of the basidial initial (transverse in the basidial lumen). In the other pattern (stichic), the prophase I nucleus was located in the median portion of the basidial initial, never the apical, with the spindles oriented parallel to the long axis of the immature basidium (longitudinal in the basidial lumen). Much later, BOIDIN (1951) added general observations on the placement of meiosis II division figures to JUEL's basic descriptions.

Over the years, observations of a number of taxa were made, but little emphasis was placed on the results for use in taxonomic descriptions. ULBRICH (1928) recognized that the clavarioid fungi exhibited both chiastic and stichic basidia. From the presumably stichobasidial forms, he segregated two genera, *Stichoramaria* (fruit bodies branched, stichic basidium) and *Stichoclavaria* (fruit bodies unbranched, stichic basidium). *Stichoramaria* was a superfluous name for *Clavulina* SCHROETER. *Stichoclavaria* was founded on *Clavaria falcata* ss. JUEL, but JUEL's concept was not true to the original taxon by that name

proposed by FRIES (1821). *Stichoclavaria* was neglected for lack of an identifiable type species (see below), and probably because of the difficulty in ascertaining its primary character.

JUEL (1898) considered the orientation of division spindles an important indication of taxonomic relationships, and MAIRE (1902) proposed a new phylogenetic chart of the basidiomycetes based on basidial nuclear behavior. DONK (1933) and OLIVE (1953) did not totally accept MAIRE's conclusions, but used nuclear behavior as a supporting character in otherwise classical taxonomy. Today the character remains controversial perhaps due in part to the lack of explanation of its mechanism. If the character is regarded as important in the consideration of taxonomic and phylogenetic relationships, then knowledge of the factors which control the distinct nuclear behavior patterns must be achieved.

The size and shape of the basidium have been thought to dictate nuclear behavior in that basidium. Stichobasidial behavior has been related to small cylindrical basidia and chiasibasidial behavior to clavate basidia (BOIDIN, 1951; VAN OVEREEM, 1923). DONK (1964) believed that this orientation was more likely a combination of factors determined not only by spindle length but also the resistance offered by the cytoplasm and its inclusions (such as vacuoles and other bodies). In both theories the pattern of nuclear behavior is not directly genetically controlled.

On completion of the divisions of meiosis, the four haploid nuclei may enter either of two developmental series. In the first series, the four-nucleate stage is followed by a mitotic division, with the position and orientation of the division figures variable in the upper portion of the basidium. A single nucleus may migrate through each sterigma leaving the basidium with four "residual nuclei" (PENANCIER, 1961). If a mitotic division does occur in the spore, it may happen prior to or soon after release, producing haploid homokaryotic dikaryons. Lastly, all eight nuclei may migrate to the spores, producing haploid heterokaryotic dikaryons. In the second developmental series, no mitotic division follows the four-nucleate stage. Each spore is initially a haploid monokaryon but may complete a mitotic division before or after release of that spore from the sterigma.

Material and Methods

Hymenial tissue from several fruit bodies of each taxon observed was fixed and stained according to CLÉMENÇON's (1968) technique. Best results were obtained when the tissue was boiled for greater than 60 s, with 90 to 120 s optimum. In some cases good results were achieved when the tissue was washed in 50 percent acetic acid prior to boiling in the acetocarmine stain. Squash mounts were examined with

a Wild Heerbrugg M 20 research microscope using both brightfield and phase optics.

I. *Cantharellus minor* PECK.

History. *Cantharellus minor* has long been accepted as a "typical" *Cantharellus*, but its stature and consistancy is similar to some *Hygrophorus* species. CORNER (1966) did not question its placement in *Cantharellus*, and HESLER and SMITH (1963), when monographing *Hygrophorus*, did not consider this name in relation to that genus. Conversely, SMITH (1968) described *C. minor* from Michigan (perhaps as a misapplied name) with no consideration as to its possible placement elsewhere.

PETERSEN (1976) examined PECK's type specimen and found the gill trama to be parallel. This was the first report of parallel arrangement of hyphae in the gill trama in a cantharelle, whereas such differentiation has been found quite frequently in the Agaricales, including *Hygrophorus*. On this character alone, *C. minor* would be allied with the section *Hygrocybe* (parallel arrangement in the gill trama) of *Hygrophorus*.

Pigmentation of *C. minor* has been found to be similar to other species of *Cantharellus* (FIASSON, et al., 1970). Several carotene pigments were extracted and identified from collections of *C. minor* from the southern Appalachian Mountains. Conversely, preliminary data on *Hygrophorus* has shown pigmentation in most infrageneric groups of that genus to be noncarotenoid. On this evidence, *C. minor* would appear appropriately placed in *Cantharellus*.

Finally, meiotic nuclear behavior in the Agaricales (including *Hygrophorus*) has been reported as chiastobasidial, while those species of *Cantharellus* which have been examined exhibit exclusively stichobasidial behavior (JUEL, 1916).

Results. Undifferentiated hymenial elements, presumably very immature basidia, were dikaryotic, cylindrical (1.8 to 2.5 μm diam) and subtended by clamp connections. The nuclei stained readily and were approximately equal in size (1.4 to 2.2 μm diam). Within the lightly stained cytoplasm were scattered small vacuoles with small refringent droplets also evident and persisting through all stages of basidial maturation (Fig. 1).

After karyogamy, the resultant interphase nucleus was large (3.4 to 5.0 μm diam). During the prolonged prophase period the basidial initial became narrowly clavate, with the nucleus located near the basidial median, but never in an extreme distal or proximal position of the cell. Cytoplasmic vacuoles were generally both distal and proximal (Fig. 2).

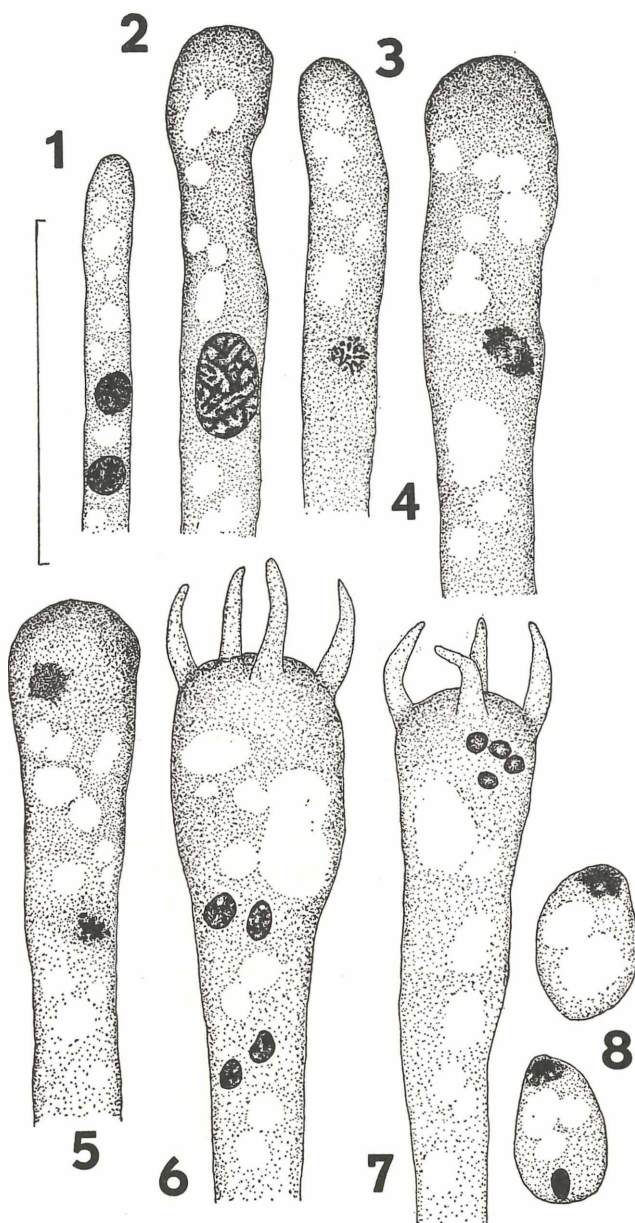


Plate 1

Fig. 1—8. *Cantharellus minor*. 1. Dikaryotic state in basidial initial. 2. Prophase I. 3. Metaphase I. 4. Anaphase I. 5. Telophase I. 6—7. Four-nucleate stage. 8. Spores-uninucleate and binucleate. Standard line = 20 μ m

Leptotene and zygotene stages were not observed, but chromosomal condensation toward pachytene was evident in the regularly shaped, granular nucleus. Diplotene was represented by intensification of the granular appearance and an observable strand-like configuration, followed by further condensation during diakinesis.

Condensation of chromatin material was most noticeable at metaphase I (Fig. 3), but no metaphase plate was discernible. Spindle orientation was oblique and placement was in the median third of the immature basidium. Chromosomes separated irregularly during anaphase I (Fig. 4), and the telophase I nuclei were peripheral with observable membranes. During meiosis I, the cytoplasm became denser distally with more numerous proximal vacuoles.

Meiosis II divisions were asynchronous; nuclei were not densely staining; placement and orientation of the spindles were irregular, but never strictly distal (Fig. 5). The resultant four haploid nuclei each were approximately 2 μ m diam, and somewhat condensed when sterigmata formed (Fig. 6—7). Sterigmata number was (2)—4—(6). Several instances of four-nucleate stages were observed, as well as a single post-meiotic division. In no case were there fewer nuclei than sterigmata. A single nucleus migrated through each sterigma, and the spores were released as haploid monokaryons (Fig. 8), the single nucleus invariably in juxtaposition to the hilar appendix. A subsequent mitotic division resulted in a second polar nucleus, and mature spores included refringent cytoplasmic inclusions (Fig. 8).

Conclusions. *C. minor* was found to exhibit stichobasidial nuclear behavior similar to the generalized type described by JUEL (1898) and BOLDIN (1951). Several instances of a single post-meiotic mitotic division were observed, but this did not appear to be common. In all basidia observed the eventual number of nuclei was greater than the number of sterigmata (with four sterigmata and spores observed most frequently). These data on *C. minor* agree with earlier reports that the genus *Cantharellus* was stichobasidial (MAIRE, 1902; JUEL 1916).

Cantharellus has been postulated as intermediate between the Agaricales and the agaricoid Aphyllophorales. Some investigators have felt this relationships might be best explained between the genera *Cantharellus* and *Hygrophorus* (HESLER and SMITH, 1963; PETERSEN, 1971). The long cylindrical basidia and the waxy appearance are the significant characters shared by both genera. HESLER and SMITH (1963), though, felt that *Cantharellus* (interwoven trama) may have evolved to *Hygrophorus*, sect. *Camarophyllopsis* (interwoven gill trama). Although *Cantharellus* has been found to contain no species with chiasmatobasidial behavior, HESLER and SMITH (1963) believed that this should not preclude derivation of *Hygrophorus* and from *Cantharellus*.

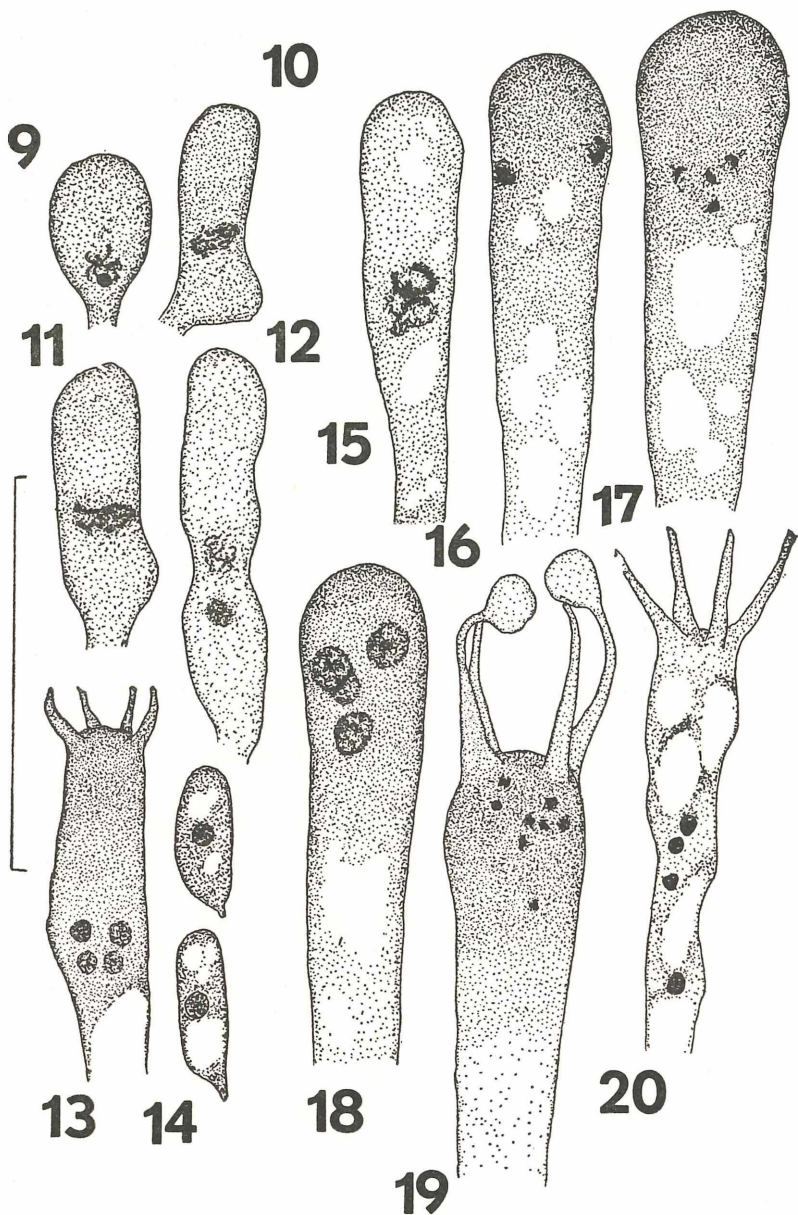


Plate 2

Figs. 9–14. *Multiclavula mucida*. 9–11. Prophase I showing distal elongation. 12. Telophase I. 13. Four-nucleate stage. 14. Elongate spores

Figs. 15–20. *Clavulinopsis fusiformis*. 15. Prophase I. 16. Telophase I. 17. Anaphase II. 18. Four-nucleate stage. 19. Eight-nucleate stage with sterigmata. 20. Effete basidium with 4 “residual nuclei.” Standard line = 20 μ m

ARPIN & FLASSON (1971) have introduced *Gerronema* as a possible candidate for relationships with *Cantharellus*. *Gerronema* shows strong tendencies toward parallel gill trama (SINGER, 1975), and deposits significant amounts of carotenoid pigment within the fruit bodies. Conversely, at least *Gerronema chrysophylla* (Fr.) SINGER (the only species thus far investigated) exhibits chiasitic nuclear behavior (KÜHNER, personal communication).

II. *Multiclavula mucida* (FRIES) PETERSEN

History. ULBRICH (1928) proposed the genus *Stichoclavaria* based on JUEL's observation of stichic basidia in *Clavaria* "*falcata*" auct. non FRIES. As this was the only species with unbranched fruit bodies exhibiting stichobasidial nuclear behavior, he segregated the taxon from the chiasmobasidial species of *Clavaria*.

From JUEL's (1916) descriptions it is evident that he misapplied the name *Clavaria falcata*. The organism he described and illustrated produced elongate spores and supernumerary sterigmata, neither of these characters found in *C. falcata* (= *C. acuta* teste DONK, OLEXIA). A comparison of the descriptions of FRIES (1821) for *C. falcata* and *C. mucida* show how easily this confusion might arise. Although *Clavaria* (= *Multiclavula*) *mucida* is now known to occur on wood, FRIES acknowledged two forms, one of which was on soil, the habitat of *C. falcata*.

In order to discover the real identity of *Stichoclavaria*, it is necessary to search for a terrestrial, white, unbranched fruit body, with agglutinated hymenium, elongate spores and supernumerary sterigmata. This list of characters satisfies the descriptions of both Juel and Fries. The poorly pigmented fruit bodies of *Multiclavula corynoides* (PECK) PETERSEN, which occurs in Sweden, would seem a likely choice. Studying nuclear behavior in *Multiclavula* would be necessary to establish any relationship. If stichobasidial, *Multiclavula corynoides* might be proposed as synonymous with JUEL's misapplication of *Clavaria falcata*. If the identity of *C. falcata* sensu JUEL non FRIES is revealed to be a *Muticlavula*, then *Stichoclavaria* might be taken as the correct name for *Multiclavula* PETERSEN (1967).

Results. Undifferentiated hymenial elements, presumably very immature basidia were dikaryotic, cylindrical (1 to 1.5 μ m diam) and subtended by clamp connections. The nuclei were approximately equal in size and the cytoplasm stained evenly without any visible cytoplasmic inclusions.

After karyogamy, the resultant interphase nucleus was large, without an evident nuclear membrane. A prominent nucleolus was present until late stages of prophase (Fig. 9). During the prolonged prophase period, the metabasidium became elongated distally, with the

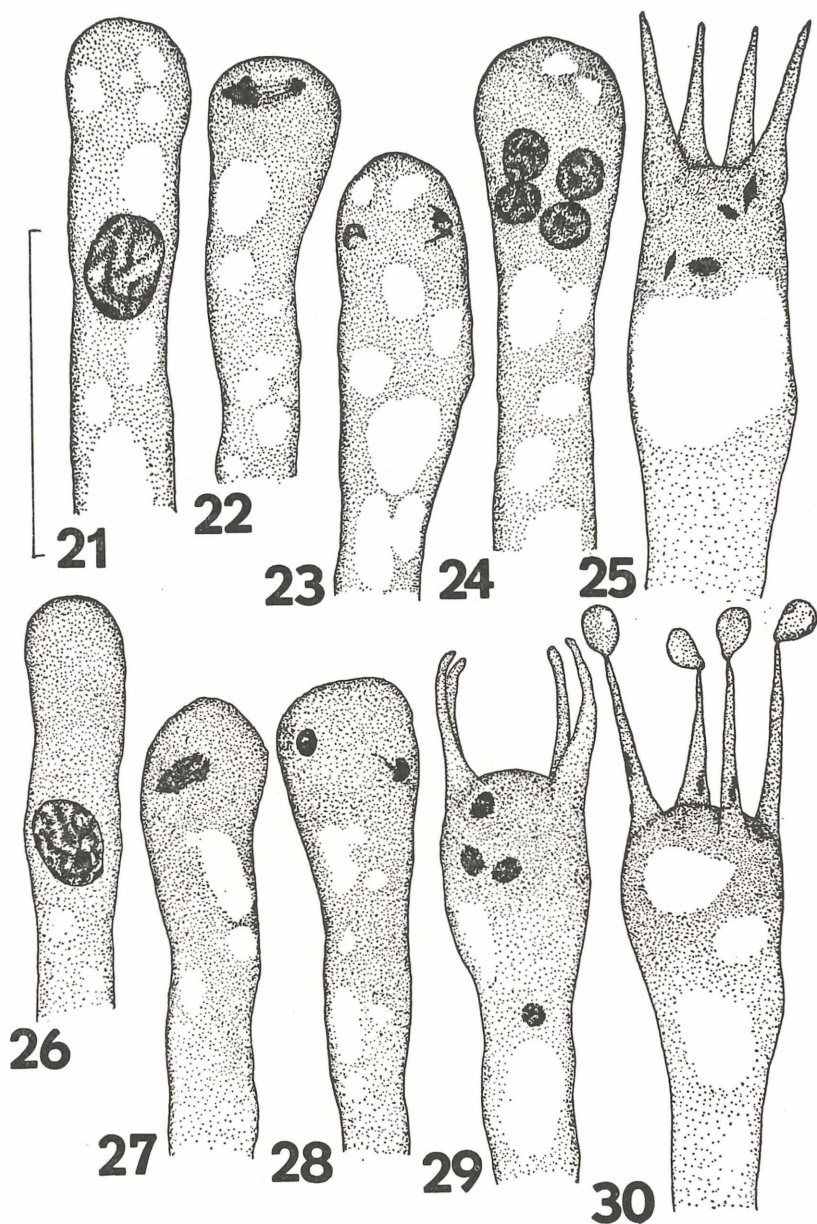


Plate 3

Figs. 21–25. *Clavulinopsis amoena*. 21. Prophase I. 22. Anaphase I. 23. Telophase I. 24. Four-nucleate stage. 25. Nuclei condensed, moving to sterigmata

Figs. 26–30. *Clavulinopsis aurantio-cinnabarina*. 26. Prophase I. 27. Anaphase I. 28. Telophase I. 29. Four-nucleate stage. 30. Nuclei moving through sterigmata. Standard line = 20 μ m

bulge of the probasidium still discernible (Fig. 10—11). The divisions of meiosis were not clearly observed but separation during anaphase I was longitudinal and the chromatin masses were not significantly separated at telophase I (Fig. 12). Meiosis I nuclei were located in the mid-region of the basidium, not distally.

The four nucleate stage was observed in basidia with mature sterigmata (Fig. 13). No further mitotic divisions were evident and the spores were released as haploid monokaryons with the nucleus centrally located (Fig. 14).

Conclusions. *Multiclavula mucida* was found to be stichobasidial. Basidial development, size and shape in *M. mucida* are very different from those of other stichic taxa. The division is clearly longitudinal, but spindle separation is not as great as in other stichobasidial organisms, e. g. *Cantharellus minor*.

With its stichic basidia, *M. mucida* may be similar to JUEL's (1916) sense of *C. falcata*. JUEL's description of nuclear behavior agrees well with the results for *M. mucida*. In both cases the spores are clearly elongate and 1—2-guttulate, these not characteristic of *Clavaria falcata* (= *C. acuta*). JUEL (1916) also described an agglutinated hymenium, characteristic of *M. mucida*.

Multiclavula corynoides, a species found in Sweden, would be a likely choice for the taxon to which Juel misapplied the name *Clavaria falcata*. One species of *Multiclavula* (i. e. *M. mucida*) has been found with stichic basidia, and on this basis, *M. corynoides* would likely also be stichobasidial.

The results indicate a strong possibility that JUEL (1916) was looking at a *Multiclavula* when he described *Clavaria falcata*. ULBRICH's (1928) recognition of clavarioid forms with stichic basidia was fortunate. While the identity of *Clavaria falcata* sensu JUEL can never be definitely established, the results here indicate that *Stichoclavaria* should be reconsidered as the correct name for the *Multiclavula* complex.

III. *Clavulinopsis* VAN OVEREEM

History. *Clavulinopsis* VAN OVEREEM (1923) was proposed to accommodate taxa of simple clavarioid forms, red to orange color, with basidia exhibiting distorted, often misplaced sterigmata thought similar to those of *Clavulina* SCHROETER. The type species is *Clavulinopsis sulcata* VAN OVEREEM [= *Clavulinopsis miniata* (BERKELEY) CORNER]. The generic name was not generally adopted until CORNER (1950) saw it as a companion genus to *Clavaria*, with clamp connections on the hyphae of the trama, and *Clavaria* lacking tramal clamps. Several taxa were transferred to *Clavulinopsis* and PETERSEN (1968) subsequently monographed the genus for North America.

CORNER (1950) recognized some infrageneric groups within *Clavulinopsis*. One group produced spores with small, papillate hilar appendices, and included the type species *C. sulcata* (as *C. miniata* (BERK.) CORNER). A second group produced spores with stout, protruding hilar appendices. A less definable third group is characterized by elongate spores with "medium sized" hilar appendices.

This taxonomic distinction was reinforced by the reaction of the hymenium in sulfuric acid (VAN OVEREEM, 1923). Differences in carotenoid pigments were detected macrochemically. The major distinctions proposed by CORNER (1950) were supported by the reactions of the hymenium in iron salts (DOTY, 1950) especially with added ethanol (PETERSEN, 1968, 1971). Among the taxa tested, the hymenium of the taxa producing stoutly apiculate spores showed a green reaction in iron salts, whereas those with weakly apiculate spores showed no reaction at all. Biochemical techniques have been used to further clarify this distinction. Fruit bodies of weakly apiculate-spored taxa which have been examined exhibited carotene pigments (FIASSON, et al., 1970), while *C. fusiformis* (stoutly apiculate spores) seemed to deposit a substituted xanthophyll rather than the carotene pigments (JAMESON, 1973).

PETERSEN (1971) reported that the strongly apiculate-spored group seemed to be world wide in distribution, while the weakly apiculate-spored group appeared to be confined to a pantropical belt extending northward only in the eastern United States and Asia.

Nuclear behavior in the genus was first described by JUEL (1916). He examined *Clavaria muscoides* (= *Clavulinopsis corniculata*) and described it to be chiasmobasidial without a third division sequence. PENANCIER (1961) noted the chiasitic basidia and four "residual nuclei" in *Clavulinopsis fusiformis*. To this time, all taxa examined for nuclear behavior patterns have been members of the strongly apiculate-spored group.

ARPIN & FIASSON (1971) stated the opinion that a carotene pigmented taxon could not be derived from a non-carotene pigmented taxon. The implications of such a theory are serious in the fungi where relatively unrelated groups exhibit similar pigments. PETERSEN (1976b) has postulated a phylogenetic relationship between the non-carotene-pigmented group of *Clavulinopsis* (stoutly apiculate spores, green reaction in iron salts, world wide distribution) and *Clavariadelphus*, also without carotene pigments. This scheme leaves the carotene pigmented group of *Clavulinopsis* (weakly apiculate spores, no reaction in iron salts, basically tropical) unassigned in any phylogenetic pathway.

The several possible candidates as relatives of the carotene pigmented group might be *Cantharellus* and its allies. All taxa within

Cantharellus (carotene pigmentation) are known to be stichobasidial (JUEL, 1916) and an examination of nuclear behavior in the carotene pigmented group of *Clavulinopsis* would help to clarify such a possible relationship. Comparison of the nuclear behavior in the two infrageneric groups of *Clavulinopsis* might reveal differences supporting the infrageneric taxonomy now based on other characters.

In the present study, the carotene pigmented group was represented by *C. aurantio-cinnabarina* and *C. amoena*. The non-carotene pigmented group was represented principally by *C. fusiformis* and supported by observations of *C. corniculata* and *C. laeticolor*.

a. *Clavulinopsis fusiformis* (Sow. ex Fr.) CORNER

Results. *Clavulinopsis fusiformis* does not exhibit a discernibly different pattern of nuclear behavior from *C. aurantio-cinnabarina* through meiosis I (Fig. 15—16). Two minor differences were observed in the lack of an evident prophase I membrane (Fig. 15) and the spindle orientation more variable than in the other *Clavulinopsis* species. While the spindles were distal and transverse, they were observed as far as 7 μ m from the basidium apex and with an angle as great as a 65°.

The divisions of meiosis II follow a pattern not discernibly different from the other studied species of *Clavulinopsis*. Eight-nucleate stages presumably resulted from mitotic divisions coincident with sterigmata initiation. Nuclei were somewhat condensed when they migrated to the spores, with four nuclei remaining to degenerate with the collapsed basidium. The spores were released as haploid monokaryons, the nucleus in juxtaposition to the hilar appendix. No subsequent mitotic division in the spores was observed.

b. *Clavulinopsis corniculata* (Fr.) CORNER and *C. laeticolor* (BERK.) PETERSEN

Because dried specimens were used to prepare microscope mounts, observations were less accurate in these taxa. The cytoplasm of the basidium did not return to its original position during the staining procedure, instead remaining somewhat irregularly deposited inside the basidial wall. Deeply stained areas were readily observable and considered to indicate the placement of nuclei. In both species, rehydrated basidia with 6 to 8 nuclei were observed, as well as collapsed unstained basidia with residual nuclei. The number of nuclei indicate a division sequence similar to that in *C. fusiformis*. Spores on release were uninucleate in both species.

c. *Clavulinopsis amoena* (ZOLL. & MOR.) CORNER

Clavulinopsis amoena (Fig. 21—23) exhibited a pattern of nuclear behavior through meiosis I not discernibly different from *C. aurantio-*

cinnabarina. Chromosomal separation during anaphase II was evident in the midregion of the immature basidium. The spindles were at approximately the same level in the basidium, observed to be both perpendicular and parallel to the others. The resultant four nuclei were approximately 2 μm diam, granular and membrane-bound (Fig. 24). No mitotic division followed, and the nuclei were somewhat condensed when sterigmata were formed. Coalescence of the proximal vacuoles was evident and a single nucleus migrated through each sterigma (Fig. 25). The spores were released as haploid monokaryons with the nucleus invariably in juxtaposition to the hilar appendix. Within the spores no mitotic division followed.

d. *Clavulinopsis aurantio-cinnabarina* (SCHW.) CORNER

Undifferentiated hymenial hyphal tips, presumably very immature basidia, were cylindrical, approximately 2.0 μm diam, subtended by clamp connections, and dikaryotic. The prominently stained nuclei were approximately equal in size (1.5 to 2.0 μm diam). Small scattered vacuoles were evident within the lightly stained cytoplasm, and appeared to enlarge and coalesce during later stages of development.

The post karyogamic interphase nucleus was large (approx. 4 μm diam) and a nuclear membrane was evident (Fig. 26). During the prolonged prophase period, the basidial initial became narrowly clavate with the nucleus variously placed, but never distal or proximal in the immature basidium. Leptotene and zygotene stages were never observed, but chromosomal condensation toward pachytene was evident in the regularly shaped, granular nucleus. Diplotene was represented by an intensification of the granular appearance and an observable strand-like configuration, followed by further condensation during diakinesis.

At metaphase I, condensation of chromatin material was greatest and the nucleus located distally, but no metaphase plate was discernible. Spindle orientation was transverse and frequently at a slight angle. Chromosomes separated irregularly during anaphase I (Fig. 27). Telophase I nuclei were peripheral with observable membranes (Fig. 28). During meiosis I, the cytoplasm became more dense distally with more numerous proximal vacuoles.

Meiosis II divisions were asynchronous, nuclei were not densely staining with placement and orientation of the spindles irregular but always in the distal third of the basidium. The resultant four nuclei were approximately 2 μm diam, and somewhat condensed when the sterigmata were formed (Fig. 29). No mitotic division followed. A single nucleus migrated through each sterigma and the spores were released as haploid monokaryons (Fig. 30). The single nucleus was invariably

located adjacent to the hilar appendix, with no subsequent nuclear division within the spore.

Conclusions. *Clavulinopsis aurantio-cinnabarina* and *C. amoena* were found to be chiasmobasidial with two standard meiotic divisions producing four daughter nuclei, all of which migrate to the spores. In *C. fusiformis*, *C. corniculata*, and *C. laeticolor* similar meiotic divisions are evident with the four-nucleate stage followed by a mitotic division sequence. Four of the resultant nuclei migrate to the spores and four "residual nuclei" remain in the collapsed basidium. These observations on nuclear behavior can be added to the existing list of infrageneric characters (cf. Table I).

The significance of the third division sequence and the "residual nuclei" is unknown as is the significance of the orientation of division spindles. It could be postulated that two taxa exhibiting a different orientation of the spindle apparatus are more distantly related than taxa merely displaying the presence or absence of a third division sequence and four "residual nuclei". To further understand the significance of this character, additional taxa of *Clavulinopsis* should be investigated to discover completely its distribution within the genus. *Clavulinopsis corniculata* and *C. laeticolor* would best be investigated with fresh material as observations on dried material are not so conclusive as those with fresh.

With CORNER's monograph on the clavarioid fungi came acceptance of the genus name *Clavulinopsis* and a recognition of two infrageneric groups based on spore morphology. This initial dichotomy has been further reinforced by the subsequent observations listed above (Table I). Consideration of pigmentation indicates a possible relationship between the non-carotene complex of *Clavulinopsis* and *Clavariadelphus*. The carotene group remains without a known relative.

A study of the nuclear behavior of these taxa does not clarify completely the infrageneric groups of *Clavulinopsis*. *Cantharellus*, consistently carotene pigmented, has been exclusively described as stichobasidial, while the representative of the carotene-pigmented, weakly apiculate complex of *Clavulinopsis* (*C. amoena* and *C. aurantio-cinnabarina*) were found to be chiasmobasidial. A relationship between this infrageneric group of *Clavulinopsis* and the genus *Cantharellus* is therefore difficult to establish for it would be based primarily on the presence of carotene pigmentation.

Nuclear behavior in the second infrageneric group of *Clavulinopsis* (stoutly apiculate spores, non-carotene pigmentation) was found to be chiasmobasidial similar to the genus *Clavariadelphus*. This complex of *Clavulinopsis* exhibited a third division sequence with four "residual nuclei." The genus *Clavariadelphus* also exhibits this type of chiasmobasidial division (PENANCIER, 1961). In this case the fine details of the division process are found to be more nearly similar.

Table I
Infrageneric Characters in *Clavulinopsis*

Character	Group I	Group II
	Inc. <i>C. amoena</i> and <i>aurantio-cinnabarina</i>	Inc. <i>C. fusiformis</i> , <i>C. laeticolor</i> and <i>C. corniculata</i>
Spore morphology	Weakly apiculate	Stoutly apiculate
Chemical reactions		
Macro-Fe ₂ SO ₄	No reaction	Green reaction
Biochemical	Carotene deposition	Non-carotene deposition in <i>C. fusiformis</i> , sub. xanthophyll
Geographical Distribution	Pantropical belt	World wide
Nuclear behavior	Chiastobasidial without a third division	Chiastobasidial with four 'residual nuclei'

Specimens Examined

Cantharellus minor. Sugar Cove off Cades Cove, Great Smoky Mountains National Park, Tennessee, 30. viii. 75, det. R. H. P., TENN 40235.

Clavulinopsis aurantio-cinnabarina. Cades Cove, Great Smoky Mountains National Park, Tenn., 12. viii. 75, det. R. H. P., TENN 40236.

Clavulinopsis amoena. Cades Cove, Great Smoky Mountains National Park, Tenn., 12. viii. 75, det. R. H. P., TENN 40237.

Clavulinopsis fusiformis. Roaring Fork Nature Trail, Great Smoky Mountains National Park, Tenn., 20. viii. 75, det. R. H. P., TENN 40238.

Clavulinopsis corniculata. Sweden, Lycksele Lappmark: Tärna, 5. ix. 74, det. R. H. P., TENN 39774.

Clavulinopsis laeticolor. Sweden, Lycksele Lappmark: Tärna, 5. ix. 74, det. R. H. P., TENN 39799.

Multiclavula mucida. Savage's Garden, Lake City, Anderson Co., Tenn., 15. x. 75, det. R. H. P., TENN 40158.

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