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Life History and Developmental Processes in the Basidiomycete *Coprinus cinereus*

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INTRODUCTION

Coprinus cinereus (Schaeff. ex Fr.) S. F. Gray is one of two model organisms commonly used to study developmental processes in the homobasidiomycetous fungi. Unlike the other model organism, the bracket fungus *Schizophyllum commune*, *C. cinereus* is a typical mushroom (246, 335, 338, 517). Although it is of limited edible value (10), studies of *C. cinereus* may be used to understand the development of numerous edible basidiomycetes which fail to grow and/or produce fruiting bodies in the laboratory and are not readily accessible to genetic approaches (84, 255a). *C. cinereus* was introduced early as an object for studies of development (26, 39, 46, 50, 53, 58), mainly because of its relatively short life cycle, which can be completed in the laboratory within 2 weeks (343). The natural substrate of the species is horse dung (50, 58), but it also grows and fruits well on various artificial media (73, 292, 406, 508a). Over the decades, the fungus has been isolated under various names including *cinereus*, *delicatulus*, *fimentarius*, *lagopus*, *macrorhizus* f. *microsporus*, and *radiatus*. The names *lagopus* and *radiatus* were also attributed to other *Coprinus* species, making it difficult to analyze the older literature and to be certain which fungus was dealt with. There is thus no guarantee that all articles listed in this paper were indeed on *C. cinereus*. The *Coprinus lagopus* of Borriss and Madelin, for example, has sometimes been interpreted to be *Coprinus radiatus* (344), but because of its fundamental character, the work is included here. At present, all isolates interfertile with *C. lagopus* sensu Buller are classified under the species name *cinereus* (222, 226, 344, 382), but another renaming is expected in the future. Traditionally, members of the genus *Coprinus* (commonly known as ink caps) were defined as saprophytic mushrooms whose gills and frequently the entire cap autodigest at maturity, giving rise to an inky black fluid that drips to the ground (10). Recent phylogenetic studies based on large-subunit rDNA sequences, however, indicate that the traditional genus *Coprinus* is polyphyletic. Unfortunately, the type species, *Coprinus comatus*, nests within the lepiotoid fungi while most other

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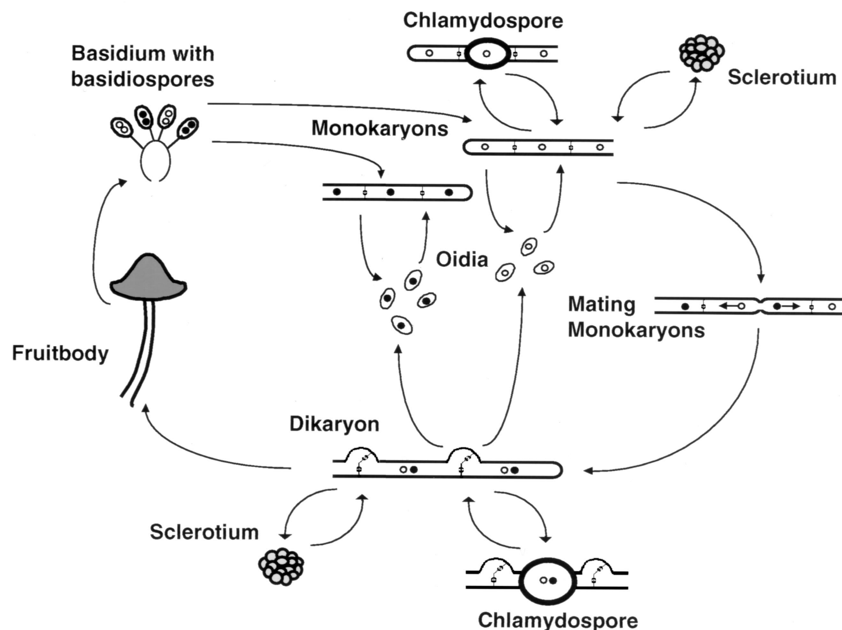

FIG. 1. Life cycle of *C. cinereus*.

Coprinus species including *C. cinereus* are placed close to *Psathyrella* (177, 178, 192).

C. cinereus is a heterothallic basidiomycete. Two main types of mycelia are distinguished in its life cycle, the infertile monokaryon and the fertile dikaryon (71, 176). *C. cinereus* has a wide-ranging developmental potential in both the monokaryotic and the dikaryotic mycelial stages (Fig. 1). This potential ranges from the fruiting body (carpophore, basidiocarp, basidiome), with the meiotic basidiospores localized within the gills (314, 338) (see below), to mitotic aerial spores (oidia) and mitotic submerged spores (chlamydospores) to the multicellular structures of sclerotia, mycelial cords, pseudorhizas and rockeries (56, 60, 171, 261, 371, 385) (see below). There is considerable flexibility in the shapes formed and in when and where these different organs develop (89, 91, 171, 463; U. Kües, J. D. Granado, Y. Liu, E. Polak, and M. Aebi, unpublished data; E. Polak, M. Aebi, and U. Kües, submitted for publication). Fungal differentiation is clearly not a rigid process but is tolerant to imprecision in fungal morphogenesis, probably enabling the fungus to react to adverse conditions. Fungal morphogenesis is organized in an array of developmental pathways, or subroutines (335), which are genetically and physiologically distinct. These subroutines run in parallel or in sequence, and the order followed determines the final outcome (338–340). Numerous molecular, genetic and cytological techniques are now available (9, 41, 71, 101, 125, 126, 145, 267a, 283, 343, 366, 386, 388, 390, 391, 430, 446, 508b, 537, 539, 540, 543) to unravel these routes and we are beginning to gain insight into the fascinating regulatory mechanisms of development in *C. cinereus*.

GROWTH AND STRUCTURE OF THE MYCELIUM

Monokaryons and Dikaryons

Monokaryons arise from germination of the haploid binucleate basidiospores or, alternatively, from germination of the uninucleate haploid oidia. During germination of the basidiospores, a single germ tube displaces the spore pore cap. Similarly, a single germ tube is formed by the oidium. Nuclei within the germ tubes divide, and septa may be formed between the daughter nuclei; alternatively, the germ tubes may stay aseptate through several cycles of nuclear division. Multinucleate side branches emerge, while septum formation occurs in the older portions of the germtubes to yield cell segments with one or only a few nuclei. The tip cells of the main hyphae and those of side branches remain multinucleate during further growth (26, 169). The literature contains reports of the older monokaryotic mycelium having only one nucleus per hyphal cell (452). However, nuclear staining of aerial mycelium of various strains revealed that in most cases up to half of all hyphal cell segments contain not just one but two and sometimes even three nuclei (385; E. Polak, personal communication). Thus, the primary mycelium of *C. cinereus* does not fulfill the strictest definition of a monokaryon, i.e., a specific homokaryotic mycelium with just one nucleus per cell (4, 121). Nevertheless, we prefer to continue calling the primary mycelium a monokaryon, since this term is traditionally used in *C. cinereus* (70, 75, 266, 343, 391), and thus follow the less stringent definition given by Hawksworth et al. (164) of a mycelium as having genetically identical haploid nuclei. For the geneticists, the term "monokaryon" nicely targets the most important difference from the dikaryotic mycelium, which typically contains two genetically distinct haploid nuclei in its cells (26, 175a, 187).

Cultures of monokaryons differ greatly in growth rate and also in their morphological appearance, primarily due to variations in the amount and structure of the aerial mycelium produced (Polak et al., submitted). The distance between branches varies between strains but branches usually form in a relatively wide angle of about 70 to 75°. Hyphae of monokaryons are usually thin, with a diameter of about 3 μm (58, 226; Polak et al., submitted). They are generally characterized by simple septa (26, 58, 475) with a dolipore, as is typical for the basidiomycetous fungi (132). The dolipore is barrel shaped due to the swollen edge of the cross-wall around the pore. Parenthosomes, dome-shaped double membranes thought to be a

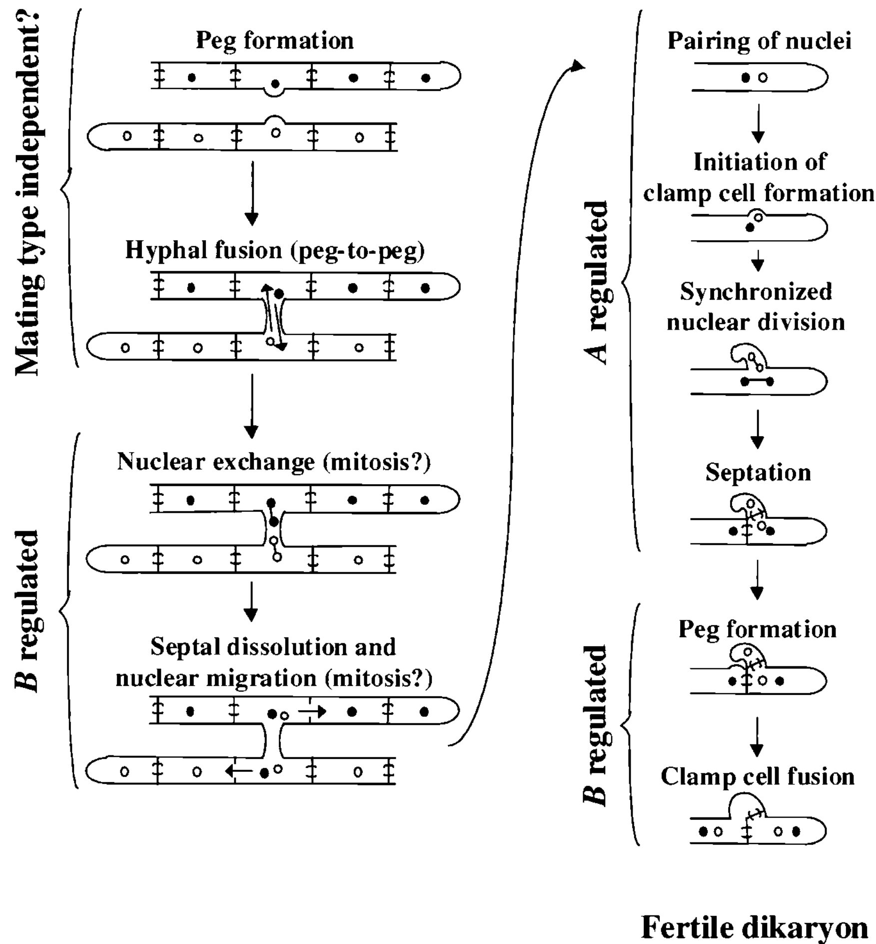

FIG. 2. Dikaryon formation following peg-to-peg fusion of hyphae of two compatible monokaryons. This model has been composed from observations by Buller (59), Iwasa et al. (187), and Raudaskoski (410). For a discussion of *A* and *B* mating-type control in the process of hyphal fusion and dikaryon formation, see references 79, 172, 410, and the text.

modified part of the endoplasmic reticulum (ER), cover the dolipore swellings and the pore channel to form the septal pore cap. Perforations within the membranes allow cytoplasmic continuity through the parenthosome barrier and between adjacent cellular compartments, giving the hyphae a coenocytic character. Passage of smaller organelles such as mitochondria is possible; however, migration of larger organelles such as nuclei is blocked (299, 348, 437).

Dikaryons arise upon fusion of monokaryons of different mating types (Fig. 2), either by hypha-hypha fusion or by fusion of hyphae with germinating or resting oidia (26, 75, 223). Cellular fusion (anastomosis) may occur between two hyphal tips (tip-to-tip fusion), between a hyphal tip and a lateral hyphal wall (tip-to-side fusion), between a hyphal tip and a lateral swelling of a hypha (tip-to-peg fusion), or between lateral swellings of two neighboring hyphae (peg-to-peg fusion) (59, 410, 440). Upon fusion, nuclei enter the mycelium of the opposite mating type and, with dissolution of the hyphal septa (69, 75, 132), migrate through the hyphae until they reach a hyphal tip cell (26, 58) (Fig. 2). In *C. cinereus*, the speed of nuclear migration is between 1 and 3 mm h^{-1}, which is up to 20 times faster than that of the hyphal tip growth (58, 236, 460; for a compilation of data for various basidiomycetes, see reference 64). Buller (58) found that migration takes place mainly through the outer part of the colony, and he assumed that migration involved the regular division of the invading nucleus. In *Schizophyllum commune*, invading nuclei apparently do not densely colonize the established host mycelium and there are areas through which the migrant nuclei obviously pass but in which they cannot be detected (407, 441). Niederpruem (361) monitored nuclear movements over short distances in living hyphae in compatible matings of *S. commune* and did not observe any mitosis. The observations in *S. commune* suggest that there may be no or little nuclear division during nuclear migration in basidiomycetes (361, 407, 441). Other authors, however, dispute this conclusion. At least directly after hyphal fusion, at the initial stage of nuclear exchange and migration, there are sometimes nonsynchronous (265, 409) and often also synchronous mitotic divisions of the two nuclei while they are together in the fusion compartment (410, 471). In addition, synchronous nuclear divisions in "migration" hyphae have been visualized by indirect immunofluorescence microscopy

(410). The age of the hyphae strongly influences the rate of nuclear migration (425) and might also have an effect on the mitotic activity of the nuclei in the fusing hyphae (M. Raudaskoski, personal communication). Whatever the situation in *C. cinereus*, once a migrating nucleus reaches a hyphal tip cell, the two types of haploid nuclei pair at average distances of 15 to 20 μm (175a, 211) and the paired nuclei divide synchronously (26, 58, 459) (Fig. 2). Simultaneously, specialized clamp cells (or hook cells) are formed at the position where a new septum will appear (26, 59, 459) (Fig. 2).

During the mitotic prophase, the nucleus localized closer to the tip will enter the developing clamp cell, and in the anaphase, it divides with a short spindle. The second nucleus stays in the hyphal cell beneath the clamp cell and divides with a longer spindle. Due to the different lengths of the spindles, the foremost of the dividing nuclei in the hyphal cell will pass the member of the other pair of dividing nuclei that is leaving the clamp cell. Septa are generated between the dividing nuclei, enclosing one nucleus into the clamp cell, one nucleus of the other type in the newly formed subapical cell, and a nucleus of each type in the newly arising hyphal tip cell. After septum formation, the backward-looped clamp cell fuses with a peg induced at the subapical cell. This fusion releases the enclosed nucleus from the clamp cell (59, 187, 464, 465) (Fig. 2). As a result of this coordinated mechanism of clamp cell formation and synchronized nuclear division, the order of nuclei reverses between the apical and subapical cell with each cellular division (187). The mechanism ensures that every cellular segment within a dikaryon contains one of each of the two distinct nuclei (26, 59, 187) (Fig. 2). However, occasionally, more than two nuclei are found within cells of a *C. cinereus* dikaryon (175a), and other species are known where the homokaryon also possesses clamp cells (225) or where a dikaryon is perfectly formed in the absence of any clamp cells (224, 459). Consistent with earlier data obtained with *S. commune* (427), recent analysis of mutant strains indicates that the actin cytoskeleton and microtubules with α_1- and β_1-tubulins play a role both in nuclear migration for dikaryosis and in subsequent nuclear positioning and movements within the established dikaryon (199, 209, 211, 410, 464, 465).

As in the monokaryon, the septa of the dikaryon have a dolipore, irrespectively of being formed between two hyphal segments or between a hyphal cell and a clamp cell (132). Biochemically, the septa of monokaryons and dikaryons are probably somewhat distinct, as suggested by in vitro enzymic dissolution of *S. commune* septa (69, 75, 519). The more resistant nature of dikaryotic septa had been suggested to be a cause of blockage of nuclear migration through septa within the dikaryon (69, 80). The literature on the cell wall composition of the monokaryotic and the dikaryotic mycelium in *C. cinereus* is unfortunately poor (42, 43, 195, 296, 298, 432). The innovative work of Marchant (298) and Bottom and Siehr (42, 43) indicates that major differences in chitin content and sugar compositions exist between the cell walls of the two different mycelial stages. In addition, Ásgeirsdóttir et al. (15) recently isolated monokaryon-specific hydrophobins. These are small, hydrophobic, cysteine-rich secreted proteins that assemble at the hyphal wall when hyphae emerge from a submerged culture into the air (116, 231, 521, 522). Visually, there are further differences between monokaryons and dikaryons. Dikaryons of *C. cinereus* tend to grow faster, with a denser, more protuberant and conspicious aerial mycelium, the hyphae are about 7 μm in diameter, and branches arise with a relatively acute angle of 10 to 45° (58, 266). Due to the vigorous, rapidly propagating character of dikaryotic mycelium, outgrowth of a dikaryon from a cross of compatible monokaryons is easily detected. In the ideal case, there are four positions where outgrowth will be observed. Two dikaryotic sectors will arise at the junction of the growing monokaryotic colonies, where their hyphae met and fuse. Two other dikaryotic mycelia are generated at the outward sides of the two monokaryons after migration of nuclei through the opposite mycelium (58, 158). Since only the nuclei, not the mitochondria, migrate, these latter dikaryons are distinguished from each other by their mitochondrial content. In contrast, the dikaryotic sectors arising from the junction zones of the monokaryotic colonies are expected to be mitochondrial mosaics due to mixed hyphal populations with distinct mitochondrial DNA populations. Usually, such mixed dikaryotic mycelia rapidly segregate for one mitochondrial type. Although mitochondrial inheritance in *C. cinereus* is basically uniparental, recombined mitochondrial DNA is occasionally found in places of hyphal anastomosis (23, 75, 117, 118, 306; for a recent review of mitochondrial inheritance and recombination, see reference 420).

Following dikaryon formation, there is no habitual restriction to hyphal fusion with other monokaryotic or dikaryotic strains, but, in contrast to monokaryons, dikaryons do not accept invading nuclei (237, 456, 457, 460). However, they are capable of contributing fertilizing nuclei to a haploid monokaryon, resulting in a new dikaryon (57, 58, 69); this reaction has been termed the Buller phenomenon (400). "Legitimate di-mon matings" (for "dikaryon-monokaryon matings") are those where both kinds of nuclei in the dikaryon are of compatible mating type to the nuclei of the monokaryon. In these cases, heterokaryotization of the monokaryon occurs readily. Either one or both types of the nuclei from the dikaryon migrate into the mycelium of the recipient monokaryotic partner, giving rise to one or two new dikaryotic mycelia. Occasionally, both nuclei from the dikaryon replace the original resident nucleus of the monokaryon (237, 238, 304, 401, 457). In di-mon matings, as in matings of compatible monokaryons, mitochondria are not exchanged but mitochondrial mosaics may arise by a mixed hyphal population (304, 306). In hemicompatible matings, where one nuclear type of the dikaryon is incompatible with the nuclei of the monokaryotic partner, only the compatible nuclei might enter the monokaryon or, alternatively, both kinds of nuclei invade the monokaryon and replace the resident nucleus (304). In illegitimate matings, where all nuclei are incompatible due to differences at either one of the two mating-type loci (see below), heterokaryotization of the monokaryon may occur but only after a delay during which compatible nuclei are generated by somatic recombination (58, 401). Exchange of nuclei between different dikaryons is also possible despite the blockage of nuclear migration, but only in areas where hyphae of both strains intermingle. New dikaryons are thought to form either by outgrowth of fused cells after a fresh sorting of the original pairs of nuclei or by dikaryotization of monokaryotic hyphae that occasionally are observed in the growing front of a dikaryon. Somatic recombination between nuclei has never been observed in dikaryon-dikaryon combinations (456), probably due to the low frequency with which nuclei of the different strains are found together within the same cell.

One of the most remarkable aspects of the life cycle of most homobasidiomycetes is the temporal and spatial separation of cellular fusion from nuclear fusion. Karyogamy normally occurs in the fruiting bodies within the specialized cells, the basidia. It is directly followed by meiosis, thereby restricting the diplophase to a single nuclear generation (283, 469) (see below). The extended dikaryotic growth phase, together with the unusual mating system developed in *Coprinus* and other basidiomycetes (see below), has special consequences for the

understanding of the individual fungus. The free fusion between any mono- and dikaryotic mycelia and the variety of donating, accepting, and expelling of nuclei allows the formation of genetic mosaic colonies composed of genetically different sectors. However, somatic incompatibilities (mycelial antagonisms) lead to processes that rapidly separate newly formed and original dikaryons, despite their history of hyphal fusions and a common nucleus, ensuring that different dikaryons can represent discrete individuals. The vegetative self-nonself recognition of dikaryons is associated with pigmented zones, sparse hyphae or, less commonly, tight hyphal knitting, and an increased production of sclerotia at the interface of colonies. In most cases, the nuclear genomes but occasionally also the mitochondria seem to determine somatic incompatibility. Usually, mitochondrial differences are tolerated and a mitochondrial mosaic behaves as one individual (304; for a further discussion of somatic incompatibility and the problem of fungal individualism, see references 122, 227, 412, and 511).

Other Heterokaryons and Homokaryons

Dikaryons are only one type of heterokaryon found in *C. cinereus*. Dikaryon formation is governed by the two independent mating type loci, *A* and *B*. For a mating to be successful, monokaryons must be different at both loci (for recent reviews, see references 79, 172, and 245) (see below). However, monokaryons can fuse independently of whether different mating-type specificities are present (438, 440). If monokaryons differ in the *B* but not in the *A* mating-type loci, a so-called common *A* heterokaryon is formed that is not distinct in hyphal morphology from the monokaryon, although such strains usually grow less vigorously and more slowly than their component monokaryons. If strains differ within the *A* but not the *B* loci, a common *B* heterokaryon results which grows as vigorously as a dikaryon and which is characterized by formation of unfused clamp cells at the hyphal septa. Common *B* heterokaryons may form fruiting bodies but not as readily as does the dikaryon. In contrast, fruiting body formation in common *A* heterokaryons is the exception (399, 460, 459; for further review, see references 75, 76, and 407). Usually, common *A* heterokaryons are not stable and can be recognized and kept as such only under strong selection pressure (forced heterokaryon), e.g., by selection for complementation of auxotrophies. Similarly, unstable clampless common *AB* heterokaryons can be isolated by a forced mating of monokaryotic strains of the same mating type but with different auxotrophies. By contrast, common *B* heterokaryons are normally quite stable. Like dikaryons, common *B* heterokaryons have been reported to act as donors but not as acceptors of nuclei upon fusion with suitable monokaryons. In contrast, common *A* and common *AB* heterokaryons will usually act both as donors and as acceptors of nuclei, probably also because they frequently produce hyphae with only one type of nucleus (455, 459, 460).

Normally, it is the dikaryon that produces the fruiting bodies (see below). However, under specific conditions, monokaryons may also form fruiting bodies, e.g., under total nutritional depletion (159, 503, 508a). Certain mutations outside of the mating-type loci (*su-A* [103]), *fis*^{c} [324, 373, 480, 491], *pcc1*, and *CopD5* [356, 357]) also lead to formation of fruiting bodies, karyogamy, and meiosis on monokaryons. These mutations are all accompanied by the formation of unfused clamp cells at hyphal septa (356, 357), and the *su-A* mutation is known to block nuclear acceptance (103). A specific class of mutants comprises homokaryons with defects in the mating-type loci that overcome the self-incompatibility of monokaryotic strains. Such strains, commonly called *Amut Bmut* homokaryons, are

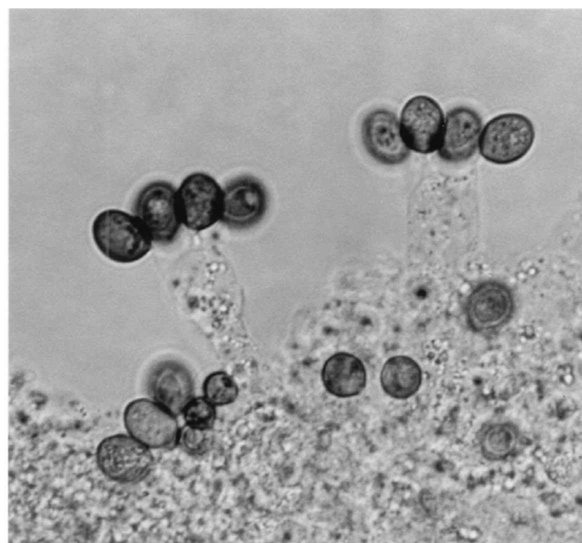

FIG. 3. Basidia with mature basidiospores of homokaryon AmutBmut (*A43mut B43mut*). Courtesy of J. D. Granado.

fully self-compatible and will initiate fruiting-body development under certain environmental conditions (452; see below). Depending on the general genetic constitution of the strain, fruiting-body initials and primordia will mature and karyogamy, meiosis, and the production of four basidiospores will occur within the gills of the fruiting body (165, 452) (Fig. 3). *Amut Bmut* homokaryons resemble dikaryons in their vigorous growth and hyphal morphology. They have fused clamp cells at the hyphal septa, but their distribution is usually not as regular as in dikaryons, and septa with unfused or no clamps are frequently been detected (452; U. Kües, unpublished data). The nuclei in aerial cells of *Amut Bmut* homokaryons are distributed in similar patterns to those of related monokaryons (385), but in submerged mycelium a fairly strict binucleate distribution has been reported (452). Although fully self-compatible, *Amut Bmut* homokaryons might mate with any strain in the junction zones of a cross, irrespective of which wild-type (self or nonself) or mutant mating types are present in the mating partner. However, heterokaryons formed with strains of related mating types appear to be short-lived and unstable. Nuclear acceptance of *Amut Bmut* homokaryons might be restricted but donation by nuclei into monokaryons is possible (269; Kües, unpublished).

To generate *Amut Bmut* homokaryons, independent mutations were selected in the *A* and *B* mating-type loci and combined into the same nucleus by crosses (165, 452). *Amut* homokaryons with only a mutated *A* locus mimic common *B* heterokaryons and are characterized by mycelia with unfused ("false") clamp cells at some but usually not all septa. *Amut* homokaryons may have one, two or occasionally even three nuclei per cell (103, 165, 452) at frequencies comparable to what we have found in monokaryons (384, 385). *Amut* homokaryons are hemicompatible and form stable dikaryons with any monokaryotic strain as long it has a different *B* specificity (103, 165, 452). In mating, *Amut* homokaryons may act as both donors and acceptors of nuclei (Kües, unpublished). *Bmut* homokaryons are also hemicompatible. They mate bilaterally and accept and donate nuclei in crosses with monokaryons as long as these differ in the *A* mating-type locus. *Bmut* homokaryons have simple septa like normal monokaryons (165, 452). In contrast to the analogous *Bmut* homokaryons of *S.*

commune (243, 361), the dolipore septa are not disrupted in the *C. cinereus Bmut* homokaryons and the nuclear distribution within the cells is even over the entire hyphal length as in monokaryons (165, 452).

Somatic Diploids

Although the diplophase is normally restricted to the basidia in the life cycle of *C. cinereus*, nuclear fusion occasionally occurs within the vegetative mycelium of heterokaryons. Diploid mycelia can be selected from common *A* and common *AB* heterokaryons by plating and germinating uninucleate oidia at frequencies ranging from approximately 10^{-3} to 10^{-4} (68, 187, 355). There are no reports in the literature on the rescue of diploids from common *B* heterokaryons or from dikaryons, but indirect evidence for the infrequent existence of diploid nuclei comes from the observations of somatic recombinations (98, 237, 401, 457, 458).

Diploid oidia of common *A* and of common *AB* heterokaryons have increased cell size, with a single enlarged nucleus that is twice the size of a haploid nucleus. Germinated hyphae are significantly broader than those of the monokaryotic parents (68, 187, 355, 364). Diploid common *A* and common *AB* mycelia readily mate with monokaryons and with other diploid common *A* strains, provided that these strains contain other *A* mating-type genes. However, common *A* diploids serve only as nuclear donors in matings, whereas common *AB* diploids both donate and accept nuclei (77, 80, 98, 364). In agreement with their different behavior in nuclear acceptance, septal dissolution was not detected in common *A* diploids, in contrast to common *A* heterokaryons, indicating that the cytological difference between the two nuclear conditions has an impact on the mating behavior of the mycelium (364). Possibly due to uneven nuclear distribution within colonies of common *A* heterokaryons (78, 455), common *A* diploids and common *A* heterokaryons also differ in complementation efficiency of metabolic functions whereas common *A* diploids and ordinary dikaryons usually behave similarly (78, 105, 367, 472). However, bringing genes together in a single nucleus in common *A* diploids or separating them into two haploid nuclei within dikaryotic cells can also cause changes in expression, as observed with certain resistance genes (267, 365).

Diploid mycelia are often fairly stable—only 0.5% of oidia produced by such mycelia were found to be haploid (68, 78)—but treatment with the fungicide griseofulvin can induce haploidization by a gradual loss of chromosomes (364). Most interestingly, diploid-haploid and diploid-diploid pairings produce dikaryons in which the diploid nuclear components are unstable in the vegetative growth phase, indicating that the dikaryotic situation is preferred over the diploid. Loss of chromosomes in such dikaryons is also progressive as aneuploid and haploid nuclei are recovered from these colonies (68, 78, 397). Finally, it is interesting that common *A* diploids are not fully compatible even if they are distinct in their *A* mating-type loci. In dikaryons formed by such common *A* diploids, the produced clamp cells at first fail to fuse, but progressive haploidization, eliminating one of the two *B* chromosomes from the diploid nuclei, eventually results in a compatible situation and clamp cell fusion (78).

ASEXUAL SPORE FORMATION

Oidiophores and Oidia

Monokaryons of *C. cinereus* have for a long time been known to constitutively produce abundant uninucleate asexual spores on specialized aerial structures (oidiophores). These spores are rod shaped, and because of this shape, they are called oidia (26, 47). Until recently, dikaryons were believed not to form these mitotic spores (48, 70, 234), but their production has been observed after light induction (232, 452) (Fig. 4). Likewise, formation of oidia on *Amut* and *Amut Bmut* homokaryons is under light control, whereas *Bmut* homokaryons and common *A* heterokaryons behave like monokaryons and constitutively produce numerous oidia (232, 385, 452). Common *B* heterokaryons are also reported to produce abundant oidia in the light (459); due to the presence of different *A* mating-type genes within these strains, repression of oidiation in the dark is expected (232, 261) (see below) but was not tested. Common *A* and common *AB* diploids also give rise to oidia, and spore production is presumably constitutive (68, 78, 364). Extensive use of oidia has been made in single-cell purification of cultures, in generation of uninucleate protoplasts for transformation, and in providing isolated uninucleate cells in classical and modern mutagenesis techniques (30, 31, 68, 145, 366, 386, 388). Regardless of their importance in genetic studies, attention was only recently drawn to the cytological process of formation of oidia (385; Polak et al., submitted). Under certain genetic conditions, oidiation is light induced, and light acts at the level of oidiophore formation, which has enabled the whole process of sporulation to be monitored over time in microslide cultures (385).

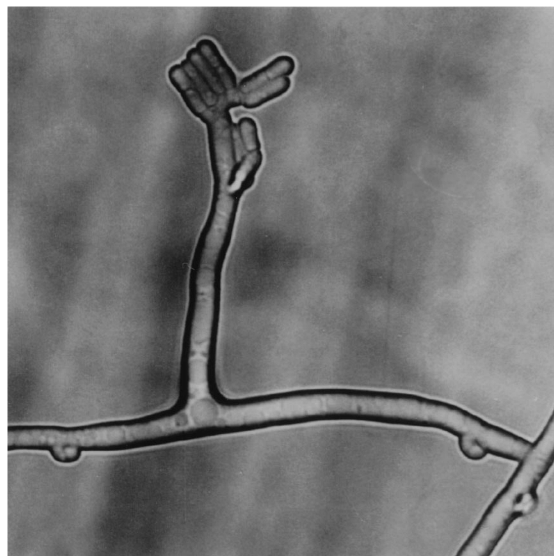

FIG. 4. Young oidiophore in the aerial mycelium of dikaryon FA2222 (*A5 B6*) × 306 (*A43 B43*). Note the clamp cells at the septa of the hyphae and the absence of clamp cells on the oidiophore. Courtesy of E. Polak.

Oidiophores are formed predominantly in the aerial mycelium (47, 385), although in most strains small numbers of oidiophores can regularly be detected in the submerged mycelium of agar cultures (Polak et al., submitted). Not every cell of the aerial mycelium becomes an oidiophore foot cell, i.e., the hyphal cell that will give rise to the oidiophore. Unlike the oidiophore foot cells, undifferentiated aerial cells vary greatly in length, indicating that the former are physiologically predetermined (Polak et al., submitted). Development starts with the protrusion of a young oidiophore from its foot cell (385) (Fig. 5). Subsequently, a nucleus in the foot cell divides, one daughter nucleus migrates into the bulging young oidiophore, and a septum is formed which separates the first oidiophore stemcell from its foot cell. The stem cell elongates and may

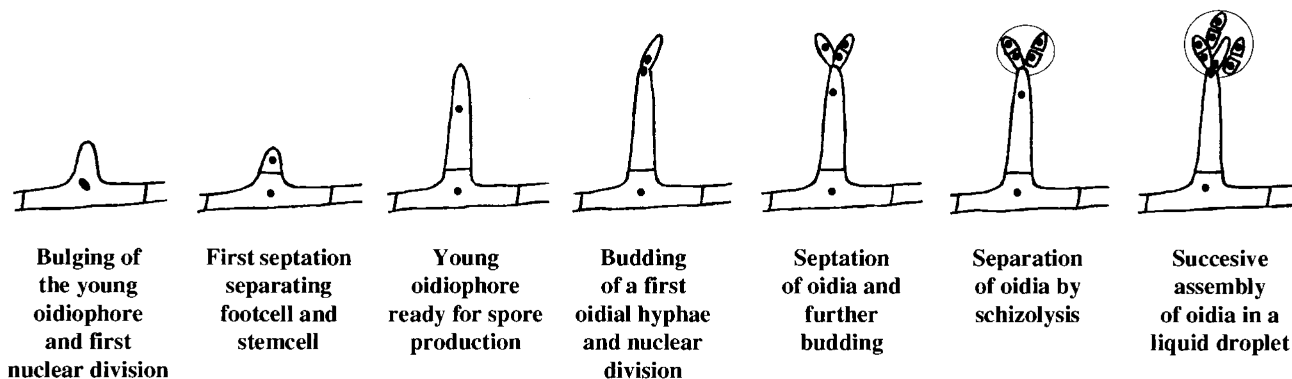

FIG. 5. Model of the development of oidiophores and oidia in *C. cinereus*.

divide once or twice, and side stems may branch from the cells of the main stalk. From the tip of stem cells of both main and side stalks, short, oblong oidial hyphae bud off one after the other. Successive nuclear divisions within the stem cells ensure that each oidial hypha is provided with a nucleus before it is separated from the stem cell by septation. Within an oidial hypha, a further nuclear division occurs followed by formation of a septum that separates the oidial hypha into two equally sized cells. Eventually, these cells are released by schizolysis of the septa between the oidial hypha and between the oidial hypha and its stem cell. A few hundred free spores are successively collected in a sticky liquid droplet secreted at the tips of the oidiophores (385) (Fig. 5). Since their mode of generation involves budding and septum schizolysis, oidia are classified as arthroconidia (228, 385). Mature haploid spores average about 2 by 4 to 6 μm in size, and mature diploid oidia measure about 3 by 7 μm (68, 364, 385; Polak et al., submitted). Oidia are enclosed by mucilage and possess a double-layered primary cell wall with hair-like structures, except at former sites of cell attachments, where a single-layer secondary cell wall is present (168, 169, 385). These secondary walls are later involved in the germination of the spores (168). Oidia are distinguished as "wet" spores due to their strong hydrophilic character (15, 222). Consistent with this, proteins with the characteristic properties of hydrophobins are not detected on oidia (15), unlike the "dry" hydrophobic spores of other fungal organisms, which are coated with hydrophobins (116, 231, 518, 521, 522). Oidia of *C. cinereus* are not wind-borne spores. Instead, they stick to flies and other insects attracted by the horse dung substrate and are thereby distributed to new substrates (47). Independently of mating types, oidia attract hyphae of colonies—a process called oidial homing—and act as spermatia in matings with compatible *C. cinereus* cells (223) (see above). Most interestingly, they also attract and fuse to hyphae of other related coprophilous fungi. Upon fusion, somatic incompatibility reactions are initiated, leading to the death of the foreign hypha. Oidia thereby act as a killing agent of opponents competing for the same limited substrate (223).

Analysis of various *C. cinereus* strains showed that oidiophore formation is not a fixed cytological process. Oidiophores may have simple stems or may be branched, and the stem cells may not elongate or may totally be absent (26; Polak et al., submitted), indicating that the different steps in oidiophore development, as defined in Fig. 5, are independent of each other and that some may be omitted without terminating development. To denote the main structural differences, four main types of oidiophores have been defined. Type 1 oidiophores have unbranched elongated stems and produce oidial hyphae at only their tips. Type 2 oidiophores form oidial hyphae at the tip of a main stem and also at the tip of side branches; oidial hyphae may also bud directly from the uppermost stem cell (type 2A) and from stem cells beneath (type 2B). In contrast to these more advanced structures, type 3 oidiophores do not elongate their stem cells. Type 4 oidiophores are those lacking a stem cell, where oidial hyphae bud off either singly (type 4A) or in bundles (type 4B) from cells of the aerial hyphae. These various types of oidiophores occur within the same aerial mycelium of all strains so far analyzed, although at strain-specific frequencies (Polak et al., submitted).

Chlamydospores

Chlamydospores are large, thick-walled mitospores of variable forms and with condensed cytoplasm. They are found in brown patches present on the mycelial mating of older cultures of dikaryons (6, 71, 121, 266) and, occasionally, on certain monokaryons (26, 261) (Fig. 6). The generation mode of this type of spore in *C. cinereus* is not well documented. In general, chlamydospores may arise endogenously in cells of the vegetative hyphae following compression of the cytoplasm (chlamy-

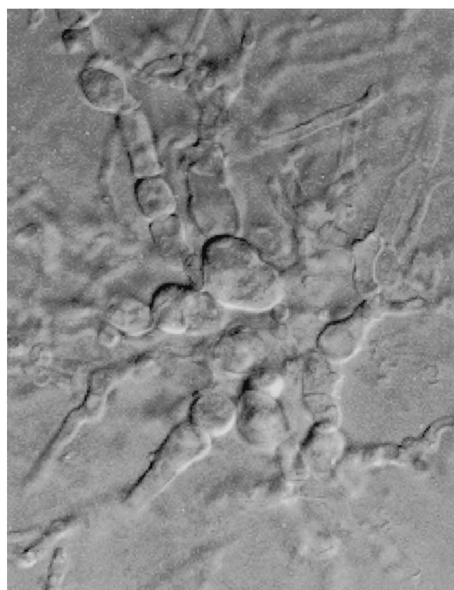

FIG. 6. Young chlamydospores in the submerged mycelium of monokaryon 218 (*A3 B1*).

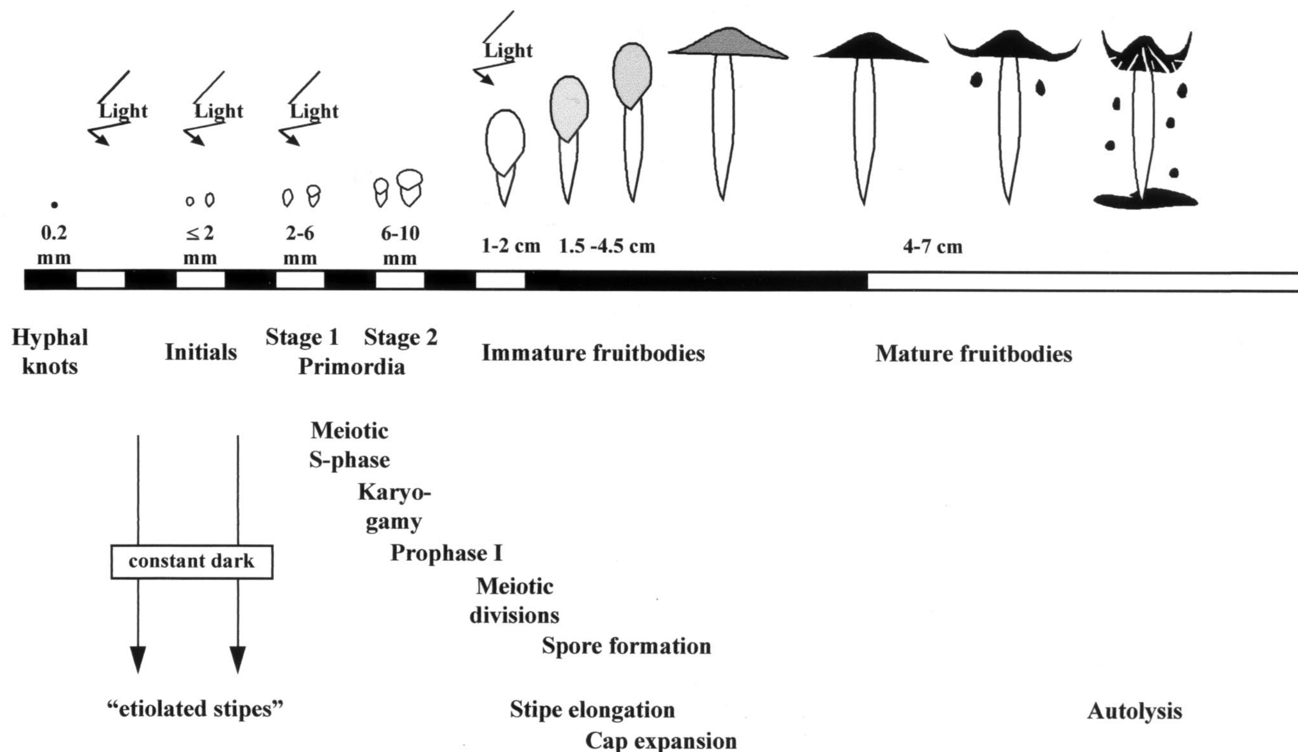

FIG. 7. Fruiting-body development of homokaryon AmutBmut (*A43mut B43mut*) in a 12-h-dark/12-h-light regime (light intensity, 50 to 75 $\mu E\ m^{-2}\ s^{-1}$; light source: Osram L36W) at 25°C and 90% humidity (Boulianne et al., submitted; Kües, Granado, et al., unpublished). Dark periods are indicated by black boxes, and light periods are indicated by white boxes. "Light" arrows indicate time points where light positively influences a developmental process: the first signal causes the induction of initial formation, the following two induce gill development in the cap and suppress the formation of etiolated stipes, which will appear when, instead, cultures are transferred in constant dark. Further on, light will induce premeiotic DNA replication and another signal influences meiosis. For details on karyogamy and meiosis, see the text. Note that changing the light intensities and/or the length of light incubation time might change the length of the intervals for the different developmental steps, especially the course of initial and primordium formation and the length of meiosis (U. Kües and J. D. Granado, unpublished data; B. C. Lu, personal communication).

dospores in the strictest sense) or by transfer of the compressed cytoplasm from a hyphal cell into a bud (blastocyst) (95). Diagrams found in some publications (6, 121, 266), combined by occasional observations in our laboratory (U. Kües and E. Polak, unpublished data), suggest that both generation modes exist in *C. cinereus*.

Despite their poor cytological description, chlamydospores have been used to collect component monokaryons from dikaryotic mycelia. Chlamydospores from dikaryons generally contain one nucleus of each parental type. Dikaryotic chlamydospores germinate with either one germ tube or two germ tubes, one at each end. When two germ tubes are present, each will receive one nuclear type. Monokaryotic hyphal cells can be isolated by microsurgery using a sharp scalpel before the germ tubes newly dikaryotize each other (121, 266). However, the fact that oidia production has now been observed in dikaryotic cultures after light illumination simplifies the process of monokaryotic culture isolation, but there is normally an uneven recovery of the two nuclear types (175a, 383).

FRUITING-BODY DEVELOPMENT

Developmental Course of Fruiting

Fruiting-body formation is the most complex developmental process in the life cycle of *C. cinereus*. Fruiting-body development involves a dramatic change of the growth pattern from a relatively regular three-dimensional loose mesh of free, undifferentiated hyphae to a compact multihyphal structure composed of many different cell types that associate with each other in distinct hypha-hypha interactions (335, 337, 338). Fruiting-body formation in *Coprinus* is a rapid process. From the first sign of fruiting (formation of initials from hyphal knots) to maturation (autolysis of the cap of the mature fruiting body), it takes about 4 to 5 days (263, 277, 344, 353, 450) (Fig. 7). To initiate and continue fruiting-body development, several environmental signals are called for, of which dark and light periods are the most important (see below). Indeed, fruiting-body development is perfectly synchronized to the light-dark rhythm fixed by the normal day-night cycle (21, 40, 184, 203, 277, 350, 351, 353, 476) (Fig. 7). Hyphal knots are formed in the dark (261, 330), and light then induces the formation of globose fruiting-body initials. Within the initials, cellular differentiation begins, but a further light signal is needed to develop primordia with distinctive cellular tissues (21, 184, 203, 277, 350, 351), otherwise the initials will grow into elongated structures with underdeveloped caps (see below), variously called pseudorhizas (32, 56, 60) dark stipes (353, 476) or etiolated stipes (40, 120). Following another dark period, light is needed to complete meiosis within the basidia, while stipe elongation and cap maturation take place in parallel. Meiosis will be finished by midnight, and basidiospore formation and cap opening occur in the early-morning hours. Within a few more hours, the cap will autolyze and the black basidiospores will be released within a brown liquid (283, 286, 353) (for further details of light regulation, see below).

FIG. 8. Hyphal knots in the vegetative mycelium of monokaryon 218 (*A3 B1*) that were formed in the aerial mycelium the dark after transformation of the strain with the *A43* mating-type gene *a1-2* (left). When the cultures are transferred to a 12-h-light/12-h-dark regime at 25°C, primordia develop (middle); when they remain in the dark, sclerotia form from hyphal knots (right) (261).

Early Stages

Fruiting-body development in *C. cinereus* is monocentric: a hyphal knot (also referred to as a hyphal tuft [335] or nodulus [93, 94]) forms as a single independent organ from which a fruiting-body initial may arise (302, 303). In the literature, there is no sharp distinction between a hyphal knot and an initial, and the difference between the initial and the primordium is not easy to understand due to the different uses of these terms by different authors (see, e.g., references 93, 94, 303, 335, 338, and 344). Hyphal knots as defined by Reijnders (413, 415) occur in various tissues of basidiomycetous fruiting bodies and their primordia (e.g., in the stem, veil, and cap). Reijnders (413, 415) defines hyphal knots as aggregates of hyphae that form small communities consisting of an induction hypha with the surrounding hyphae brought under its influence (for further discussion, see reference 338).

Work in our laboratory focuses on fruiting-body initiation. This has made it necessary to define the initial hyphal knot in fruiting-body formation of *C. cinereus* more specifically as areas of intense localized branching of undifferentiated hyphae within the vegetative mycelium (R. P. Boulianne, Y. Liu, M. Aebi, B. C. Lu, and U. Kües, submitted for publication). (Fig. 8, left). Mature hyphal knots are about 0.2 mm in size (201, 302, 344; Y. Liu, personal communcation). Microscopic studies revealed that the simplest hyphal knot arises from just a single hypha that will intensely ramify with short branches, which in turn give rise to further generations of branches with restricted tip growth (46; Liu, personal communication). In the more common case, hyphal knots originate from more than one generative hypha. Branches of neighboring aerial hyphae will grow toward and alongside each other and possibly merge by anastomosis through the lateral hyphal walls to form an intricate and easily distinguishable lattice. Such locally restricted interlacings will serve as the active center for the intense production of short hyphal branches. Hyphal cells within the resulting bunches of branches are often of a globose or inflated morphology (201, 302; Liu, personal communication). The process as described so far occurs in the dark and is repressed by illumination with blue light (261, 330). However, continuation of development toward fruiting-body formation is light dependent (277, 350) (Fig. 8, middle), indicating a major change in regulation and the beginning of a new, distinct developmental phase. This new phase includes a switch from a (purely) ramifying to an aggregating mode of hyphal growth and results in the formation of a round, aggregated body of tightly interwoven hyphae (95, 335, 338; Boulianne et al., submitted). For this reason, we restrict the definition of a hyphal knot to the locally restricted bunch of hyphal branches which is formed in the dark and which does not necessarily involve hyphal aggregation (Boulianne et al., submitted). These dark-formed structures are not fruiting-body specific but also serve as precursors in the dark-dependent development of sclerotia (330) (Fig. 8, right) (see below). Thus, the formation of globose hyphal aggregates from hyphal knots in the light is the first fruiting-body-specific stage (330, 338), and these structures are referred to as the fruiting-body initials (see also references 263, 344, and 450). This distinction between hyphal knots (i.e., the primary nodules of Clémençon [93, 94]) and initials (in their early appearance, the secondary nodules of Clémençon [93, 94]) has recently been confirmed by using molecular markers. Two different galectins, Cgl1 and Cgl2, belonging to a β-galactoside sugar binding subgroup of the lectin family, had been isolated from *Coprinus* mushrooms of a wild-type dikaryon and an *Amut Bmut* homokaryon (44, 96; Boulianne et al., submitted). Expression of Cgl2 in the *Amut Bmut* homokaryon has been shown to correlate with hyphal knot formation and to be repressed by light, whereas Cgl1 expression starts with the development of initials and is light-induced (Boulianne et al., submitted). Mutants have served before to elucidate fungal development (95), and we generated a collection of mutants from an *Amut Bmut* homokaryon by restriction enzyme-mediated DNA integration (REMI) and UV mutagenesis (145; Kües, Granado, et al., unpublished). Among these mutants, we identified a number of strains with specific defects in fruiting-body initiation, having a block either before or directly after hyphal knot formation (*knt* and *prm*, respectively). Most interestingly, we found one mutant that formed hyphal knots but produced neither Cgl1 nor Cgl2, some knotless strains that produced only Cgl2, and mutants that formed knots but no initials and produced either only Cgl2, or, in rare cases, both galectins at a low level. These classes of mutants correlate well with the distinction of hyphal knot and initial and a two-phase regulation of development (Boulianne et al., submitted; Liu, unpublished). Galectins are thought to be involved in hypha-hypha aggregation (44, 96), and the results obtained with the mutants indicate further that galectins are not essential for hyphal knot formation (Y. Liu, M. Aebi, and U. Kües, unpublished data), consistent with the notation that aggregation is not essential for hyphal knot formation.

In the hyphal knot, there is a noticeable reduction in the chitin content with respect to that in the vegetative hyphae

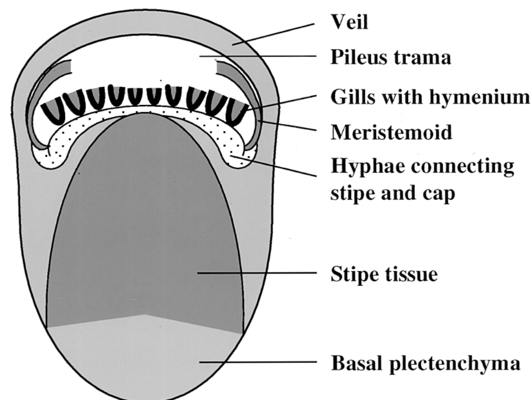

FIG. 9. Schematic presentation of a slightly tangential section of a primordium. The main tissue organization is indicated. Further details are described by Reijnders (413, 414).

(201). However, the globose hyphal aggregate of the initial, the "primordial bud" (277), is the first structure that shows clear histological differentiation. It is enclosed within a coat of large, vacuolated, and mainly outwardly directed hyphae covered with various amounts of amorphous material that protect a compact core of prosenchymal tissue. In the young initial (about 0.2 mm in diameter), this core of heavily branched short cells is only loosely grouped, but in older initials (up to 0.5 mm in diameter), the cells are tightly twisted and fixed together (303, 500). The densely packed cells in the core are rich in glycogen, and between the cells, a large amount of mucilaginous material is present which is probably involved in aggregation. Anastomosis and presumably exchange of cytoplasm occur frequently between adjacent cells. Septa between core cells are usually surrounded at one or both sides by a parenthosome and an additional hemispherical cap also composed of ER membranes. In contrast, cellular fusions do not occur between the large hyphae of the outer layer and the septa are dolipores with normal parenthosomes (500). The current lack of suitable molecular markers makes it difficult to give any information about the possible mechanisms involved in defining the further morphogenesis of the structures which eventually lead to distinctly differentiated tissues within the core area. Since the fruiting-body embryo is initiated within a hyphal agglomeration and is protected by outer layers of large cells (veil cells), which rupture later in development, fruiting-body formation in *C. cinereus* is classified as hemiangiocarp (95, 335, 512) (Fig. 9). Most important is the change in polarity: the lower and the upper parts of the core of the initial give rise to the fruiting-body stipe and cap, respectively (303, 362). It is not clear when the change from undirected hyphal growth to a defined polarity is determined, and the responsible physiological determinants are also unknown. As a step forward in elucidating this problem, a promising method of vital staining with Janus green has recently been developed to identify initials easily and to study the physiological processes involved in fruiting-body initiation (430).

Following the definitions of Moore and coworkers (263, 344, 450), up to a maximal size of 2 mm we will call the developing globular, later more oval aggregation the initial. Staining of fixed material indicated that the first cytological differentiation within the aggregate becomes obvious at a size of about 0.4 to 0.7 mm. Differentiation starts visibly in the upper third of the aggregate, the prepileus region. This ventral area is still prosenchymal and is the base for the upper peripheral cells (pileus trama) and, underneath, the ring of cells in which polysaccharides (glycogen) accumulate. Cells in the middle part of the initial line up to give rise to the stipe tissue, whereas cells in the lower third are randomly orientated to form the basal plectenchyma, representing a tissue of tightly packed hyphal cells not belonging to the stipe. A distinct mushroom shape emerges at a size of 0.8 to 1.0 mm, when hyphal tissue grows from the subapical region in an outward direction to give the annular boundaries of the pileus (303, 335, 344, 362, 414).

The whole complex is surrounded by a marginal veil of hyphae which originate from the top of the pileus (303, 344, 353, 362, 414, 422, 424). Veil cells are large, multinucleate, and septate, but they lack clamp connections (277). With an increasing size of 1.5 to 2 mm, a dense band develops which clearly defines the boundary of the hymenium and stipe (277, 333, 344, 362, 414, 422, 424). To suppress the formation of etiolated stipes and to continue hymenium development (referred to as day 0 by Lu [277]), light is needed at this stage (277). In the lateral part of the cap, between the trama of the cap (pileus) and the differentiated veil cells, a zone of cell division (meristemoid) of strictly parallel hyphae appears (413, 414). Glycogen deposits can be detected in the basal plectenchyma and in the hymenium (89, 197, 303, 344). The hymenium differentiates further into dome-shaped rudiments, which eventually will become the gills (lamella), which carry the basidia in their outer hymenial cell layer (89, 277, 333, 413, 414) (Fig. 9). Primary gill formation proceeds from the edge closest to the stipe toward the cap and from the margin to the apex of the cap (277, 333, 422, 424). Autodigestion of the cells in areas of the gill cavities has been proposed to be the origin of gill construction (277, 282), although the cell debris and the multivesicular and membraneous residual bodies seen in electron micrographs and taken as remnants of degenerating cells possibly represent fixation artifacts (335, 337, 338). Support for the occurrence of morphogenetic cell death as part of the programmed process of primordia development comes from studies with *Agaricus bisporus* and other mushrooms. In *Agaricus*, programmed cell death repeatedly occurs during establishment of the hymenial chamber within the primordia (339, 478, 479). It has been suggested that this cellular autolysis contributes to the formation of the primary extracellular matrix (ECM) (479).

Light is essential to enter the next stage of development (203, 277, 351) (Fig. 7), termed stage 1 primordia by Moore and coworkers (263, 344, 450), day 1 primordia by Lu (277), and stage 0 by Kamada et al. (203). Light induces hymenium differentiation and ultimately karyogamy (203, 277, 351) (see below), but the nuclear prefusion phase is long (taking about 24 h) (479). During this time, stage 1 primordia grow from about 2–3 mm to 7–9 mm in diameter. They are characterized by well-developed gills containing basidia of about 12 μm and cystidia (large sterile cells sized between 20 and 25 μm) at their surface (263, 344, 402, 450). Gills are essentially vertical plates arranged radially around the stipe. Primary gills are connected with their tramal tissue of their apex to the outer layers of the stipe; consequently, they have a hymenium at both their sides but not at their edge. With increasing primordium size, space for further gills becomes available within the cap. Secondary and lesser ranked gills are formed by bifurcation of the primary gills. Secondary gills grow radially outward, away from the stipe, by a replication fork-like movement of the gill organizer (a hypothetical formative element in the tissue at the extreme end of the gill cavity) into the trama of the primary gills. As the gill cavity moves outward, it expands tangentially, making room for a new gill organizer to appear, which initiates further gill splitting (89, 333, 414, 422, 424). When space becomes

available, further gills may arise from prosenchymal tissue as folds of the cap. Gills of this kind appear as convoluted plates usually in the most apical regions of the cap (89, 422; for further reading on the process of gill formation, see references 95, 335, 337, and 338). Due to their mode of formation, secondary gills are not attached to the stipe. Therefore, their hymenium is continuous over the gill edge. At the edge of the secondary gills, there is an increased number of cystidia (333, 414, 422, 424). The hymenium develops as a layer of similar-sized palisade-shaped cells by branching from sister hyphae of the prosenchymal subhymenium. This hymenial layer of cells is occasionally interrupted by larger cystidia (90, 179, 344, 422–424). Hymenial cells have clamp cells, and the nuclei stay paired, indicating that the dikaryotic stage is preserved (277, 344). During further development of stage 1 primordia, the basidia change from a cylindrical to a club-shaped structure (402). Glycogen accumulates in the subhymenium and cystidia and in the basal plectenchyma of the stipe (263, 344, 450). The timing of this stage is difficult to determine, and this makes it particularly difficult to compare the observations on primordium development made by different researchers (21, 203, 277, 344, 351). Karyogamy is therefore used as a reference point (277). Karyogamy occurs toward the end of this phase and is considered, according to Lu's definition, to have begun when 5% of the basidia have undergone nuclear fusion (277, 402) (see below). At this point, by the beginning of the following day, tissue development in the cap is completed (277).

Stage 2 (day 3) primordia (Fig. 7) are 6 to 10 mm (occasionally up to 15 mm) tall. Meiosis starts within the basidia (see below), which are now 15 to 18 μm long. The cystidia enlarge up to 45 μm. Primary gills are still connected to the stipe, but the gills begin to separate. Initially, the veil of stage 2 primordia is still intact, but it becomes more and more free. In the cap, more glycogen accumulates, while the glycogen content in the basal plectenchyma decreases (263, 277, 344, 450). Galectin distribution has been analyzed in stage 2 primordia. Galectin antibodies localize preferentially to the veil cells, to the outer layer of narrow hyphae of the stipe, and to the apex of the primary gills connected to the stipe (Boulianne et al., submitted). Significantly, these different tissues (called in specialist terms lemmablem [the external tissue of the cap] and lipsanoblem [the external tissue of the stipe], respectively) are functionally related in protection of the inner primordium tissues, and at least the veil cells of the cap are dispensible at later stages and degenerate or are discarded (95, 155). To a lesser extent, galectins are also present in the gill trama and the inner tissues of the stipe. Galectins are found attached to cell walls and in the extracellular matrix and, within the cells, localized in vesicles and in the dolipores (Boulianne et al., submitted). Consistent with the immunolocalization studies, Northern blot analysis indicates high expression of galectin genes in stage 1 and stage 2 primordia, but at later meiotic stages (late pachytene/diplotene, metaphase I) at the transition to the next developmental stage (fruiting-body maturation) galectin expression is halted in both the cap and the stipe (85).

The further development of stage 2 primordia into mature basidiocarps takes another 24 h (263, 277, 344, 353, 394, 450). Maturation consists of at least four processes: stipe elongation, basidium maturation (including meiotic divisions and spore formation), pileus expansion, and autolysis of the pileus (see below).

Structure and Development of the Stipe

The mature stipe is a thin-walled hollow cylinder with two types of hyphae, i.e., narrow and wide hyphae. It has been found that 23 to 54% of all hyphae are narrow. Most of these narrow hyphae are concentrated at the exterior of the stipe, but they are also found at the lumen and in between the wide, inflated, and highly vacuolated hyphae that make up most of the interior tissues (39, 156). The narrow hyphae resemble vegetative hyphae, since they clearly have clamp cells and form interconnections independent of the inflated hyphae (39). This network of narrow hyphae has been suggested to act in nutrient translocation from stipe to cap (188, 335, 338). Cytologically, the cell walls of the narrow hyphae at the different locations differ from each other and from those of the inflated hyphae, as indicated in various staining experiments (39, 139, 156) and by a different immunohistochemical response with antigalectin antibodies (Boulianne et al., submitted). On the whole, the composition of cell walls of the stipe seems very much like that of monokaryotic hyphae and is very different from that of vegetative dikaryotic hyphae (298). However, compared to the monokaryotic mycelium, the overall chitin content is increased in the stipe (298), consistent with the facts that chitin synthesis is especially active in stipe formation (106, 137, 140, 143) and that the chitin synthesis inhibitor polyoxin D suppresses stipe elongation (144). Chitin microfibrils, 7 to 25 nm in diameter, are indeed a major component of the walls of stipe cells. They are arranged as shallow helices transverse to the long axis of the cell. Two-thirds of these helices are left-handed, and one-third are right handed (140, 195, 210). In contrast, chitin microfibrils are randomly orientated in the vegetative mycelium; the shift to a parallel transverse arrangement can occur in hyphal knots of only 0.1 to 0.2 mm in diameter, although at this point it is still incomplete (201).

Stipe growth is mainly the result of manifold cell elongation rather than cell division (39, 99, 142, 196). However, in the very young primordium, stipe cells are cuboid or polyhedral, and proliferation still occurs in the apex meristematic region of the stipe (39, 155, 302). At the stage of karyogamy, many of the cells inflate and become cylindrical, and it is obvious that these enlarged cells lack clamp connections, in contrast to cells found in the central yet closed region of the stipe (39, 155, 156, 277). During stipe elongation, inflated hyphae inflate further but only vertically; the width of the stipe cells remains almost constant (155, 156, 335, 337, 338). However, the proportion of narrow hyphae declines as the stem grows from 45 to 70 mm, indicating that normal vertical stem extension involves both an increase in the cross-sectional area of inflated hyphae and recruitment of narrow hyphae into the inflated population (156, 335, 337, 338).

The enlarged stipe cells are usually multinucleate, and more nuclei are progressively produced by mitosis as the cells grow by vertical elongation (277, 449). Indeed, there is a linear correlation between the length of the stipe and the numbers of nuclei found within the elongated cells. There are between 2 and 8 nuclei in stipe cells of 2- to 4.5-mm primordia, about 16 at a primordial size of 5 to 7.5 mm, and more than 150 when the stipes are longer than 20 mm. In 29% of stipe cells, nuclei are present in uneven numbers and there is no indication of synchronized nuclear division (142, 449). The increase in the number of nuclei is indicated by the dramatic increase in DNA content 3 h before the onset of rapid stipe elongation (142, 202). In contrast, the RNA content increases continuously with stipe maturation and the protein content is constant (141, 202, 344). The young stipe contains large amounts of glycogen inclusions, whereas glucans, including glycogens, are almost absent in the fully expanded stipe, probably because they serve as a source of cell wall precursor material (32, 195, 197, 198). Apart from glycogen inclusions, insoluble protein inclusions were also detected which first increase but then decrease in

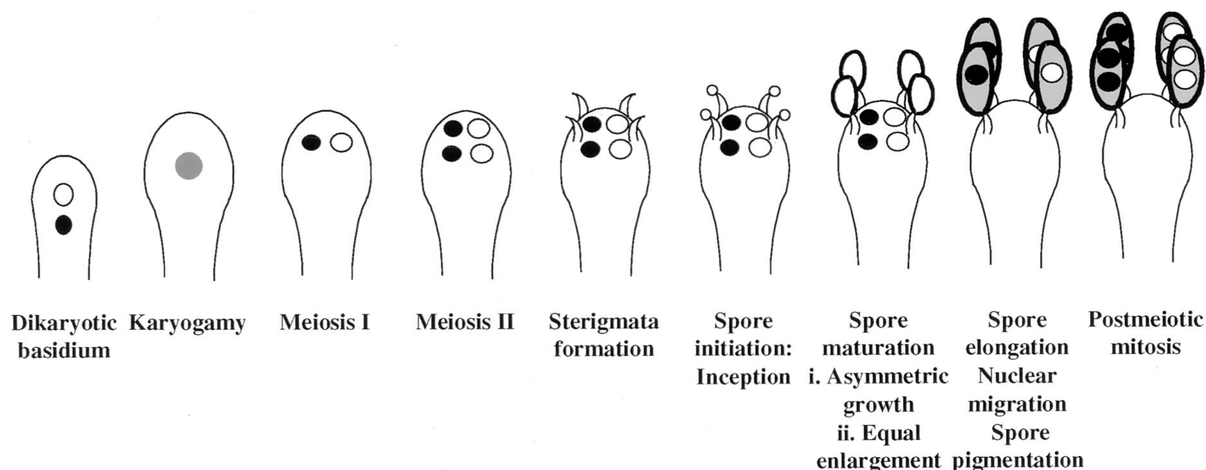

FIG. 10. Karyogamy, meiosis, and basidiospore formation.

size with progressive stipe development (32). This is most interesting, since, apart from the intercellular compartments and cell walls, the galectins have been localized to vesicles within stipe cells of stage 2 primordia and young elongating fruiting bodies (Boulianne et al., submitted).

Decapitation of the stipe before meiosis arrests stipe expansion, showing that the cap is needed for the early development of the stipe (39, 99, 138, 150, 195). Consistent with this, grafting experiments revealed that during meiosis, the cap produces a diffusible substance acting on basidiocarp maturation, including stipe elongation (200). Rapid stipe elongation correlates with the end of meiosis 8 h after the nuclei in the bulk of basidia have fused (155, 202). Although the cap still influences the absolute length a stipe can achieve, in the postmeiotic basidiomes the stipe and cap develop independently from each other. Also, the stipe does not need to be connected to the vegetative mycelium, indicating that stipe elongation is an autonomous endotrophic event requiring no exogenous nutrients, growth factors, or water (39, 99, 138, 142, 155). Elongation is not evenly distributed over the length of a stipe. The ultimate apex of the stipe does not extend much, although in general the cells in the apical half elongate most, in contrast to the cells of the basal half, which show reduced stretching, and the cells in the base, which show no stretching at all (39, 99, 156, 196, 198, 344). Stipe cells elongate in an intercalary fashion by diffuse extension in which the extension of the cell surface is not confined to the hyphal tip but occurs throughout the whole cell (139, 141, 156, 195). The stipe has to be formed quickly and as strongly and economically as possible. Therefore, cell walls have to be plastic but also rigid to withstand the high turgor pressure. Plasticity is given by the ordered arrangement of chitin helices, and rigidity is given by cross-linking between chitin and glucans (195, 196, 198). Throughout elongation, the chitin content stays constant and insertion of new chitin microfilaments occurs over the whole length of the cell in a uniform intercalary fashion, probably mediated by a constant unfastening and resealing of linkages between chitin and glucan (139, 141, 197, 210). Consistent with active cell wall hydrolysis playing a role in the mechanism of stipe elongation, stipes are rich in chitinases and glucanases (204, 205, 207).

An average stipe may elongate 80 mm in less than 12 h (195, 341, 449). It is very strong in its longitudinal axis and withstands pressures of 7×10^4 N m^{-2}, a fact impressively shown by the occasional documentations of fungal breaks through asphalt (58, 142, 327). Rapid stipe elongation requires high turgor pressures (142, 327), and throughout elongation the osmotic value stays almost constant at 0.45 to 0.5 M (99, 195). This high turgor must be actively maintained, probably by organic metabolites which have not yet been identified (39, 141, 142, 338). Trehalose and polyols have been excluded as the sole osmotic stabilizers, since the concentration of the former decreases during elongation whereas the latter are hardly present in stipes at all (141, 142, 338, 406). Amino nitrogen compounds and urea have also been implicated in osmostabilization, but their contents are low and decline with development (123, 142, 344). Regularly in fruiting-body development, shortly before rapid stipe elongation, clear or sometimes yellowish droplets are excreted at the region where the cap with the gills is attached to the stipe (241; Kües, unpublished). These droplets are rich in potassium oxalacetate, but it is not known whether this contributes to the high turgor pressure of the stipe (241). Cox and Niederpruem (99) reported that a brown gel was present within the lumen of young stipes but disappeared during elongation, and this has also been discussed as a source of an organic osmotic stabilizer (195). Since no sugars or other substances have been found to be of prime importance, cocktails of simple carbohydrates together with inorganic ions are anticipated to control the osmotic pressure in stipe elongation (338, 344).

Developmental Processes in the Basidia

Basidiospore formation. Basidia are the only *C. cinereus* cells that express developmental comittment. Probasidia can easily be arrested in development (86, 277, 285), but once meiosis is initiated, maturation of basidia is an autonomous, endotrophic process (86, 314) (Fig. 10). The basidium usually arises as the terminal cell of a hyphal branch and is separated from the subjacent cell by a dolipore septum with a well-formed septal cap at the side of the subjacent cell (312, 314). The cytoplasm in the probasidia is relatively simple with numerous free ribosomes, few vacuoles, mitochondria, and limited ER. At the time of nuclear fusion, glycogen is evident at the basidial base. An increase in the amount of rough ER is observed at the end of prophase I, and ER extends throughout the cell in the postmeiotic basidium. Usually, as basidiospores form, a vacuole at the base of the basidium gradually expands to fill the cell (169, 314).

Basidiospore formation starts with the development of sterigmata. These begin as broad bumps and subsequently elongate in a manner reminiscent of hyphal tip growth. They curve toward the adaxial side and are characterized by a thin, three-layered cell wall thinner than that of the basidium. It is not clear whether the sterigmal wall is a continuation of the basidial wall (311, 314) (Fig. 10). In contrast, the wall of the basidiospore is multilayered and the spore wall layers change constantly during development of the spores, with permanent wall setting occurring only at the end of development (313, 314). During spore formation, numerous microtubules are oriented longitudinally in the sterigmata, and Golgi vesicles carry carbohydrates to the developing spore and spore wall (310–312). The first stage of basidiospore formation (stage 1, inception) is characterized by the spherical enlargement of the sterigma apex (Fig. 10). Typically, the basidiospore is asymmetrically positioned on its sterigma because of an unequal initial growth toward the abaxial side (stage 2, asymmetric growth) (Fig. 10). Later, the basidiospore enlarges spherically, a peripheral ER develops, many Golgi and other vesicles and mitochondria are present, and the number of wall layers rises (stage 3, equal enlargement). In the last stage of development (stage 4, elongation) (Fig. 10), the spore grows longitudinally and less Golgi vesicle but new microtubules are found within the spore. A pore cap develops at the spore apex and covers the germ pore, and the walls thicken extensively; within 2 h, the spores become pigmented (184, 193, 313, 314). Nuclei migrate into the spores at stage 4 (239, 313), although other authors report earlier nuclear migration (402). The cytoplasma of stage 4 spores resembles that of mature, ungerminated spores. At the mature spore, two papillas are seen; one is the spore cap, and the other is the hilum, the scar at the point of former attachment to the sterigma (169, 193, 316). Mature spores are partly submerged in a mucilaginous-like secretion (169, 193). Mature basidiospores measure 9.5 to 13 by 6 to 7 μm (376, 500).

In parallel with basidiospore development, a wall thickening, the hilar appendix body, forms and projects from the sterigma/spore base (313). Although spores of *C. cinereus* are released mainly by autodigestion of the cap (53, 56, 58, 185), liquid droplets (Buller's drops) are collected at the hilar appendix (315, 316) in the characteristic way needed for the ballistic discharge of basidiospores (55, 182, 328, 515). A secondary mode of spore release in *C. cinereus* by ballistospore ejection is consistent with the occasional shedding of spores before autolysis of the cap (95, 184, 315; Kües, unpublished).

Karyogamy, meiosis, and postmeiotic mitosis. A remarkable feature of *C. cinereus* is the natural synchrony of karyogamy and meiosis—60 to 85% of all basidia within a given cap will always be in the same developmental phase during all stages of meiosis. In general, the basidia at the bottom of the gills are slightly more advanced in their development than are those at the apex (53, 55, 155, 271, 402). Synchronization of karyogamy and meiosis occurs through light impulses (286, 324) and is thought to be a consequence of spore liberation by autodigestion of the cap, since this limits the time during which mature basidiospores can be produced on the gills (53, 55). This unique property of synchronizing basidial development has made the fungus a classical object for studying meiosis (100, 283, 389, 391, 419). Each mushroom cap contains 10^7 to 10^8 meiotic cells (404), which provides sufficient material for cytological and biochemical analysis at any stage. When carefully prepared, a few gills can be removed at successive time points from a single developing mushroom without resulting in any apparent effects on development, and progeny will still be left for genetic analysis (239, 271, 283). Moreover, because of the control by environmental signals (275, 278, 286) meiosis can be monitored in a regular and predictable manner (402). *C. cinereus* has a total genome size of 37,500 kb (115, 539) distributed over 13 chromosomes (176, 371, 391, 392, 535), although only 10 linkage groups have been defined genetically so far (71, 366). In the developing meiotic cells, all 13 chromosome pairs can easily be studied jointly by light microscopy using rapid fixation and staining techniques and by surface spreading and electron microscopy (176, 239, 283, 288, 392, 466).

At the early stage of basidial development (Fig. 10), the dikaryotic probasidium contains two oval haploid nuclei, one from each monokaryotic parent. Each nucleus consists of a relatively large nucleolus and a hyaline portion (271, 239, 324). Similarly, probasidia of *Amut Bmut* homokaryons are binucleate, and the process of karyogamy, meiosis, and basidiospore formation is as in dikaryotic basidia (452; J. D. Granado, personal communication; B. C. Lu, personal communication). In contrast, *Fis*^{c} monokaryons often have only one nucleus in the probasidium, but after a mitotic division, no obvious difference between dikaryotic and homokaryotic fruiting bodies was detected (324). As the binucleate basidium develops, the nuclei come in close contact and fuse to a dumbbell-shaped nucleus with two nucleoli. The nucleoli combine into a large spherical nucleolus, and the now diploid nucleus becomes oval (239, 324). Simultaneously with nuclear fusion, the two spindle pole bodies (SPBs) also fuse (176, 279).

At the beginning of the meiotic S phase, premeiotic DNA replication takes place to duplicate the chromatids. Not unusually for fungi, the premeiotic S phase takes place before the onset of karyogamy (90, 216, 280, 286, 373). Before nuclear fusion, the chromatin appears diffuse in the light microscope, but after fusion individual chromosomes can be distinguished (271). The subsequent first meiotic division is cytologically subdivided into prophase I (condensation of chromosomes, chromosome pairing, formation of the synaptonemal complex, SC), metaphase I (arrangement of paired chromosomes at the equatorial plate), anaphase I (total separation of the bivalents, migration to the poles), and telophase I (formation of two nuclei) (176, 239, 271, 283, 402). Prophase I is classified by five steps: chromosome condensation and alignment (leptotene), synapsis (zygotene), appearance of recombination nodules (pachytene), desynapsis (diplotene), and transition to metaphase (diakinesis) (176, 271, 288, 402) (Fig. 11). In leptotene and zygotene, the two nucleoli are generally seen fused before the chromosomes are completely paired (288). The initial contact and alignment between homologous chromosomes often take place at either one or both telomeres before the chromosomes condense and zip up throughout their length with formation of the tripartite SC (176, 272, 281, 288), a proteinaceous core of two parallel lateral elements separated by a central region of 100 nm which holds the paired condensed homologues close together (272, 281; for reviews, see references 326, 419, and 534). As soon as synapsis is complete, the chromosomes remain closely paired for approximately 2.5 h. In the next 2 h they are pulled slightly apart (288). Chromosome breaks are present during zygotene. Their correction is completed by breakage-reunion before mid- to late pachytene (175), when DNA repair synthesis occurs extensively (286). Recombination nodules, small, dense proteinaceous structures connected to chiasmata and recombination processes (283, 326, 419, 534), are readily identified in the central region of the SC (Fig. 11). A first early type is more frequent and randomly distributed over the bivalents. Fewer, nonrandom late nodules become larger and surrounded by chromatin during pachytene and diplotene, and by late diplotene these are replaced by small chromatin condensations, the chiasmatas. During diplotene, the SC is eliminated from the bivalent arms but the

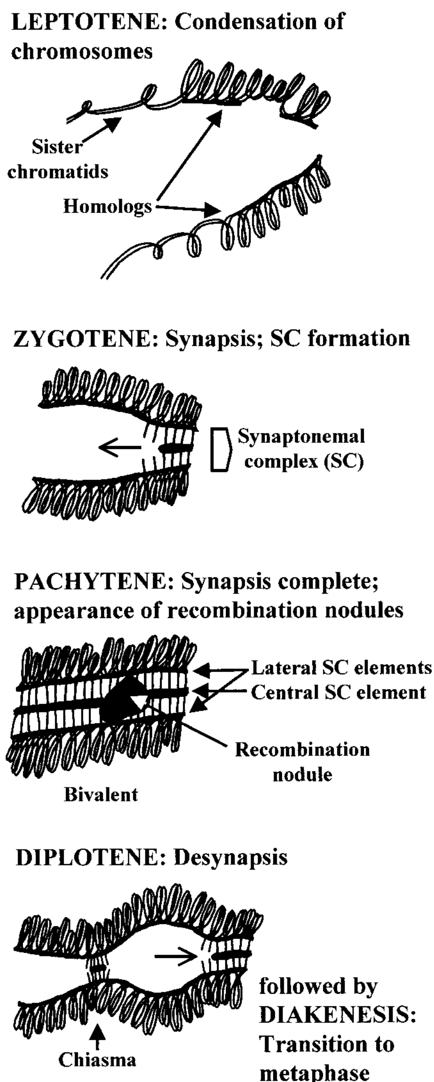

FIG. 11. Meiotic prophase I. Pairing of homologous chromosomes and the formation and disassembly of the synaptonemal complex. Arrows indicate the direction of SC formation in zygotene and the direction of desynapsis in diplotene (for further information, see references 326, 419, and 534).

process is delayed at the centromeres and the chiasmata (175). At early diplotene, the chromosomes are somewhat elongated and the so far single SPB divides. In late diplotene, a pair of duplicated SPBs, each 0.3 μm in size, become visible (271, 279, 288, 404) and the two bivalents are pulled apart, but the centromere regions remain fused at least until early diakinesis (175, 288). At metaphase I, the chromosomes are highly electron dense, consisting of closely packed chromatin fibrils, and congregate at the equatorial region between the two SPBs. Microtubules connect the chromosomes to the SPB, and other microtubules link up the two centrosomes. The two sets of homologous chromosomes separate at anaphase I, often in an asynchronous manner, and assemble at the poles. Later in telophase I, the chromosomes become uncoiled, and in the interphase, the fine structure of the new nucleus resembles the prefusion nucleus (239, 271). *C. cinereus* has a closed meiosis; in contrast to initial reports (239, 272), the nuclear membrane remains intact throughout the whole process of meiosis (175, 469). The ends of the SC (telomeres) remain anchored in the nuclear envelope throughout meiotic prophase (175, 270).

Soon after interphase, the two daughter nuclei begin the second meiotic division and pass quickly into prophase II, metaphase II, anaphase II, and telophase II. This second division takes about 1 h and occurs in the same plane as the first division (Fig. 10). In most cases, this plane is transverse to the long axis of the basidium. The two spindles of meiosis II are in parallel to each other and considerably smaller than those of meiosis I. After chromatid separation, each of the now tetrad nuclei appears as a special compact body. The nuclei elongate and migrate toward the tip of the basidium, where, in the meantime, four perpendicular sterigmata begin to project on the margins of the basidial apex and the four basidiospores are formed, into which the nuclei migrate (155, 239, 402, 469). Bleaching of the mature black basidiospores with hypochlorite (Javelle water) followed by nuclear staining (503; E. Polak and Y. Liu, personal communication), transmission electron micrographs (169), and DNA measurements (202) indicate that a postmeiotic mitosis follows nuclear migration in the spores. In contrast, Chiu and Moore (90) maintain that postmeiotic mitosis occurs before spore formation. However, pictures showing nuclear migration into the spores at the four-nucleus stage or pictures showing eight nuclei within the basidium are not available.

Meiotic recombination. Although meiosis is an autonomous, endotrophic process, it can still be influenced by environmental signals and chemical treatments (88, 280, 285, 411). Arrest of premeiotic S phase by high temperature and light shortens the length of the meiotic cell cycle, in particular diplotene, by several hours after release of the arrest. In contrast, cold treatment at pachytene prolongs the pachytene stage (285). High and low temperatures appear to affect different steps in recombination—heat treatment at late S phase, at karyogamy, or at pachytene will lead to an increased recombination frequency, indicating that repair activity is not turned on until pachytene (272, 280, 283, 287, 403). Cold effects on recombination are very stage specific and are effective only in pachytene with a maximal increase of recombination (272, 280, 284, 285). These observations correlate with a DNA-nicking programme active in the premeiotic S phase, at karyogamy and pachytene, and in the repair program in pachytene and diplotene (274, 280), consistent with the results of radioisotope-labeling experiments (280, 284) and the cytological studies (176). Meiotic recombination frequencies are also altered by ionizing radiation and divalent cations, which causes DNA breakage at S phase, karyogamy, and pachytene (276, 403), and by hydroxyurea, which acts on premeiotic DNA replication and on pachytene-diplotene repair replication (469).

DNA molecules must be broken and rejoined to mediate genetic exchange. The synchrony of karyogamy and meiosis within the *C. cinereus* fruiting bodies makes it easy to monitor stage-specific enzyme activities and makes this an excellent system in which to isolate the respective proteins. Thus, a meiotic endonuclease with DNA-nicking activity was purified from basidiocarps during the late premeiotic S phase, karyogamy, and pachytene stages of meiosis (287, 290, 329). Cloning of the gene encoding this enzyme using antiserum against a λgt11 cDNA expression library failed, since the highly expressed galectins copurified with the endonuclease (85, 96). A second enzyme from the karyogamy-pachytene stages is an endo-exonuclease with single-strand-specific exonuclease activity (289), and another prophase I endonuclease also preferentially digests single-stranded DNA (240). DNA polymerases have been identified from zygotene-pachytene (300, 428) and pro-metaphase I (431). A meiotic protein factor specific to

prophase I stages enhances the activity of the zygotene-pachytene DNA polymerase (135). The highest enzyme activities of DNA ligases occur at pachytene, and a corresponding enzyme has been characterized (301).

Other observations related to meiosis. In fruiting bodies of a diploid-haploid dikaryon, basidiospore formation is strongly disturbed, probably because meiosis does not proceed as normal. It has been found that 20% of all basidia have an aberrant number of spores, in most cases five. The absolute number of spores per fruiting body is strongly reduced, and large numbers abort in development. The few spores that mature are irregular in size and extremely variable in shape. Numerous spores seem to have two germ tubes. Many germinated spores fail to grow further or grow only poorly, suggesting that large numbers of unbalanced aneuploids are produced (68). Contrary to the paradigm in higher eukaryotes that only two homologues can pair at one location regardless of the number of homologues present (309, 360), there is almost exclusively triple pairing in meiosis of triploid nuclei of *C. cinereus*. Trivalents exhibit double SCs with three lateral components and two central regions. This configuration arises when sister chromatids of the central homologue have different synaptic partners. The trivalent configurations are maintained unaltered throughout pachytene, and at least the centromeres remain associated until mid-diplotene. At mid- to late pachytene, recombination nodules are found in both the central regions. Sometimes, unpaired arms associated with central region material and attached recombination nodules project from the trivalents. Breaks and gaps in trivalents are common which probably arise from earlier losses of portions of chromosomes in the vegetative divisions (397, 408).

Chromosome translocations are common in *C. cinereus* (176, 301, 392, 541). Reciprocal translocations have been mapped between chromosomes 3 and 5 and between chromosomes 1 and 9 (176, 392). Pairing and SC formation between translocation chromosomes and their normal homologues give rise to translocation quadrivalents. These are more often involved in interlockings and have more chromosome breaks than normally aligned bivalents do. Rarely, translocation quadrivalents are converted into two heteromorphic bivalents, probably because crossovers prevent the resolution (176). In *C. cinereus*, basidiospore viability can be poor; this is sometimes related to certain chromosomes (269, 330, 388), but it has not yet been established whether this relates to translocations as found in other fungi (379).

C. cinereus has an extensive chromosome length polymorphism that can be monitored in crosses (7, 391, 523, 535, 539, 541). Occasionally, crosses lead to new sizes of chromosomes in F_1 progeny, indicating that recombination took place between homologs (8, 54, 540).

Meiotic recombination rates vary at different chromosomal locations (8, 126, 257). There are about 60 to 90 copies of the tandemly repeated rRNA genes (units of 9.3 kb with each one copy of each of the 18S, 5.8S, 26S, and 5S genes) in the *C. cinereus* genome. Meiotic recombination in these repeats is inhibited, although breakage and rejoining reactions within rDNA are frequent throughout the life cycle (82, 393).

The nuclear genome of *C. cinereus* is extensively methylated at CpG sequences. Variation of the methylation pattern may arise during vegetative DNA replication. However, patterns of methylation are usually faithfully maintained through mitosis and also through meiosis; in most cases of meiosis, methylation patterns segregate 2:2 (124, 536, 537).

Mechanisms have been described in the filamentous ascomycetes *Neurospora crassa* (RIP, for "repeat-induced point mutation") and *Ascobolus immersus* (MIP, for methylation induced premeitotically) which detect and methylate cytosines in duplicated DNA sequences specifically in the dikaryotic stage in a premeiotic genome-wide homology search prior to karyogamy. Cytosine methylation is maintained through meiosis and accompanied by silencing of duplicated genes and, in *N. crassa*, by C-to-T transitions. Gene inactivation in *N. crassa* is permanent, whereas that in *A. immersus* is reversible (435a). As shown in *trp1*$^+$ transformants, de novo methylation of repeated DNA sequences (limited to CpG sequences) also takes place in the dikaryotic stage in *C. cinereus*. Methylation triggers gene silencing which is reversible, as in *A. immersus*. C-to-T transitions as in *N. crassa* were not observed. De novo methylation of duplicated sequences in *C. cinereus* has thus all the features of MIP, although the general level of methylation is low and gene inactivation is rare compared to *A. immersus*. It has thus been proposed that methylation of duplicated sequences in *C. cinereus* serves to mark ectopic repeats prior to meiosis in order to avoid translocations resulting from ectopic recombination (124).

DNA integrated by transformation into the *C. cinereus* genome is often stable in mitosis as well as in meiosis (30, 318), but this is not always the case (101, 124, 126, 145; A. P. F. Bottoli, personal communication).

Cap Maturation

With progressing meiosis, the hymenium within the cap differentiates fully. In the immature stage, the hymenium lacks the close packing of sterile hyphal elements (paraphyses), which may provide some stability in later stages (277, 344, 394, 402, 422). In late stage 2 primordia, at the end of prophase I, binucleate paraphyses emerge as outgrowths of binucleate subbasidial cells, increasing the width of the gill from 100 μm to 300–400 μm (90, 394, 395, 422–424). In the postmeiotic cap of the immature fruiting body (10 to 20 mm in size; stage 3 immature fruiting bodies [263, 344, 450] [Fig. 7]), the paraphyses expand from 3–4 μm to 8 μm, incorporate glycogen, vacuolize, and take on their characteristic rectangular shape. Inflation of paraphyses makes a major contribution to cap extension, which starts within the 1.5-h period between the ending of meiosis and the beginning of sterigma production (123, 155, 344, 423). Basidia begin to form sterigmata and spores when they measure around 20 μm (344, 394) (Fig. 10). Each basidium is surrounded by about five paraphyses, and consequently the basidia are displaced from each other (123, 312, 394, 422). Although comparably low in numbers (8% of all the hyphal tips of the juvenile hymenium become cystidia [423]), the solitary cystidia are very prominent on the gill surfaces due to their final length of about 60 μm (193, 344). The cystidia also accumulate glycogen (312). Cystidia are commonly believed to function as spacing organs to keep the hymenial surfaces apart during the development of basidia and basidiospores (54, 55, 193), to aid in evaporation of moisture and other volatile substances (439), and to enable ballistic spore release (55). Moore and coworkers suggest another role for cystidia in anchoring the gills to each other in order to provide a robust stabilization of the loosely arranged gill tissues and pull them into the typically radial-parallel arrangement due to the tension exerted by cap expansion (89, 179, 335, 337, 338). Cystidia are regularly spaced over the hymenium surface at both sides of the gills. As they grow, cystidia come into contact with the opposing gill face. Collision of the tips of the cystidia with cells of the opposite hymenium induces the latter to vacuolize and to adhere firmly to the cystidia. Cells whose differentiation is determined by attaching a cystidium have been named cystesia (179). Mutants lacking cystidium-

cystesium connections have a distorted hymenium, and the cap rolls up prematurely (89). Initially in cap expansion, gills are still physically connected to the young stipe, but eventually, after onset of rapid stipe elongation and by the time sterigmata appear, the stipe-hymenium boundary breaks up, separating the stipe from the gills by a clear zone (338, 344, 394, 422). When primary gills pull away from the central stipe, marginal, often multinucleate cystidia arise from the multinucleate gill trama, probably to protect and stabilize the apex of the primary gills (90, 277). The cystidia on the edge of a gill are more oval than the solitary facial cystidia, which are mostly binucleate and only occasionally uninucleate or multinucleate (90, 193).

During fruiting-body maturation, there are no further cell divisions and most changes in the shape of the cap depend on cell expansion (338, 344). Cap expansion correlates temporally and proportionally with stipe elongation, which lifts up the cap for more effective spore dispersal (155, 344). At a size of 15 to 45 mm (stage 4 immature fruiting bodies [263, 344, 450] [Fig. 7]), about 3.5 h after sterigma production at the time of basidiospore pigmentation, hymenial cells become vacuolated and glycogen disperses from the subhymenial tissue (155, 310, 312, 344). Within a further 8 h, the fruiting body adopts its final size and the cap fully expands, with outward upward and curling of the initially vertical oriented gills (58, 263, 338, 344, 450) (Fig. 7). Cap expansion is associated with a considerable cellular uptake of water, and this is probably osmotically driven (123, 338, 344) (see below). Cap expansion remains constant and continues in the still intact tissues even in the final autodigestive phase, possibly by utilizing substrates provided by the already digested cells (338, 344). Autolysis is clearly part of the developmental program of fruiting-body formation (55, 58, 344) and starts at the edge of the gill closest to the stipe (422), like karyogamy, meiosis, spore formation, and pigmentation (338, 402, 424). Autolysis of the mature cap is caused by cell wall degradation by chitinases, which are released into the wall from vacuoles in senescing gills about 8 h after the spores begin to blacken and 7 h after rapid elongation and opening of the cap start. Autolysis affects all cap tissues, the lamellae, and the interior trama but not the outer veil layers. The chitinase is produced 2 h in advance and is also not effective on stipes or the vegetative mycelium (155, 184, 185). Apart from the chitinases, proteases and glucanases have also been identified in extracts and autolysates of *C. cinereus* caps (184, 323, 338).

Mutant Analysis

Variants in fruiting-body development were first isolated by UV and chemical mutagenesis in dikaryons. The yield of variants was surprisingly high, with about 15% of a total of ~11,000 isolates displaying a change in pattern of development (461–463), of which a large proportion were temperature sensitive (466). Component nuclei of dikaryotic isolates have been found to carry naturally recessive alleles acting negatively on fruiting. This suggests that the mutations induced in dikaryons are not all dominant but, rather, that phenotypes are due to a mixed genetic background with naturally recessive and newly mutated alleles. The alleles present in the unmutated dikaryons obviously complement each other for fruiting (269, 330, 353). *Amut Bmut* homokaryons are able to fruit, and their use in isolating developmental mutants has a number of advantages over the use of dikaryons. First, it is clear that all genes essential for fruiting are present in an active form. Second, because of the presence of a single haploid genome, all possible mutations will be detected, regardless of whether they are dominant or recessive. Third, to ease the mutagenesis procedure, oidia with a single haploid nucleus can be used (388, 389). Because of these advantages, it is nowadays rather common to use *Amut Bmut* homokaryons and other fruiting homokaryons in UV and in REMI mutagenesis (45, 89, 101, 145, 213–215, 354, 389, 543; Kües, Granado, et al. unpublished) unless a phenotype can also be expected in the monokaryotic growth phase (206, 208, 209, 498, 538, 542). Following UV irradiation of *Amut Bmut* or *CopD5* oidia (with a 10% survival rate), 30 to 40% of all germinated clones have a defect in fruiting, and similar percentages have been determined after REMI mutagenesis (145, 354; Kües, Granado, et al., unpublished). In comparison, auxotrophic mutations are rare, with ≤1% (354; Kües, Granado, et al., unpublished). The large number of developmental mutants in *Amut Bmut* homokaryons and in dikaryons suggests that development is affected by defects in various housekeeping genes in addition to fruiting-specific genes, although some of the mutants may also carry more than one mutation (354, 463; Kües, Granado, et al., unpublished). One-third to one-half of the mutants with defects in fruiting are also defective in mycelial growth and/or oidiation, and two-thirds of clones abnormal in oidiation are also defective in fruiting, reflecting the fact that regulation and execution of fruiting and oidiation are probably closely related (383; Kües, Granado, et al., unpublished).

Mutants with mutations in fruiting-body development have been categorized into eight major groups: mutants without hyphal knots (*knt*), mutants blocked after hyphal knot formation (*prm*), mutants with primordia that do not form mature fruiting bodies (*mat*), mutants with a short fruiting body where the stipes do not elongate (*eln*), mutants with fruiting bodies where the cap does not expand (*exp*), mutants with white fruiting bodies that do not form basidiospores (*spo*, sometimes also called *bad*), mutants with combined defects in expansion, elongation and/or sporulation, and other mutants that do not fit into these categories (214, 215, 354, 389, 463; Kües, Granado, et al., unpublished). The unclassified group of strains include such interesting mutants as those forming well-proportioned miniature fruiting bodies of 1 to 1.5 cm (dwarfs or bonsais) and mutants forming etiolated stipes in both the dark and the light (45, 215; Granado, personal communication). Our group has concentrated on analyzing *knt* and *prim* mutants (269; Kües, Granado, et al., unpublished). The defect in fruiting-body initiation of the first *prm* mutant has now been overcome by introduction of a gene cluster that seems to act in initial induction and primordium maturation (Liu, personal communication). Sequencing data suggest that the cluster contains a gene for a cyclopropane fatty acid synthase (a specific methyltransferase for membrane-bound unsaturated fatty acids postulated to exist only in bacteria [149]), a gene for a putative ADP-ribosylation factor (a member of the RAS superfamily of small GTPases involved in vesicle formation and trafficking [4, 33, 109, 426]), and a gene for a kinesin that may be linked to transport of vesicles and other organelles (157, 448). These putative gene functions promise to become very interesting, since the galectins have been localized in vesicles within the primordia and the young fruiting body and in the heterologous host *Saccharomyces cerevisiae*, galectins are secreted by a nonclassical pathway (Boulianne et al., submitted).

Temperature-sensitive mutants with defects in hyphal growth often also exhibit a defect in stipe elongation (323). In one temperature-sensitive hyphal growth mutant, the mutated gene *hyt1*, encoding a novel protein, has been identified, but in this case it is not known whether stipe elongation is also affected (206). However, a specific defect in stipe elongation has recently been complemented in an *eln* UV mutant. The gene isolated, *eln2*, is constitutively expressed independently of fruiting and was found to encode a cytochrome P450, with 31%

amino acid identity to enzymes of the CYP64 family (354a). This family includes the oxidoreductases of the filamentous ascomycetes *Aspergillus parasiticus* and *Aspergillus flavus* that convert *O*-methylsterigmatocystin to aflatoxin (221, 387, 531). Another gene, *ich1*, has been cloned by complementation of a natural *mat* mutant with deformed "fig-shaped" primordia that are lacking a differentiated pileus. The *ich1* gene is specifically expressed in the pileus. The protein is 1,353 amino acids (aa) long, but the last 590 aa, including a six-times-repeated sequence, are dispensable for function. The remaining part of the protein contains three positively charged sequences suggested to be nuclear localization signals (NLSs), and the protein is therefore believed to act in the nucleus, for example in the regulation of expression of other genes required for the development of the pileus (353). However, another interesting motif is present in the protein, with a sequence of IVDVGG GIA...15...E...94...ADFV at positions 483 to 605 (cf. the Ich1 protein sequence given in reference 353), which is typical of the *S*-adenosylmethionine binding domain in non-nucleic acid methyltransferases (154, 229). This motif therefore suggests a totally different enzymatic function. Most interestingly, a Blast search revealed that Ich1 has low identity (ca. 20%) to *O*-methyltransferases from *A. parasiticus* and *A. flavus*, which are involved in the conversion of sterigmatocystin to *O*-methylsterigmatocystin and of dihydrosterigmatocystin to dihydro-*O*-methylsterigmatocystin (220, 473, 529, 530). Aflatoxin has recently been connected to the development of sclerotia and conidiospores in *Aspergillus*; when aflatoxin production is missing, development is blocked, and when aflatoxin is overexpressed, development is increased (49, 152, 473, 474). It is therefore likely that aflatoxin plays a biological role in development and that one possible function would be in signaling. In *C. cinereus*, it is probably not the polyketide aflatoxin that is produced within the tissues of the primordia but some other, probably analogous substances. It is striking that the *ich1* mutant fails to develop a differentiated pileus at the apex of the primordial shaft whereas in the *eln2* mutant the tissues of the stipes are composed of meandering cells and are disturbed in their organization (353, 354a). *ich1* dikaryons still form normal "etiolated" stipes in the dark (353), indicating that the mutant can reach the developmental stage at which a darkness-induced factor from the cap can bring about maturation (200). It is thus possible that Eln2 produces a metabolite that will signal the stipe to organize its tissues properly and, when further modified by Ich1 in the pileus, will determine further development of the cap and stipe. With this in mind, it will be interesting to test the behavior of an *ich1 eln2* double mutant.

Much attention has been given in mutant analysis to the stages of karyogamy, meiosis, and basidiospore formation in fruiting-body development. Mutants with defects in meiosis and spore formation are easy to recognize by their white caps, since it is the mature basidiospores that color the cap of *Coprinus* black. Kanda et al. (214) identified at least six different genes acting at meta-anaphase I in meiosis in a collection of white cap mutants. Two other genes act in sterigma formation following meiosis, 13 genes are involved in prespore formation, and 4 genes contribute to nuclear migration into the spores (214). Other studies report defects in premeiotic DNA replication and meiotic prophase I, but the majority of defects appear to be localized at the stage of meta-anaphase I (216, 389, 396, 397, 405, 435, 466, 498, 502, 538, 539, 542). From γ-radiation-sensitive mutants exhibiting defects in chromosome condensation and synapsis in meiosis, an epistasis group of *rad3-9-11-12* has been defined (405, 498, 538, 542). The first genes involved in meiosis and DNA repair (*rad9*, *rad11*/*mre11*, and *spo11*) have been isolated by mutant complementation and by a two-step, semirandom PCR recovering DNA inserts of a REMI mutant ((101, 130, 539, 542). Mre11 has a well-studied homolog in the yeast *Saccharomyces cerevisiae* which acts in double-strand break repair (83, 153, 349, 495). Spo11 of yeast is a topoisomerase II-like protein that is also involved in catalyzing meiotic double-strand breaks (219). Rad9 of *C. cinereus*, however is a novel, proline-rich protein required for meiotic chromosome condensation and synapsis (435), indicating that studying meiosis and recombination in *C. cinereus* will add new aspects to the cytological and mechanistic knowledge we have from studies with *S. cerevisiae* (for further information on meiotic recombination, see reviews in references 100, 380, 417–419, and 534). Homologous sequences to Rad9 from human (AB019494) and *Drosophila* (AF114160) are now deposited in GenBank. The latter, being a chromosomal adherin homolog, had been implicated in gene activation by remote enhancers (421). Rad9 is homologous to Mis4 of *Schizosaccharomoyces pombe* and Scc2 of *S. cerevisiae*, which are sister chromatid cohesion molecules (adherins) that prevent premature separation of sister chromatids in anaphase of mitosis (127, 321, 421). Rad51, homologous to RecA of *Escherichia coli*, has a central place in meiotic homologous recombination and functions in sequence identification, strand exchange, and branch migration (28, 151, 359, 467, 532). An orthologous gene of the *S. cerevisiae RAD51* gene, *Ccrad51*, has been isolated from *C. cinereus* by a PCR approach using degenerate primers. The gene does not complement any of the *rad3*, *rad9*, *rad11*, and *rad12* mutants and maps to chromosome 1, unlike these other genes, indicating that *Ccrad51* represents a new gene (446, 542).

OTHER MULTICELLULAR STRUCTURES: SCLEROTIA, MYCELIAL CORDS, PSEUDORHIZAS, AND ROCKERIES

Sclerotia of *C. cinereus* are globose, radial, symmetrical, multicellular, persistent resting structures of about 0.25 mm that have been observed in both mono- and dikaryons within the aerial and submerged mycelia (262, 330, 511). They appear to arise from hyphal knots (330, 510; Kües, unpublished) but only when the fungus has been kept for a longer period in the dark (262, 342). The mature sclerotium possesses an outer uni- or multilayered rind composed of cells with thickened walls with melanin inclusions. The rind encloses a medulla of a mass of bulbous cells that are oval or more irregular in shape and, depending on the strain, are more or less thick-walled (171, 507, 509, 510). The internal cells found within the medulla very closely resemble chlamydospores. Indeed, the appearance of chlamydospores is often temporally and spatially associated with the formation of submerged hyphal knots and sclerotia (507, 510; Kües, unpublished), and a hyphal knot might completely turn into chlamydospores, giving rise to nests of spores (Kües, unpublished) (Fig. 6). Development of sclerotia and often also chlamydospores correlates with the abundant occurrence of thick-walled inflated hyphal segments in the mycelial matting of older monokaryotic and dikaryotic cultures (262, 294), and all these differentiations are believed to be related (262, 507, 510). Glycogen accumulates within the inflated hyphal cells and, if not relocated to the fruiting body (292, 294), the polysaccharides seem to be transported to the sclerotia to build up the glycogen storage found in their internal inflated hyphae (190, 338, 342, 510). Sclerotia of *C. cinereus* will germinate to give rise to a vegetative mycelium and do not serve in initiation of fruiting-body formation as in other basidiomycetes (335, 338).

Like many other saprophytic basidiomycetes, on certain substrates (e.g., horse dung) *C. cinereus* forms linear vegetative

organs by the parallel aggregation of morphologically similar hyphae (Kües, unpublished). Such linear organs are called mycelial cords and are thought to provide a main translocation route for nutrients (34, 35). Mycelial cords must be distinguished from the pseudorhizas, which are functionally analogous to soil rhizomorphs (transport of nutrients) but developmentally analogous to indefinitely extending fruiting-body stipes (56, 60, 95, 335, 338). Formation of pseudorhizas (etiolated stipes, dark stipes) occurs in the dark after induction of fruiting-body formation, either at the initial stage or if stage 1 primordia are transferred to the dark before complete gill development and induction of karyogamy (32, 40, 56, 60, 353, 476; Granado, personal communication). To form these structures, the basal plectenchyma of fruiting-body initials (Fig. 9) extends for many centimeters (often 20 cm or more) to drive the tip with the immature cap and stipe tissues toward any source of light. Elongation of the etiolated stipes occurs by cell proliferation (40, 56, 60, 277; Granado, personal communication). Within the basidia there is no karyogamy, not even after transfer into the light (277; Granado, personal communication) (see above). Following light incubation, the underdeveloped fruiting-body tissues at the apex of the elongated structure will be abandoned in favor of the production of new initials that quickly arise over the whole length of the etiolated stipes (120, 476; Granado, personal communication).

Rockeries are white callus-like masses up to several millimeters in size; they are made of densely packed hyphae, and their function is unknown. Their formation requires light, and their occurrence is epistatic over the development of fruiting bodies (371). Rockeries have so far been observed only on developmental mutants (215, 371; Kües, unpublished), and it is possible that these structures are artifacts due to defects in the normal developmental pathway of fruiting-body formation.

REGULATION OF DEVELOPMENT

Developmental processes in fungi are controlled by environmental and nutritional signals (120, 344, 335, 338). Generally in fungi, mating-type loci are the genetic master regulators of sexual development and, as seen in *C. cinereus*, sometimes also of asexual development (172, 248, 252) (see below). Environmental and nutritional signals are probably linked to the mating-type loci via signal transduction pathways enabling the coordination of gene expression with physiology and environment (36, 107, 249). In *C. cinereus*, mating-type loci and their products have been extensively analyzed and are relatively well understood, but their links with physiology and environment still have to be unraveled.

Mating-Type Loci

C. cinereus, like many other homobasidiomycetes, is an outbreeding organism with a tetrapolar incompatibility system determined by the two mating-type loci *A* and *B*. "Tetrapolar" refers to the fact that four different types of basidiospores arise from meiosis: AxBx, AxBy, AyBx, and AyBy, where x and y represent the different mating-type specificities of the parental haploid nuclei. Since the two mating-type loci must be different for a successful mating (see above), each spore has a 25% probability of finding a fully compatible partner within the tetrad it comes from. This reduction of outcrossing per tetrad is compensated for in the whole natural *Coprinus* population by acquisition of multiple specificities for each of the two mating-type loci. From *C. cinereus* isolates from the wild (102, 104), Raper (407) calculated that there are about 160 different *A* and 80 different *B* specificities, resulting in a total of 12,800 different mating types. However, estimates obtained from other samples are even greater, with 240 different specificities for each of the two loci, suggesting 57,600 different mating types (50, 64, 235). Even using the lower of the two estimates, a general mating probability of >98% and thus inbreeding repression is achieved (for extensive discussions, see the papers by Hiscock et al. [172–174]).

Other well-understood multiallelic mating-type systems are present in the tetrapolar basidiomycetes *Ustilago maydis* and *S. commune*. The *A* mating type locus of *C. cinereus* is homologous to the *b* mating type locus of *U. maydis* and to the *A* mating type locus of *S. commune*, whereas the *B* mating type locus of *C. cinereus* is homologous to the *a* locus of *U. maydis* and the *B* locus of *S. commune* (79, 172, 194, 245, 246, 496). It has been proposed to combine the *A* mating loci of *C. cinereus* and *S. commune* and the *b* locus of *U. maydis* under the unifying name *matT* and the *B* mating type loci of *C. cinereus* and *S. commune* and the *a* locus of *U. maydis* under the name *matP* (172).

Regulation by mating types. Analysis of common *A* and common *B* heterokaryons of *C. cinereus* (see above) (Table 1) shows that the *A* and the *B* genes regulate different cellular functions during mating and dikaryon formation. The genes at the *A* mating-type locus control the pairing of the two parental nuclei within the dikaryon and induce clamp cell formation, synchronized nuclear division, and consecutive septum formation (Fig. 2). Following monokaryon fusion, the *B* genes are responsible for septum dissolution and nuclear migration. In the established dikaryon, *B* genes control the fusion of the clamp cell with the subapical cell after synchronized nuclear division and thus control the release of the nucleus initially trapped within the unfused clamp cell (459, 460) (Fig. 2). Commonly, events prior to mating and cellular fusion are assumed to be independent of the mating-type loci and self-nonself recognition is said to occur only intracellularly (76, 79, 245). Reports on effects of mating-type loci on hyphal fusions are contradictory. Some authors observed no apparent differences (438), whereas others noticed a reduction of total fusions in common *B* matings (440). However, it is possible that hyphal fusions occur by different functional means. For example, hyphal cells fuse to ease translocation and supply of nutrients throughout a mycelium (375), and it would be difficult to distinguish fusions formed for such vegetative reasons from fusions formed specifically to enter sexual development (172). Barrages, i.e., discrete zones of poor growth between colonies caused by an aversion for one another, have been observed between *C. cinereus* mycelia of different *A* specificities and the same *B* specificity (186). A more recent study of *Lenzites* showed that such barrage formation is related to the action of a diffusible pheromone, suggesting that extracellular effects take part in self-nonself recognition (170). Molecular analysis of the *B* mating-type genes has established in *C. cinereus* (153a, 374, 377) and also in *S. commune* (167, 497, 516) that the *B* locus encodes pheromones and pheromone receptor genes. Pheromones and pheromone receptors of different specificities are complementary (see below), and it is not obvious whether or how this can relate to the observation of barrage formation in common *B* matings. In contrast, a complementary action of pheromones and pheromone receptors of different *B* loci easily explains an increase in fusions involving mutually attracted pegs observed in common *A* matings of *S. commune* (410). Adding to the confused situation, attraction between oidia and hyphae of *C. cinereus* has been shown to occur independently of mating type (223), and in *S. commune*, diffusible substances exist that induce self and nonself fusions (1, 2, 508). It is also interesting that *B* pheromone expression in *S. commune* dra-

TABLE 1. Influence of activated mating-type pathways on morphology, mating, and sexual and asexual reproduction[a]

Mating-type pathway	Mycelial condition	Mycelial morphology[b]	Formation of oidia[b]	Mating behavior[b]	Fruiting-body initiation[b]
A off *B* off	Monokaryon	Simple dolipore septa; 1–2 nuclei per hyphal segment	Constitutive	Bilateral	− (occasionally +)
	Common *AB* heterokaryon	Monokaryon-like; unstable	Constitutive?	Bilateral	?
	Common *AB* diploid	Monokaryon-like; broad hyphae; enlarged oidia	Constitutive?	Bilateral	?
A on *B* off	Common *B* heterokaryon	Unfused clamp cells; vigorous growth; relatively stable	Light controlled?	Unilateral donor?	+ (less readily)
	Common *B* diploid	?	?	?	?
	Amut homokaryon	Unfused clamp cells; vigorous growth	Light controlled	Bilateral	?
	A on transformant	Unfused clamp cells; vigorous growth	Light controlled	Bilateral	+ (less readily)
A off *B* on	Common *A* heterokaryon	Monokaryon-like hyphae; retarded growth; unstable	Constitutive	Bilateral?	− (occasionally +)
	Common *A* diploid	Monokaryon-like but broader hyphae; enlarged oidia; fringed growth	Constitutive?	Unilateral donor	?
	Bmut homokaryon	Monokaryon-like	Constitutive	Bilateral?	?
	B on transformant	Simple dolipore septa; occasionally septal dissolution; poor growth	Constitutive	Unilateral donor	−
A on *B* on	Dikaryon	Fused clamp cells; 2 nuclei per hyphal segment; vigorous growth	Light controlled	Unilateral donor	+
	Amut Bmut homokaryon	Fused clamp cells; 1–2 nuclei per hyphal segment; vigorous growth	Light controlled	Unilateral donor	+
	A on *B* on transformant	Fused clamp cells; 1–2 nuclei per hyphal segment; vigorous growth	Light controlled	?	+

[a] Compilation of data from the literature (for references, see the text) and of unpublished experiments of U. Kües, M. J. Klaus, and E. Polak.
[b] Where a property was not tested, a question mark is used. For formation of oidia, question marks refer to cases where sporulation was tested only under some conditions. For mating behavior, question marks refer to reports whose results are contradictory to observations on strains having an analogous genetic condition.

matically increases at the time of or shortly after cell fusion in both self and nonself combinations (497). One might therefore consider the possibility that *B* pheromones have both a self and a nonself function, as has been reported for mating-type pheromones in the ciliate *Euplotes raikovi* (172, 174, 499). It is far from clear whether there are extracellular actions of *B*-encoded pheromones on hyphal attraction and fusion in homobasidiomycetes, and experiments with isolated pheromones are needed to solve this problem (for further discussions, see references 172 and 410).

Since the *A* mating-type locus encodes two types of proteins with homeodomain motifs (253) (see below), defining a certain class of transcription factors (62, 63), an intracellular action is more appealing. It is not known whether the *A* mating-type products are positive or negative regulators of development, since morphological observations do not show whether a regulatory effect is direct or indirect. Analysis of monokaryons transformed with *A* genes of another specificity ("*A* on" transformants) revealed a negative function of compatible *A* genes on the production of oidia and positive effects not only on the formation of clamp cells but also on the formation of chlamydospores, hyphal knots, and fruiting-body initials (232, 258, 261, 307, 358, 477), consistent with the earlier observations with common *B* heterokaryons and *Amut* homokaryons (see above) (Table 1). The mating-type-encoded transcription factors of *C. cinereus* and other basidiomycetes (*S. commune* and *Ustilago* spp.) are related to the mating-type-encoded transcriptions factors **a1** and α2 of the ascomycetous yeast *S. cerevisiae* (62, 63, 76, 253), and these always act as transcriptional repressors (191). In contrast, the α2-related homeodomain transcription factor Pm of the *mat1-P* mating-type locus of *S. pombe* appears to be an activator of transcription (501). With the isolation of the *C. cinereus* galectin genes, whose expression is induced by compatible *A* mating-type products (Boulianne et al., submitted), the first possible target genes are available with which to address whether *A* mating-type proteins act as direct positive regulators.

The effects of the activated *A* pathway in common *B* heterokaryons, *Amut* homokaryons, and "*A* on" transformants are consistent, with the one exception of mating behavior (Table 1). Common *B* heterokaryons are said to be unilateral donors (460), whereas *Amut* homokaryons and "*A* on" transformants were found both to accept and donate nuclei (240a; Kües, unpublished). However, since half of all wild-type isolates fail to accept nuclei (306), one has to be careful in judging the results of unilateral donation of nuclei. Ongoing research with crosses of *A* on transformants and *B* on transformants of the same monokaryotic background indicates that activation of the *A* pathway does not block nuclear acceptance whereas activation of the *B* pathway does so (240a). This appears to contradict reports of bilateral mating behavior of common *A* heterokaryons. However, as mentioned above, common *A* heterokaryons are very unstable and frequently produce monokaryotic hyphae expected to behave as both nuclear donor and nuclear acceptor (459). Furthermore, the bilateral mating behavior observed with some (142) but not all (Kües, unpublished) *Bmut* homokaryons may be because *Bmut* products do not function as strongly in regulating development as compatible wild-type *B* combinations do (165, 232, 377).

The *A* mating-type locus and its products. Molecular analysis of various haplotypes of the *A* mating-type locus (i.e., *A2*, *A5*, *A6*, *A42*, and *A43*) revealed that the 20- to 25-kb sized loci contain a variable number of genes effective in activation of *A*-regulated pathways when transformed into a compatible

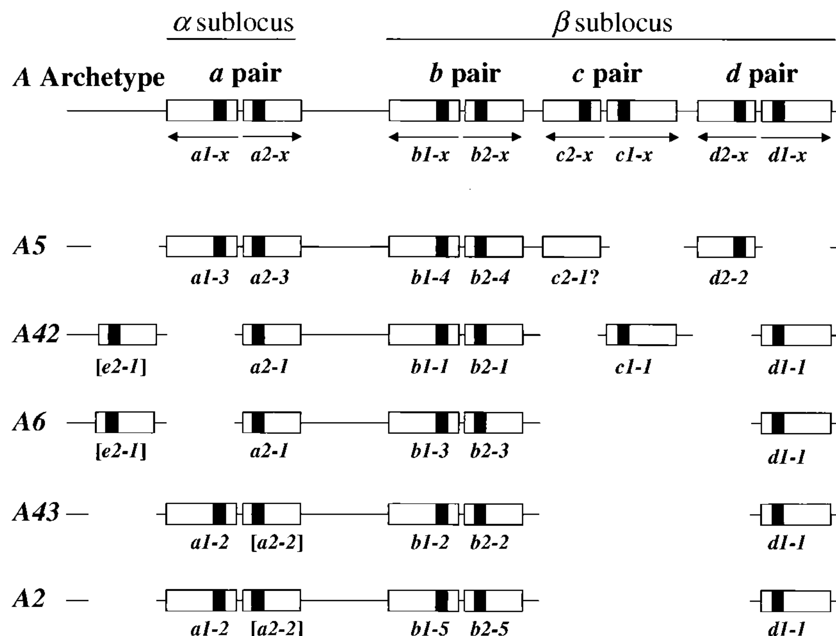

FIG. 12. Structure of the *A* mating-type locus of *C. cinereus*. The postulated *A* archetype consists of four paralogous pairs of divergently transcribed genes that encode two classes of homeodomain transcription factors (the direction of transcription is indicated by the vertical arrows). One gene pair (the *a* gene pair) is localized in the α sublocus, and the other three (the *b*, *c*, and *d* gene pairs) are localized in the β sublocus (top). Note that the *a* pair and the *b* pair are inversely orientated to the *c* pair and the *d* pair. Within the white boxes, representing the genes, the regions responsible for the homeodomains are indicated by the black boxes. Lettering in gene names refer to gene pairs; the first number of a gene name indicates the type of gene defined by the encoded homeodomain (HD1 or HD2, respectively), and the second number refers to the respective allele (255, 378). Five natural *A* haplotypes have been characterized so far (bottom). None of them contains the full set of possible genes. *A* haplotypes can share genes; for example, *d1-1* is present in *A42*, *A6*, *A43*, and *A2* but not in *A5*. To induce sexual development in the dikaryon, it is enough if the two *A* haplotypes differ in one of the pairs, for example in the *b* gene pair, which is the only different gene pair in *A43* and *A2*. In some cases, genes are transcribed but their products are not active in induction of sexual development (*a2-2* from *A43* and *A2*). The extra gene *e2-1* in the α sublocus *A42* and *A6* is only poorly transcribed. The gene at the position of the *c* gene pair in the *A5* haplotype has been suggested to be *c2-1*, the partner gene of the single *c* gene *c1-1* found in *A42*. Sequencing of *c2-1*, however, failed to identify the presence of a homeodomain-encoding region (76, 257, 259, 260, 378).

monokaryotic host (257–260, 358, 378) (Fig. 12). By comparing the gene arrangements within these natural loci, an archetypal *A* mating-type locus was deduced by Kües and Casselton (255) and Pardo et al. (378), which consists of three or possibly four paralogous pairs of divergently transcribed genes. One of these gene pairs, the *a* gene pair, is found at the *A*α sublocus, and the others, the *b*, *c*, and *d* gene pairs, are found at the *A*β sublocus (257) (Fig. 12). The closely linked *A*α and *B*β subloci were defined by classical genetics. The functionally redundant α and β subloci are separated by 0.07 map unit and are freely recombinable due to a 7-kb noncoding region of conserved DNA sequence. In contrast, the gene pairs at the β sublocus are embedded in DNA of low homology, preventing any homologous recombination within the sublocus (102, 257, 291).

The paralogous nature of the *A* mating-type locus is one of the secrets of how multiple mating-type specificities have been created. For *A* function, the presence of genes of any one of the pairs is sufficient (378, 383). Thus, *A* haplotypes with different specificities can share alleles of one or more of the pairs—*A* haplotypes have different specificity as long as they differ in one of the gene pairs (257, 259, 260, 305, 378). In *U. maydis*, there is only one gene pair at the homologous *b* mating-type locus (133, 247) and development of multiple alleles of this one gene pair ensures a high outbreeding frequency (533). Multiplication of functionally redundant units, which subsequently became independent of each other, requires the development of only a very few alleles of each of the gene pairs to obtain a high outbreeding frequency, provided that these alleles are shuffled around into all possible combinations (194, 255). In accordance, in *C. cinereus* four functional variants of the *a* gene pair, nine of the *b* gene pair, and two of the *d* gene pair have so far been identified in various combinations. If all possible combinations are considered, these few alleles already enable 72 different mating-type specificities ($4 \times 9 \times 2 = 72$) (378). Looking at polymorphisms within 44 different haplotypes from all over the world, the presence of 4 *a* gene pairs, 10 *b* gene pairs, and 3 *d* gene pairs is predicted in this particular sample and, by statistical means, the total of 4 to 5 *a* gene pairs, 10 to 12 *b* gene pairs, and 3 to 4 *d* gene pairs within the whole world population (305) would be enough to fulfill the estimates given by Raper (407) and Burnett (64). Curiously, of the *c* gene pair, there is only one incomplete copy with a single gene (*c1-1*) known, present in the haplotype *A42* (257). It is not clear if this one *c* gene, although transcribed (257, 416), presents a pseudogene (378) or, for example, if it is part of a rearranged *d* gene pair (172, 251). At the position of the *c* locus in the *A5* haplotype, there is a gene that corresponds in size to other mating-type genes, and it has been suggested to be gene *c2-1*, the original partner gene of *c1-1*. However, its product lacks a homeodomain, and it is not clear if the gene is a true mating-type gene (378). Because of the general high redundancy, the *A* locus commonly appears to lose a gene of one or more of the gene pairs (260, 378). Indeed, not one natural *A* haplotype is known that has the complete set of genes postulated in the archetype (257, 259, 260, 305, 378) (Fig. 12). Occasionally, the locus might also acquire new genes, as suggested by the presence of an extra poorly transcribed gene (*e1-2*) in the α sublocus of the *A6* and *A42* haplotypes (76) and by evidence of illegitimate recombination in the *c*-*d* gene pair region (172, 251, 260).

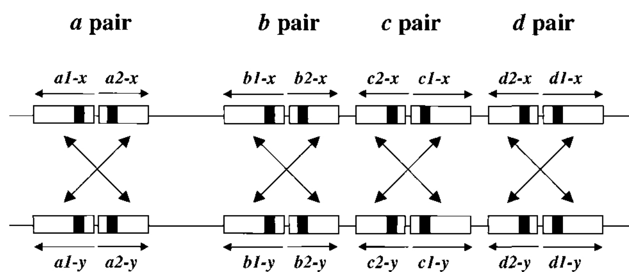

FIG. 13. The protein products of *HD1* and *HD2* genes (the gene type is indicated by the first number in their names; horizontal arrows indicate the direction of transcription) from allelic gene pairs interact with each other to induce sexual development (positive interactions are indicated by the crossed arrows). In contrast, the products of the same gene class, the HD1 and HD2 products of the same gene pair, and those of paralogous gene pairs do not. In the figure, the ideal case is shown, where all gene pair positions of two (archetypal) haplotypes contain different alleles (indicated by *x* and *y*). This leads to a high functional redundancy: each gene pair provides two functional HD1-HD2 protein combinations; with four independent gene pairs, this gives a total of 16 functional redundant protein combinations (255).

Both genes of a given *A* gene pair (*a1* and *a2*, *b1* and *b2*, *c1* and *c2*, and *d1* and *d2*) encode a homeodomain transcription factor. However, these factors belong to distinct classes that have been termed HD1 and HD2, respectively (76, 253). The HD2 motif is a typical three-helix homeodomain of 60 aa which contains the characteristic sequence WF.N.R within the third helix (the DNA recognition helix). In contrast, the HD1 homeodomain is atypical and has extra amino acids between helix 1 and helix 2 and a divergent WF.D.R sequence in the recognition helix (27, 62, 63). Strikingly, the mating-type-encoded homeodomain proteins of other basidiomycetes and of the ascomycetous yeast *S. cerevisiae* also fall into the HD1 and HD2 classes (63, 76, 172). Among these organisms, a common pattern of HD1-HD2 protein-protein interaction has been established that is crucial for regulating sexual development (194, 255) (Fig. 13). As shown by transformation studies, an HD1 protein of one mating type interacts with an HD2 protein of another mating type to induce sexual development. More specifically in *C. cinereus*, HD1 and HD2 proteins from allelic gene pairs [either from allelic *a* gene pairs or from allelic *b*, (*c*), or *d* gene pairs] have to come together by mating. Between each set of alleles, *x* and *y*, two functionally redundant interactions are possible: HD1-x interacting with HD2-y, and HD1-y interacting with HD2-x (260, 378) (Fig. 13).

Since there are several HD1 and HD2 proteins encoded within each *A* haplotype which are already expressed before mating (257, 260, 416), they have to be distinguished from each other and from those originating from another *A* locus. Paralogous genes from the same *A* haplotype and also allelic versions from other *A* haplotype are very different in sequence, with the highest conservation in the regions containing the homeodomain motifs. Paralogous genes have a DNA sequence identity between 40 and 50%, allelic genes DNA homologies between 60 and 70% (16, 131, 258, 308, 477). Domain swaps indicated that allele specificity resides within the highly variable N termini of the proteins and subsequent in vitro studies on C-terminally truncated proteins showed that the 120- to 150-aa N termini are indeed discriminating HD1-HD2 protein dimerization domains (22, 258). The N-terminal ends of HD1 and HD2 proteins from allelic gene pairs interact strongly, but N-terminal dimerization is ineffective in all other combinations (proteins of the same kind, or HD1 and HD2 proteins encoded within the same or in paralogous gene pairs) (22). Other, nondiscriminating dimerization domains were predicted to localize directly C-terminal to the HD1 homeodomains (131, 254). Remarkably, there is a significant identity between a short sequence downstream of the homeodomain in HD1 proteins to the 20-aa C-terminal tail of the homologous mating-type protein α2 of *S. cerevisiae* (172, 258) (Fig. 14). In yeast, this short tail is required for cooperative DNA binding of α2 with the HD2 homeodomain protein **a1** from the opposite

S. cerevisiae	α2	I T **I** A P E **L** A D **L** **L** S G E P L A K K K E
K. lactis	α2	T A **V** S S D **I** R N **I** **L** N
Herpes simplex	VP16	N N **Y** G S T **I** E G **L** **L** D L P D D D A P
C. cinereus	b1-1	K D **M** T P S **L** K E **Q** **L** K N D E A R R K R E
	b1-2	R D **M** T P T **L** K E **Q** **L** K N E K A R K K E K
	b1-3	K A **M** T P S **I** R E **A** **L** K K E K A S E R E E
	b1-4	K D **I** T P V **I** K K **Q** **L** K N E K I R Q R E Q
	b1-5	R D **M** A P S **L** K G **H** **W** K S E K T R G T V E
	b1-6	K D **M** T P S **L** K T **Q** **L** K N E K V R R R E E
	b1-9	R D **M** T P A **L** K E **Q** **L** K I E K A R K R Q E
	d1-1	K D **M** T P A **L** K E **K** **I** K R D A D E R R R E
S. commune	Z4	G L **E** P T E **L** A D **S** **L** N S S A V D R Q F A
	Z5	V F **Q** P S E **L** A G **T** **L** S E S T E T R P D T
U. maydis	bE1-bE7	S W **I** K Y G **V** K E **K** **V** G D W V Y D L C A A
U. hordei	bE1, bE2	S W **I** K Y G **V** K E **K** **V** G D W V Y D L V A A
U. scitaminea	bE1	S W **I** R Y G **V** K E **K** **I** G D W V Y D L V A A

FIG. 14. Comparison of a domain C-terminal to the homeodomains of HD1 proteins from *C. cinereus* and other basidiomycetes (sequences are from references 3, 16, 17, 133, 172, 247, 258, 295, 443, and 445) with the C-terminal tail of α2 of *S. cerevisiae* and the C-terminal tail of *Kluyveromyces lactis* and herpes simplex virus that can functionally replace the α2 tail in heterodimerization with **a1**. The residues shown in the α2 sequence in bold are those that interact with the **a1** homeodomain. Corresponding residues in the other sequences are shown in bold for comparison (445).

mating type. It presents the major dimerization interface with **a1** (297, 381, 444, 445), whereas the N-terminal interaction of **a1** and α2 is only of minor importance (175), possibly because protein discrimination is not required in yeast (172). There is currently no experimental evidence for C-terminal mating-type independent dimerization interfaces, in *C. cinereus*, but C-terminal dimerization of the homologous *S. commune* proteins has been described previously (11).

Further parallels exist between the yeast mating-type proteins and the *C. cinereus* HD1 and HD2 proteins. In the heterodimeric complex, the HD1 homeodomain motif of α2 is not essential for function, unlike the HD2 motif of **a1** (189, 504). Similarly, in *C. cinereus*, natural and artificial fusions between HD2 and parts of HD1 proteins and mutagenesis of the recognition helices of the HD1 and HD2 motifs revealed that the HD1 but not the HD2 motif can be eliminated without loss of function in activating sexual development and repression of oidiation (13, 232, 259). In *S. cerevisiae*, the HD1 protein α2 also forms homodimers, and these, together with the general transcription factors Tup1 and Ssn6, repress functions specific to the **a** mating type in both haploid α and diploid **a**/α cells (191). Most interestingly, recent analysis of singly transformed *A* mating-type genes in a Δ*A* knockout strain of *C. cinereus* detected a negative effect of HD1 proteins on oidia formation. For the first time, this indicates a dual regulatory function for HD1 proteins in basidiomycetes comparable to that of α2 in *S. cerevisiae* (383). In *S. commune*, homodimerization between full-length HD1 proteins has been shown in vitro (11), and it will have to be established in the future whether this is also the case for *C. cinereus*. However, in an elegant study using a heterologous onion–β-glucuronidase (GUS) expression system, Spit et al. (442) demonstrated that NLSs are present in HD1 but not in HD2 proteins, which is consistent with a dual nuclear function of HD1 proteins, one in transport of HD2 proteins into the nucleus by heterodimerization and another independent of HD2 proteins. Different HD1 proteins seem to make different use of two possible NLS sequences (NLS1 and NLS2), both found C-terminal to the homeodomains (16, 258, 477). NLS1 is essential in the HD1 protein b1-1, encoded in a *b* gene pair (442). In contrast, NLS1 can be deleted in protein d1-1, coming from a *d* gene pair, as long as NLS2 is still present (13). Introduction of an NLS into an HD2 protein can transfer the protein into the nucleus but does not render the protein independent of HD1 proteins, indicating that an NLS is not the only contribution of the HD1 partners in the HD1-HD2 heterodimeric complex (442). Using a yeast two-hybrid system, a potential transactivation domain was located in a C-terminal part of HD1 proteins known to be essential for heterodimer function in *C. cinereus* (22, 258, 477).

The potential C-terminal transactivation domain is also necessary for functional HD2-HD1 fusion proteins found in self-compatible strains carrying an *Amut* locus. Indeed, self-compatibility of all analyzed *Amut* loci is caused by the same type of mutation: a large deletion occurred that eliminated most of the β-sublocus and the 7-kb noncoding region separating α and β. The deletions led to an in-frame fusion of the *HD2* gene *a2* from the *a* gene pair with variable parts of the *HD1* gene *d1* from the *d* gene pair. In consequence, covalently linked proteins are formed whose components normally do not interact with each other (12, 13, 259, 301, 378). Interestingly, both former N-terminal domains become superfluous in such HD1-HD2 fusion proteins, consistent with their function in recognition and discrimination (13, 259). Mutations within the N-terminal domains changing the specificity of a protein such that it recognizes formerly incompatible proteins of the other type (i.e., the partner protein from the same gene pair or those proteins of the other type from paralogous gene pairs) have never been isolated. In principle, such loss-of-specificity mutations should be easy to select as gain-of-function mutations, recognized by morphological changes of the mycelium (clamp cell formation). The failure to obtain this kind of self-compatible mutants indicates how specifically, precisely, and subtly the hypervariable N-terminal recognition regions work. Data from *Ustilago* (212, 525, 526) and yeast (175) suggest that there are many different contact points in the hypervariable N termini of HD1 and HD2 proteins that, depending on the particular protein combination, may contribute negatively or positively to the interaction. Therefore, it is thought that the summation of all contacts will decide upon dimerization; between incompatible proteins, this sum results in aversion, while between compatible proteins, it results in attraction. In consequence, it is the lack of interaction between proteins encoded by the same *A* locus that determines mating-type specificity (172, 194, 264).

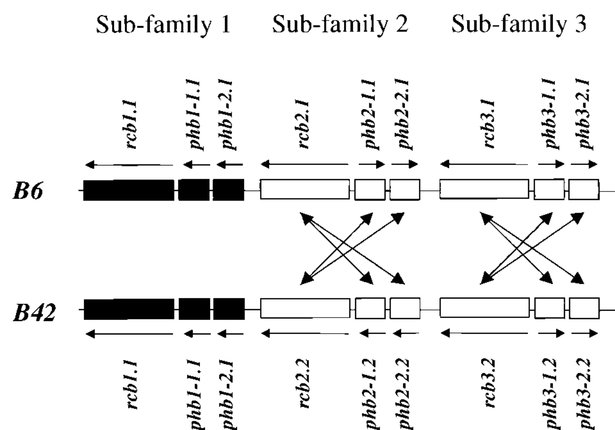

FIG. 15. Structure of the *B* mating-type locus of *C. cinereus*. Two *B* haplotypes, *B6* and *B42*, have so far been cloned and characterized. The *B* locus consists of three subfamilies of genes; each subfamily has one gene encoding a pheromone receptor and two different genes encoding distinct pheromones. As found in *A* haplotypes, *B* haplotypes of different specificities can share genes. *B6* and *B42*, for example, share the genes of the subfamily 1 but differ in the genes of subfamilies 2 and 3. Transformation studies suggest that the pheromone products of subfamily 2 interact with the pheromone receptor of an allelic subfamily 2 and that the pheromone products of subfamily 3 interact with the pheromone receptor of an allelic subfamily 3 (indicated in the figure by the crossed vertical arrows). Note that between different *B* haplotypes, the direction of pheromone gene transcription within a subfamily might change, as seen with the pheromone genes of subfamily 2 in the examples of *B6* and *B42* (79, 153a, 377). However, there is also some inconsistency in the literature in terms of the transcription direction of the pheromone genes of subfamily 1 (79, 374, 377).

The *B* mating-type locus and its products. As with multiple *A* mating type specificities, the same strategies of gene multiplication and divergence in allele sequence are followed to generate multiple *B* mating-type specificities, although the encoded gene products have totally different functions. In the *B* mating-type locus, within a region of 17 kb, there are three paralogous subfamilies of genes marked by unique allele sequences (Fig. 15). Each subfamily consists of two genes encoding pheromones (subfamily 1, *phb1-1* and *phb1-2*; subfamily 2, *phb2-1* and *phb2-2*; subfamily 3, *phb3-1* and *phb3-2*) and one gene encoding a pheromone receptor (*rcb1*, *rcb2*, and *rcb3*, respectively). Studies transforming isolated genes of one monokaryon into compatible monokaryons followed by crosses with suitable tester strains having another *A* but the same *B* specificity suggest that pheromones will recognize the pheromone receptor of allelic pairs but not those of paralogous pairs (153a, 374, 377). This is exactly in analogy to the reactions

observed between the HD1 and HD2 proteins from the *A* mating-type locus (see above). Currently, it is not known how many different alleles of each subfamily exist but, as with the *A* mating-type locus, only a few are needed to create a large number of *B* mating-type specificities. The four versions of two of the subfamilies and five different versions of the third subfamily are already sufficient to generate the 80 different B specificities ($4 \times 4 \times 5 = 80$) postulated by Raper (407). By transformation and hybridization analysis, two different alleles of subfamily 1, three different alleles of subfamily 2, and four different alleles of subfamily 3 have been identified so far (153a).

Most of the mating pheromones known from other fungi, including the **a** pheromone (**a**-factor) of *S. cerevisiae*, are short lipopeptides of 9 to 15 residues that have a modified C terminus and are generated from larger pheromone precursors (65). Likewise, *B* genes in *C. cinereus* seem to encode pheromone precursors of 53 to 72 residues that, after N-terminal processing and C-terminal modification, will give rise to mature pheromones of 11 to 13 aa. N-terminal processing is predicted to occur at a two-residue charged motif (E/DR), and the C terminus contains an essential CAAX signal (C = cysteine, A = aliphatic amino acid, X = any amino acid) for posttranslational isoprenylation and farnesylation, during which the last 3 aas are eliminated (65, 79, 153a, 374, 377). Accordingly, a C-to-A mutation within the CAAX motif severely reduces pheromone activity in vivo (377). Receptor activation tests with Rcb2.1 (from *B6*) in the heterologous host *S. cerevisiae* indicate that the *C. cinereus* pheromone Phb2-2.2 (from *B42*) is secreted from yeast *MAT***a** cells but not from *MAT*α cells, strongly suggesting that the Phb2-2.2 pheromone precursor is processed by the yeast **a**-factor maturation pathway and secreted by the **a**-factor-specific transporter STE6. A farnesylated synthetic 12-aa Phb2-2.2 peptide including the ER motif activates receptor Rcb2.1 in yeast, but the unfarnesylated peptide and shorter or longer peptides, regardless of whether farnesylated or unfarnesylated, are only weak or inactive in obtaining a receptor response (374).

The pheromone precursors of a given *B* subfamily have an overall identity between 22 and 50% and an overall similarity between 49 and 61%. More surprisingly, the predicted mature pheromones can differ totally in sequence and length, although they interact with the same pheromone receptor. In contrast, the predicted pheromones from allelic genes may differ only by 3 or 4 aa, and these must determine specificity (79, 153a, 374, 377). The pheromone receptors encoded within the same *B* mating-type locus have 40 to 50% identity and 60 to 70% similarity, whereas allelic forms may be more similar, with 80% identity and 90% similarity. The *B* pheromone receptors have significant identity to the mating-type pheromone receptors of *S. commune* and *U. maydis* and the STE3 **a**-factor receptor of *S. cerevisiae*. Like these, they belong to the rhodopsin-like receptor family, characterized by seven hydrophobic transmembrane-spanning helices (7TM-type receptors), an extracellular N-terminal tail, three outer and three cytoplasmic loops, and an inner C-terminal tail (33, 72, 108, 153a, 374, 377). Preliminary results with *S. commune* suggest that the pheromone receptors reside within the outer hyphal membrane (245), and domain swaps between receptors indicate that the first and the third extracellular loops contribute to specificity (166). Analysis of chimeric α-factor receptors of *S. cerevisiae* and *Saccharomyces kluyveri* suggests that similar interactions occur between pheromones and pheromone receptors in ascomycetous yeasts (436). Commonly, 7TM receptors are linked to an intracellular heterotrimeric G-protein that becomes activated by binding of the signaling molecule to the receptor (33, 36, 108). From mutational analysis of the *S. cerevisiae* pheromone receptors, the third intracellular loop and the C-terminal tail are implicated in G-protein activation and/or desensitization (38, 244, 447). Quite fascinatingly, the disruption of self-incompatibility observed in certain *B6mut* homokaryons (165) has now been traced to a single amino acid alteration (Q229P) at the extracellular end of the transmembrane domain VI of one of the three pheromone receptors (Rcb2.1 from subfamily 2), which rendered the pheromone receptor constitutively active. The mutated pheromone receptor was also constitutively effective in the heterologous host *S. cerevisiae*, in the absence of any activating pheromones. Receptor activity depended on the presence of chimeric Gα species (chimeras of Gpa1 from yeast and the five C-terminal amino acids of human Gα16 or of Gpa3 from *U. maydis*), demonstrating a clear link between the *C. cinereus* receptor and the yeast heterodimeric G protein specific for the mating-type pheromone response (374). Whereas the described mutation obviously causes a true constitutive activation of the downstream signaling pathway, two other kinds of *B* mutations are also expected to lead to self-compatibility. Loss of specificity of the pheromone due to amino acid changes might make it bind to its own pheromone receptor, whereas changes within the specificity determinants of a pheromone receptor might force it to accept pheromones formerly not accepted (172). Analysis of more *Bmut* loci will reveal if these classes of mutations are as difficult to obtain as loss-of-specificity mutations in the HD1 and HD2 products of the *A* mating-type locus (see above). By in vitro mutagenesis, it had been shown that a single amino acid exchange to a pheromone is sufficient to make it recognize a receptor from the same *B* haplotype. Thus, it is possible that this mutated pheromone activates its own receptor (Y. Honda and L. A. Casselton, personal communication).

Coordination of mating-type regulation. Although *A* and *B* mating-type genes regulate distinct cellular functions (see above), in the dikaryon they coordinately control functions such as cyclic AMP (cAMP) production, cAMP-dependent protein kinase activity (453, 454), repression of oidiation (232), and, as suggested previously for *Amut Bmut* homokaryons (265, 452) and now shown in *A* and *B* activated transformants, also fruiting-body initiation (240a). Strikingly, all these functions are also light regulated (203, 232, 277, 350, 351, 492). There are, however, considerable differences in the way these factors are linked in regulation. For cAMP production and cAMP-dependent protein kinase activity, both mating-type pathways have to be active and light has a stimulatory effect (453, 454, 492). In fruiting-body initiation, where light is usually required (350, 351) (see above), activation of the *A* pathway can be sufficient (258, 261, 459) but additional activation of the *B* mating-type pathway clearly promotes fruiting when light signals are provided (240a, 459; Kües, unpublished). In contrast, in formation of oidia on the dikaryon, compatible *A* products repress sporulation, light counteracts this repression, and compatible *B* products override the negative effect of light on *A*-mediated repression and, in addition, enhance the repression by *A* products in the dark (232, 261). From these various observations, it cannot be deduced whether the factors involved act before, after, or simultaneously with each other. Because *B* genes aid in repression of oidia and formation of initials but are not essential, it had been suggested that the B products modify the action of A proteins for spatiotemporal regulation of development (261, 262). It is possible that such modification occurs via posttranslational modification of mating-type proteins or via intermediate regulators, for example, by employing the cAMP produced after light induction in the dikaryon (232). In *U. maydis*, communication between the two

mating-type loci is mediated by the high-mobility group (HMG) box transcription factor Prf1 (161, 161a, 494), and cAMP has been implicated in cross talk with the pheromone response pathway (113, 114, 161a, 249, 250). For elucidation of the situation in *Coprinus*, two genes for Prf1-related HMG box transcription factors (*hmg1* and *hmg2*, respectively) and the gene encoding adenylate cyclase (*cac*) have recently been cloned from *C. cinereus* by PCR using primers deduced from *U. maydis* and other fungal sequences (41; M. J. Milner, Abstr. Fungal Genet. Conf., http://www.fgsc.net/asilo99/posterabs2.htm). A third HMG box transcription factor, Pcc1, has been identified by cosmid complementation of a monokaryon able to produce clamp cells and fruitbodies. Mutations in the HMG box, the DNA binding motif of the protein, have been identified as being responsible for the untimely fruiting-body formation and clamp cell formation observed in the strain. *pcc1* expression is upregulated in dikaryons, in strains with an activated *A* pathway, and in strains with an activated *B* pathway, suggesting that the gene might play a role in coordinating the activities of the *A* and *B* genes (356) (see above). It is interesting to note that monokaryon Fis^c, belonging to the same class of mutants as the monokaryotic *pcc1* strain (357), produces few oidia in the dark and shows a 40-fold increase in the number of oidia formed in the light at 37°C (Kües, unpublished). This observation does not exclude the possibility that light acts on *A* products and/or their genes but it suggests that light acts in parallel to the *A* products and/or affects downstream components of the *A* mating-type pathway.

Studies of certain resistance genes in dikaryons and diploids revealed differences in complementation efficiency between the diploid and the haploid-dikaryotic situation (267, 365) (see above). This might not be surprising for genes that are under direct or indirect control of the mating-type genes. In *S. commune*, for example, increasing the distance between the two nuclei within the aerial cells of the dikaryon allows expression of the *SC3* gene, which encodes a hydrophobin typically found in the monokaryon. Expression of *SC3* is down-regulated in the presence of different *B* genes, and the release of gene suppression with larger internuclear distances is thought to relate to gradients of pheromone and pheromone receptors: protein gradients from proximal nuclei will overlap, and a pheromone response will be generated which activates or suppresses genes in both nuclei. With increasing internuclear distance, dilution of *B* mating-type products along the gradients will eventually hinder any interaction between compatible *B* products and consequently interrupt nuclear communication, causing gene expression patterns to change (14, 434, 519a). In *C. cinereus*, internuclear communication is obviously interrupted in dikaryotic chlamydospores germinating with two monokaryotic germtubes (121, 266). Furthermore, nuclei in the clampless veil cells are not conjugated and are already arrested in mitosis on the very young basidiocarp (277). Thus, each veil cell nucleus is independent, and homokaryotic mycelium can be obtained from isolated, germinating veil cells (97, 277, 537). There are no reports of an uneven recovery of monokaryotic mycelia from chlamydospores and veil cells, probably because this was not systematically analyzed, in contrast to formation of oidia on dikaryotic mycelia. Single-component nuclei of predominantly one type escape by formation of oidia from the dikaryon after release of *A* repression by light induction, and gradients of mating-type products may play a role in this process. We do not know whether the *B* genes have an influence on this unequal recovery of oidia, but introduction of a compatible *A* gene into the formerly dominant nucleus reversed the relative yield of oidia (175a, 383). The use of transformants with mating-type genes to address problems on the dikaryon, such as why stipe cells have no clamp cells (277) and an apparently monokaryon-like cell wall composition (298), promises more exciting results on the interplay of *A* and *B* genes in the future. DNA integration in *C. cinereus* transformation is mainly ectopic and often occurs at multiple sites and expression levels of integrated genes vary between transformants (30, 31, 74, 145, 256, 317, 318). These features of transformation could be very useful to study the interplay between *A* and *B* at different product levels. Most importantly, for the first time in *C. cinereus*, with *A* gene and *B* gene transformants of the same strain, it is now possible to study dikaryons of totally isogenic backgrounds (240a).

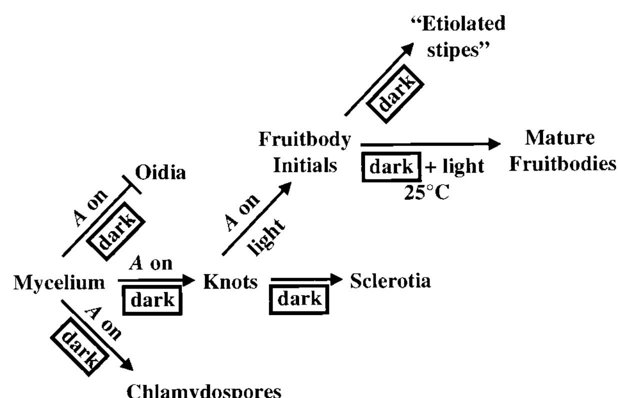

FIG. 16. Alternative developmental pathways on the dikaryon and regulation of development by dark-light conditions and by the *A* mating-type genes.

ENVIRONMENTAL AND PHYSIOLOGICAL REGULATION

Physical Factors

Environmental conditions including light, temperature, humidity and nutrients play a decisive role in determining the developmental pathways that *Coprinus* enters. On a superficial level, alternative developmental choices are possible. At each point of choice, environmental signals act, and light is probably the most important of these (Fig. 16). Light conditions will determine whether a dikaryon will form hyphal knots or oidiophores with oidia and whether the hyphal knots will mature into sclerotia or fruiting-body initials. Higher temperatures favor the development of oidia, and lower temperatures lead to fruiting-body initiation; the application of a cold shock can raise the absolute number of fruiting bodies per culture. Fruiting-body initiation and maturation need high humidity, whereas sclerotia and chlamydospores will also appear at low humidity (39, 40, 232, 261, 277, 293, 330, 352, 476, 506; Kües, unpublished; Kües, Granado, et al., unpublished). After light induction of initials, light continues to be the most important regulator: it suppresses the development of dark stipes and induces proper gill development of the cap tissues. At 48 h later in development, when gill formation is completed, light is required for induction of karyogamy at the stage of DNA synthesis prior to nuclear fusion (21, 184, 203, 277, 286, 350, 351, 476, 492) (Fig. 7). However, the situation is not as simple as this, since strains differ in their responses to light and since environmental signals other than light may influence the process. Light induction of fruiting bodies takes place at 20 to 37°C (275, 276, 476), but complementation of fruiting-body development needs more defined conditions. At 25 to 28°C, most but not all strains perform the whole program of fruiting

in continuous light (21, 275, 276, 350, 506; Granado, personal communication), but at 35°C, a 2-h dark period is required before meiotic DNA replication can proceed and complete within the following 6 h (275, 286). Certain strains will form initials in the dark, depending on the amount of ammonium in the media (352, 476) or the age of the culture (292, 293). For some specific strains, an extra, dark-dependent 2.5- to 3-h step has been observed at prophase I before they enter metaphase of meiosis, where strong light and long exposure time lead to arrest of development and the formation of abortive basidiocarps (B. C. Lu, submitted for publication). Different workers used different stage identification and different starting points, making it difficult to recognize how many different regulated steps indeed occur during fruiting-body morphogenesis (21, 203, 277, 344, 351). It is thus likely that the extra light-sensitive phase at prophase I corresponds to a light-sensitive phase at a later stage of development mentioned before in other papers (203, 324; Lu, submitted). Altogether, this yields at least five light-sensitive phases in the course of developing a mature fruiting body: the negative effect on hyphal knot formation, at least three positive effects to induce the formation of initials, maturation of primordia, and karyogamy, and another negative effect on completion of meiosis. However, light illumination before the extra-sensitive dark period at prophase I slows development and illumination after this phase accelerates development, indicating the possible presence of more light-sensitive steps (203).

Light in *C. cinereus* acts only on already established mycelium, and light response signals are not transmitted through the mycelia. Light effects are therefore local and not systemic events (232, 293). In an *Amut Bmut* homokaryon, a brief illumination of 1 min was found sufficient to induce the development of oidia and only 0.1 μE m^2 s^{-1} was needed for maximum production of oidia (232). Similarly, light requirements in fruiting are low. A 1-s light exposure and 1 ft-candle h (0.98 lx) is enough to induce fruiting (277, 293), and a 30-s exposure to 500 lx has been shown to induce karyogamy and basidiocarp maturation (203, 350). The active wavelengths in all light-controlled reactions, irrespective of whether they are negatively or positively affected, are in the blue region (400 to 500 nm) of the spectrum (40, 232, 261, 277, 278, 350, 476). The identity of the light receptor(s) in *C. cinereus* is not known, but from action spectra determined for other basidiomycetes (111, 112, 527, 528), blue light receptors are predicted to be flavoproteins. A number of blue light flavin-binding receptors (cryptochromes) have been found in plants and animals that have particular amino acid sequence identities to subgroups of bacterial and eukaryotic photolyases (67). Attempts to isolate a homologous *Coprinus* photoreceptor using primers deduced from plant cryptochromes and the closely related bacterial type II photolyases unfortunately failed (Bottoli, personal communication). However, comparison of plant and animal cryptochromes and the three major subgroups of photolyases suggested that there was repeated evolution of cryptochromes, in which different lineages arose independently from orthologous genes (67). It is thus possible that in *Coprinus* cryptochromes from other ancestries exist, possibly more closely related to the animal cryptochromes, since fungi are closer to animals than to plants (18). Moreover, other flavoproteins with photoreceptor properties are being discovered in plants (92), and the red/far-red photoreceptors (phytochromes) can also function in blue light responses (370, 398). Other candidates for blue light receptors have been proposed for the filamentous ascomycete *N. crassa* with the white collar Zn finger transcription factors WC1 and WC2. Both proteins contain PAS (PER-ARNT-SIM) dimerization domains that have identity to the xanthopsin-containing blue light photoreceptor PYP (photoactive yellow protein) from the halophilic purple bacterium *Ectothiorodospira halophila* (19, 20, 268). A further potential photoreceptor in *N. crassa* is a recently discovered rhodopsin-like protein (29).

Another fungal model system for blue light photoreception is the zygomycete *Phycomyces blakesleanus*, in which phototropism of sporangiophores (reproductive structures containing mitotic endospores) is used to monitor light response (128, 129). Mutant analysis in this fungus indicates that the photoreceptor system is also required for gravitropism (66). In the Coprini, the growing primordia and young fruiting bodies show a positive phototrophism before a negative geotrophic response takes over (53, 60, 241). Gravitropism is a postmeiotic event. It develops after an initial period of light-seeking growth in the early stages of fruiting-body development at the point of completion of meiosis (53, 55, 60, 233, 233, 347), but it is not clear whether the two types of tropism are also linked genetically in *Coprinus*. Clinostat experiments with *C. cinereus* and space laboratory experiments with other mushrooms (*Flammulina velutipes* and *Polyporus brumalis*) revealed that the basic form of a mushroom, i.e., the overall tissue arrangement of stem, cap, gills, hymenium, and veil is established independently from a gravity vector (162, 230, 336), although without gravity, stipes can be abnormally helically twisted (230). In the absence of a gravity vector, all *C. cinereus* tissues remain underdeveloped and fruiting-body development stops prior to meiosis, indicating that commitment to the meiosis-sporulation pathway requires the normal gravity vector (336); however, this is not the case in all fungi (229).

Fungus-like plant graviresponse systems divide into reception, transduction, and realization (320a, 347, 451). As in other agarics (53), the negative gravity response of the *C. cinereus* stipe is very quick. It takes a 7- to 10-min exposure to note a change in the gravity vector and about a 25-min reaction time for the first visible response (bending of the stem), which is strong (51° h^{-1}) within the first 30 to 60 min and completed in 2 to 3 h. Reaction times do not depend on the exposure time, and exposures are not additive, indicating that graviresponse is an "all-or-nothing" reaction. After reaching the maximum curvature, bending is still reversible, but if the tropic stimulus maintains, bending is rigid, indicating that gravitropic bending is a two-stage process (146, 147, 162, 163, 233, 320, 347). It is not exactly known when, where, and how gravity is sensed, but perception and response probably occur in the same tissue (163, 336). The response in horizontally placed stipes is most intense just behind the apex of the stipe and is almost absent at the apex and the base. More than half of the upper stipe can be removed without affecting the ability of the remaining stem to show gravitropic bending or its ability to compensate for curvature so induced and adjust to the vertical. However, the greater the part eliminated, the more time is needed to respond, suggesting that graviperception is gradually reduced in zones further from the apex (146, 147, 319). Gravisensing in fungi is thought to be simple and to occur, for example, just by a static gravistimulus mediated by the fungal mass or by a dynamic stimulus caused by alterations of the rate of cytoplasmic streaming and the slow sedimentation of organelles (such as the nucleus) acting as statoliths (24, 347). In *C. cinereus*, extracellular mass and/or mechanical stress have been excluded as the cause of the gravitrophic response (147). Geotropism of the stipe has been suggested to relate to a displaced distribution of the vacuole in relation to the cytoplasm, caused by a rearrangement of the cytoskeleton (142), but so far this has not been substantiated (347). Delayed and diminished gravitropic bending of stipes has been observed after treatment

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Lcc1  HWHGLFQRGTNWADGADGVNQCPISP------GHAFLYKFTPAGHAGTFWYHSH
Lcc2  HWHGMFQRGTAWADGPAGVTQCPISP------GHSFLYKFQALNQAGTFWYHSH
Lcc3  HWHGFLQEGTAWADGPAGVTQCPIAP------GHSFLYKFQAKNQAGTFWYHSH
Lac1  HWHGFFQHGTAWADGSQSVSQCPISP------GHSFEYRFPGGDQAGTFWYHSH
Lac2  HWHGFFQHQSAWADGPDGVTQCPI-PQS----GQEFEYAFNAGQEAGTFWYHSH
Lac3  HWHGLLQKGTNWADGAEGVNQCPISPASPENTENACEYRFTPAGHAGTFWYHSH
```

FIG. 17. Alignment of a copper-binding domain (110) of six different laccases of *C. cinereus*. Amino acids present in all sequences are shown in bold. Sequences for Lcc1, Lcc2, and Lcc3 are taken from reference 524a, and those for Lac1, Lac2, and Lac3 are taken from reference 41.

with the cytoskeletal inhibitor cytochalasin B, suggesting that the cytoskeleton indeed contributes to gravity perception. Since inhibitors of microtubule polymerization had no effect on gravitropism, the membrane connections of the actin microfilaments may mediate communication (146, 347, 369). In contrast, experiments with antagonists of Ca^{2+} transport and inhibitors of calmodulin have led to the conclusion that, unlike gravitropic responses in plant roots, Ca^{2+} acts in *C. cinereus* not in perception but in signal transduction (336, 368, 369). Ca^{2+}-mediated signal transduction may be involved in directing growth differentials, since the gravitropic bending of the stipe is the result of an asymmetric distribution of longitudinal cell expansion. Neither cell cross-sectional area nor cell size population structure change during bending, indicating that the growth mechanism of stipe bending is different from that of normal vertical stipe growth (148, 336, 347, 369).

Physiological Factors

C. cinereus initiates fruiting when nutrients are depleted (338, 406, 450), but only the youngest mycelium maintains fruiting competence (293, 350, 352; Kües, Granado, et al., unpublished); when a culture is too old at the point of light exposure, mycelial growth and consequently fruiting can be induced by injuring the established mycelium (145; Kües, Granado, et al., unpublished). Mycelial age also determines the execution of light-induced oidiation (232, 262), indicating a need for physiological activity to perform developmental programs upon exposure to environmental signals. Increasing concentrations of C and N sources act negatively on both fruiting-body formation and sclerotium maturation (292, 342, 476). This is also observed in the expression of galectins (Boulianne et al., submitted) and, to a lesser extent, in the production of oidia. In oidiation, absolute spore numbers are influenced by nutritional conditions (508a) but, as tested in an *Amut Bmut* homokaryon, light perception per se is not affected by nutrients (232, 508a). In principle, it is not so much an overexcess that is inhibitory, but development is particularly sensitive to balanced C/N ratios (292, 338, 352, 476). Ammonium is released by the fungus during the early stages of fruiting-body development (450), possibly to delay sclerotium maturation, which is sensitive to ammonium (476). However, the addition of free ammonium to competent mycelia also stimulates fruiting (352). Analysis of physiological effects on development have concentrated on fruiting-body formation (338). Fruiting-body initiation is inhibited by glucose and glucose analogues (302, 372, 476, 484, 485, 493). cAMP production is glucose repressed (484, 485, 493), but addition of cAMP overcomes a block in hyphal knot formation (302), initial formation, and fruiting-body maturation (480, 481, 491). High activities of adenylate cyclase and low levels of phosphodiesterase and, consequently, accumulation of cAMP were detected in light-incubated mycelia of *fis*^{c} strains and of dikaryons that form fruiting bodies but not in mycelia that do not fruit (262, 482, 491, 492). cAMP production by adenylate cyclase follows a typical pattern. The cAMP concentration in the mycelium rises slightly in the light before or during the onset of fruiting and stays high for 3 to 4 days. It then decreases rapidly due to a fall in adenylate cyclase activity and an increase in phosphodiesterase activity during primordium maturation (262, 484, 492), just before or at the time of karyogamy and early meiosis (344, 480, 482, 485). Isolated fruiting-body initials have a high cAMP content, but with primordium formation, the level of cAMP decreases. Although the levels are not as high as in the initials, the cAMP level rises again in both cap and stipe as meiosis proceeds, and it drastically drops once more in the mature fruiting body (263, 344). Accordingly, treatment of isolated basidia with cAMP allows karyogamy but blocks the process of meiosis (89). Generally, cAMP stimulates protein phosphorylation and activates a number of protein kinases (483, 484, 486, 488, 489, 491) but other protein kinases present in the mycelium are inhibited (483, 490). To really understand the actions of cAMP in developmental processes, it is necessary to use molecular biological techniques. A first step in this direction is the analysis of the adenylase cyclase gene *cac* (41). Expression of the gene is hardly influenced at all by external and internal signals (Bottoli, personal communication), indicating that enzyme activity is regulated by posttranslational activation. One possible candidate for such a regulator of adenylase cyclase is Ras (136, 322, 468). A *ras* gene has also been isolated from *C. cinereus* (41, 183), and its effects on development are being studied (Bottoli, personal communication).

Despite the relatively extensive studies on cAMP and glucose regulation, there are few other individual observations linked to induction of fruiting-body formation. Phenol-oxidase activities have repeatedly been related to fruiting-body initiation and maturation in basidiomycetes, but the relevance of this is not clear (417, 518). In *C. cinereus*, a phenol-oxidase (tyrosinase) is present in the mycelium without induction and another phenol-oxidase is specifically induced when fruiting is inhibited (372). A third enzyme, a laccase, is induced at fruiting-body initiation, and its level rises dramatically in activity during meiosis and spore formation and then decreases after spore maturation. Analysis of enzyme activity in *spo* and *exp* mutants suggests that this laccase contributes to the black pigmation of basidiospores (505). Six different laccase genes have been found in *C. cinereus* (Fig. 17). mRNA expression studies might show whether one of these is correlated with fruiting-body initiation or later stages in fruiting.

Certain cerebrosides produced in the fruiting bodies of, for example, *S. commune* and *Ganoderma lucidum* will cause fruiting-body formation when applied to dikaryotic mycelium of *C. cinereus* (325). The cerebrosides, sphingosine-based glycolipids, have been shown to repress replicative DNA polymerases (325), but how this can relate to fruiting-body induction is not obvious. Implanting from stipes, regardless of whether they are from light- or dark-grown initials, causes renewed fruiting. This

response is a very rapid one, occurring 2 to 3 days earlier than on vegetative mycelium, and a new generation of basidiomes is formed at the implants (51, 86, 476, 513). Thus, there must be a memory function for fruiting within the stipe tissues; cerebrosides may play a role in this. The potential for renewed fruiting resides especially in the parts of the fruitbody with accumulations of intracellular glycogen. This may reflect the need to attain a certain threshold level within the tissue before fruiting can be expressed (51). Nutritional transport in the vegetative mycelium of *C. cinereus* is very slow (375) and, in nature, probably even mostly blocked over longer distances by incompatibility borders in mycelial communities (520). It is therefore very possible that at least the initial stages of fruiting-body formation rely on energy and carbon sources stored in place rather than on substance transport over longer distances. Accordingly, accumulation of glycogen in inflated cells of the vegetative mycelium is also associated with fruiting-body production (294). However, only specific primordia of a culture will mature whereas most others fail, probably because young fruiting bodies initiate a flow of nutritions in their direction in preference to others (292, 335, 338). As an alternative to fruiting-body formation, glycogen in the swollen vegetative cells acts as a mobilizable source of carbon reserve for sclerotium development (342, 511).

Glycogen phosphorylase activity is stimulated (483, 484, 486, 488–491) and glycogen synthetase is inhibited (483, 487, 489, 491, 492) by cAMP. At early stages of fruiting-body development, degradation of glycogen and translocation from the mycelium to the developing fruiting-bodies have been demonstrated and are correlated with the high cAMP levels (188, 292, 294, 338). Glycogen first accumulates in the stipe tissue and then relocates to the cap of the primordium, especially into the subhymenial tissues, and is almost totally utilized in the mature fruiting body (23, 142, 312, 332, 338, 344). Glycogen phosphorylase activity in the cap increases after karyogamy at the stage of sterigma formation; the onset of large-scale utilization of accumulated glycogen is a postmeiotic event. However, inhibition studies with ammonium and analysis of white cap mutants indicated that glycogen degradation and sporulation are not closely coupled (188, 345). Glycogen synthetase activity is low during spore production but increases during basidiospore maturation (188), obviously to produce the glycogen that is found in the mature spores (37, 169, 312).

Maturation of the cap is accompanied by a specific pattern of changes in enzyme activities and metabolite levels. *C. cinereus* has two forms of glutamate dehydrogenase (5, 345). The NAD-linked enzyme is most active during vegetative growth but is also present in the stipe and cap of the fruiting body. In contrast, the NADP-dependent glutamate dehydrogenase occurs at high specific activity in cap cells of fruiting bodies but is barely detectable in stipe cells and the vegetative mycelium (450). Production of the NADP-dependent enzyme is initiated at or very soon after karyogamy at the early stage of meiosis (323, 345). Urea and urea cycle intermediates activate the NAD-linked enzyme and inactivate the NADP-linked dehydrogenase, indicating a link to the urea cycle (5, 332, 450). Glutamate dehydrogenase, glutamine synthase, ornithine acetyltransferase, and ornithine carbamyltransferase are other enzymes associated with the urea cycle and ammonium metabolism that are highly expressed in the cap but not in the stipe. In contrast, urease activity is present within the stipe and the vegetative mycelium but not in the cap (123, 332, 341). During cap development, synthesis of urea is amplified and water is driven osmotically in cells in which urea accumulates. The urea concentration in cap cells therefore remains unchanged, and it is thought that this mechanism contributes to the inflation of hymenial cells (332). The cap always contains less free ammonium than does the stipe (123, 332); this is especially important for meiosis and spore formation, which are inhibited by free ammonium and also by glutamine (87, 89, 346). It is possible that the NADP-dependent glutamate dehydrogenase and glutamine synthase act together as an ammonium-scavenging system to protect the meiotic apparatus from ammonium inhibition (119, 123, 331, 333). When ammonia is limiting, acetyl coenzyme A accumulates, and this appears to be necessary for induction of NADP-dependent glutamate dehydrogenase. Consistent with acetyl coenzyme A accumulation, the tricarboxylic acid cycle is highly active in the cap, as indicated by a strong increase in succinate dehydrogenase and isocitrate dehydrogenase activities (332). However, there is no evidence for 2-oxoglutarate dehydrogenase, and it is assumed that the 2-oxoglutarate dehydrogenase step is bypassed by a glutamate decarboxylation loop (332, 338, 341).

CONCLUSIONS AND FUTURE PERSPECTIVES

In the past, morphology in basidiomycetes has been studied mainly for taxonomic reasons. In particular, the structures of fruiting bodies have been described extensively, in far more detail than was possible to present here (95, 413–415). Mechanisms by which development in basidiomycetes is regulated and verified have mostly been neglected. Attention has been given to a few species where we are starting to gain an understanding of developmental processes (246, 335, 338, 517). *C. cinereus* is probably the best-analyzed of these. However, as indicated from the state of knowledge reviewed in this paper, the work is often only fragmentary. This paper compiles numerous individual observations made over more than 100 years of *Coprinus* research since Brefeld's introductory work (46). The majority of this work is still descriptive, and, as shown by the recent discoveries of oidia on dikaryons (232) and chlamydospores on monokaryons (261), the description of the fungus is still not complete. In fact, careful descriptions are needed before it will be possible to address developmental processes by physiological and genetic studies and to analyze the influences of the environment on development. This becomes particularly obvious when comparing the somewhat confusing literature on light control of fruiting-body development.

C. cinereus has a great capacity to adapt to changing environmental cues. Depending on the conditions, the fungus enters various paths of asexual reproduction (oidia, chlamydospores, and sclerotia) and also sexual reproduction within the fruiting body (Fig. 16). The developmental programs are not strictly fixed in their temporal course or in terms of the final shape an organ will adopt (338–340; Polak et al., submitted). With the one exception of meiosis within the basidia (86), none of the possible differentiation processes are committed steps (335, 338). As first pointed out by Moore and coworkers, this gives the fungus flexibility in expression of developmental subroutines according to the environmental circumstances and the physiological and genetic condition of the fungus (91, 338–340). Thus, after light induction, we observed production of oidiophores on hyphal knots of an *Amut Bmut* homokaryon incubated at 37°C (Liu, personal communication) and also on the cap of immature, discarded fruiting bodies in the 12-h-dark/12-h-light cycle at 25°C (Kües, unpublished). Within a given developmental pathway, other, smaller "subroutines" are recognized. For example, in the process of fruiting-body development, among other tissue formations, the formation of hymenia has been observed, and within the shaping of a hymenium, there are the parallel and successive development of basidia, cystidia, and paraphyses (338–340). Although cystidia

are normally sterile cells with a structural function, which have a shape very different from the sexual basidia, they can enter the meiotic cycle, giving another example of a break in a normal developmental program (90, 340). At the lowest level, development depends on the processes of cell elongation, cell inflation, cell division, and hyphal branching (52, 160, 340). Their interplay determines the shapes of single cells and of multicellular structures. The recent description of the various shapes that oidiophores can adopt (see above) demonstrates particular clearly how modular the development in *C. cinereus* can be (383; Polak et al., submitted). Strikingly, despite the distinct forms adapted by oidiophores, the absolute number of oidia produced by different strains is very much the same (232).

As in many other filamentous fungi, adaptation in *C. cinereus* is far broader than in other groups of eukaryotic organisms. This is because syngamy (plasmogamy) and karyogamy are temporally and spationally separated, which enables the nucleus to leave one dikaryotic partnership and to enter new dikaryotic partnerships by dikaryon-monokaryon and dikaryon-dikaryon fusions (see above). Formation of the freely distributable asexual oidia on the dikaryon (232, 383) further supports changes of nuclear partner. In terms of complementation, the genetic situation in the dikaryon in its typical case is comparable to the diploid condition found in other eukaryotes (see above). However, the continuous delay of nuclear fusion gives the haploid nucleus a unique status: the nucleus can behave as an individual! Basically, the nucleus is selfish, because it does not give up its identity. In the dikaryon, it takes advantage of the presence of a haploid partner nucleus but may drop this partner in favour of other, potentially better partners. That this nuclear partnership is not equal but has aspects of parasitism is indicated by the unequal recovery of nuclei in oidia from the dikaryon (175a). The strength of the nuclear selfishness must be very great, as indicated by the rapid decrease of the diploid into a haploid condition during vegetative growth of haploid-diploid dikaryons. In the normal case, karyogamy occurs only within the basidia after fruiting-body formation and is followed directly by meiosis and spore formation (see above). Large-scale dispersal of genetically recombinant spores as produced in the fruiting bodies might be expected to have preference over simple preservation of an established nucleus. However, fruiting bodies usually form when nutrients are limiting (see above), and it is only under such adverse conditions that nuclear identity is given up. There is thus a genetic conflict between the established haploid nuclear condition and the chance to obtain new, "better" gene combinations. The multiallelic mating-type loci in *C. cinereus* are understood to have developed in order to promote outbreeding (172–174). With the acceptance of the selfish behavior of haploid nuclei, there is a further, new aspect to the presence of multiple mating-type alleles: finding a new partner can be efficient only within an advanced mating-type system where almost every other individual has another mating-type specificity. The *A* mating-type locus obviously contributes to the strength of an individual nucleus within the dikaryon (383). This is even more interesting since mating-type genes have been proposed to have a selfish infectious character (25). Meiosis, on the other hand, has been postulated to be an evolutionary consequence of the selfish behavior of mitochondria that use meiosis to distribute within populations (181). It is probably not an accident that genes encoding mitochondrial functions have been kept in close proximity to mating-type genes or directly incorporated into mating-type loci in various organisms (420), including *C. cinereus* (81). Following hyphal fusion, mitochondria are not exchanged between two mycelia of *C. cinereus*. It is the migrating nucleus that plays an active role in establishing a new dikaryon, leaving its original mitochondria behind (see above). Within a mycelial community, there might thus be conflicts between selfish nuclei and selfish mitochondria (for further discussion, see reference 180). This suggestion is supported by the unusual observation that mitochondria can determine vegetative incompatibility in *C. cinereus* (304).

On the level of the organism, the boundaries of an individual are not strictly defined. A whole mycelial community, brought together by anastomosis of originally separate clones, may act as a single individual. An individual thus might be a chimera of genetically different mycelial parts (see above). Although there are tendencies to separate again by the practice of vegetative incompatibility (304), the formation of mycelial communities clearly has advantages for development, e.g., in the supply of nutrition during fruiting-body formation (see above). Feeding effects from other parts of a chimeric mycelium can overcome particular blocks in fruiting-body formation in regions with other unrelated nuclei, showing another case of parasitism in *C. cinereus* (269; Kües, Granado, et al., unpublished). The genetic load found in monokaryotic mycelia isolated from the wild is often suboptimal to undergo fruiting when combined in a dikaryon (261, 330), and interesting recessive mutations can be hidden within wild-type fruiting bodies (353). How delicately the genetic conditions of strains are balanced is further emphazised by the ease with which mutants with mutations in fruiting-body development can be created in a dikaryon and also in *Amut Bmut* homokaryons (213, 214, 354, 463; Kües, Granado, et al., unpublished). Mutants isolated by chance from the wild have been used to clone genes *pcc1* and *ich1* (353, 357).

As is obvious from this discussion, the mycelial life-style of *C. cinereus* raises special biological questions in terms of nuclei and definition of the individual. However, interesting biological problems of general interest can also be addressed with this fungus. *C. cinereus* is an ideal organism for the study of meiosis because of its natural synchronization within several millions of cells (see above). Because of its short life cycle and the ease with which mutants can be created, *C. cinereus* has advantages over plants in studies analyzing light and gravity perception and signal transduction (see above). Studying cytology and the genetics of development in *C. cinereus* will also reveal how alike and how different a basidiomycete is compared to other eukaryotes and, in particular, to the better-understood ascomycetous fungi including the yeasts *S. cerevisiae* and *S. pombe* and the filamentous fungi *Aspergillus nidulans* and *N. crassa*. Few genes (e.g., *cgl1*, *cgl2*, *eln2*, *ich1*, and *pcc1*) and some differentially expressed proteins of undefined function (217, 218) are to date known that are specific to the *C. cinereus* fruiting body or necessary for its formation. There have been surprising discoveries in this fungus within the small number of products so far identified from cloned genes, such as the galectins, only known in animals till now, and the putative cyclopropane fatty acid synthetase, believed so far to be a bacterium-specific enzyme. From DNA reassociation studies, 10% of the whole *C. cinereus* genome has been judged to correspond to coding sequences (514). With an average gene length of 2 to 3 kb, the fungus would have about 1,250 to 1,875 different genes within the total genome length of 37,500 kb. In *S. cerevisiae*, 5,885 genes have been identified in the genome-sequencing project (134), indicating that the estimate of coding sequences for *C. cinereus* is far too low. A total of 17% of the *C. cinereus* genes are estimated to be differentially expressed during fruiting-body formation (394, 395, 524). This large number of genes correlates well with the high frequency of mutants obtained by mutagenesis approaches in different laboratories.

Many of the genes may represent functions related to housekeeping. Others will be involved in the general coordination of developmental processes. Sexual and asexual development are regulated by the same environmental and physiological factors and, in addition, by the same genetic master regulators (see above). A major fraction of mutants are simultaneously defective in fruiting and asexual sporulation (383; Kües, Granado, et al., unpublished). With the detailed observation of the different developmental processes in wild-type and mutant strains, it should be possible to define genes specific to a given developmental pathway and genes that are generally involved in development.

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