The Basidium in Ustilaginaceae

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This essay summarizes many recent papers by the author dealing with the basidium in smut fungi belonging to Ustilaginaceae. In nearly all species, germination of the teliospore (probasidium) either leads to a structure that is obviously a 4-celled linear basidium or can be interpreted as a modification thereof.

Mycologists often divide the smut fungi (Ustilaginales) into Ustilaginaceae, with a transversely septate basidium, and Tilletiaceae where the basidium is unicellular. This system is adopted in *Ainsworth and Bisby's Dictionary of the Fungi* (Hawksworth *et al*, 1995). However, Vánky (1985), the foremost authority on smuts, is reluctant to recognize separate families. My knowledge of these fungi, developed late in life, is based almost entirely on having watched germination of teliospores (probasidia) in 40 species belonging to 14 genera. On this basis the recognition of two families appears to me to be justified. However, I would define Ustilaginaceae as smuts having a transversely septate basidium (or a modification thereof), which is prostrate on the substratum so the basidiospores (sporidia) are not directly available for aerial dispersal. This definition would exclude *Anthracoidea*, as would Denchev (1997a) who makes it the type genus of the Anthracoidiaceae, with some 60 species on *Carex* spp., in which there is an erect two-celled basidium with finely poised basidiospores which, though not ballistospores, can be liberated directly into the air (Ingold, 1989a).

The usual text-book figure of teliospore germination in *Ustilago* shows the young basidium (promycelium) as a short hypha of limited growth that divides into four cells from each of which a basidiospore is formed followed, in succession, by similar sporidia. However, although this standard pattern is widespread in this genus and its close allies, there are many species in which it is significantly different.

In passing it is of interest to compare this standard pattern with the somewhat similar situation in rusts such as *Puccinia* spp. First, in the *Ustilago* type normally no conspicuous basal vacuole occurs in the developing basidium, whereas

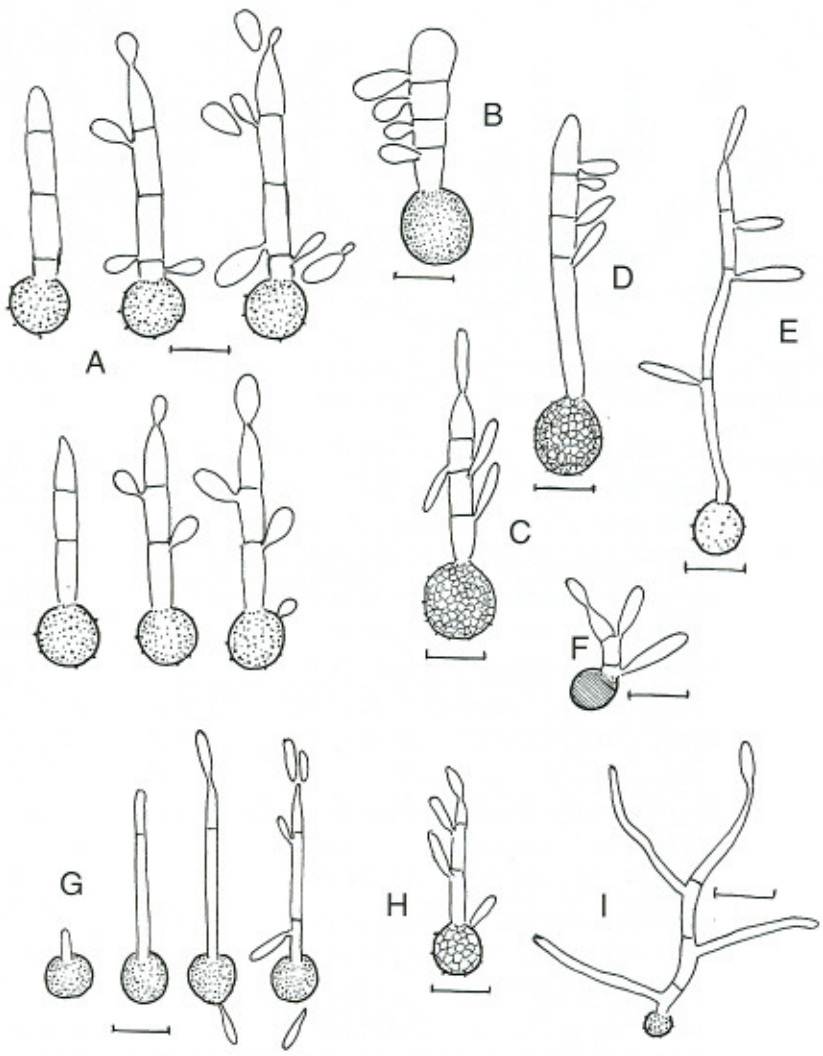

Fig 1 Basidia in Ustilaginaceae. A, *Ustilago avenae*, stages in basidial development in two germinating teliospores; B, *Bauhinus bistortarum*; C, *U. tragopogonis-pratensis*; D, *B. kuehneanus*; E, *U. trichophora*; F, *U. scitaminea* with 3-spored basidium; G, *Sporisorium tricholaenae*, stages in basidial development; H, *Bauhinus vinosus*; I, *U. hypodytes*. Bars = 10 μm.

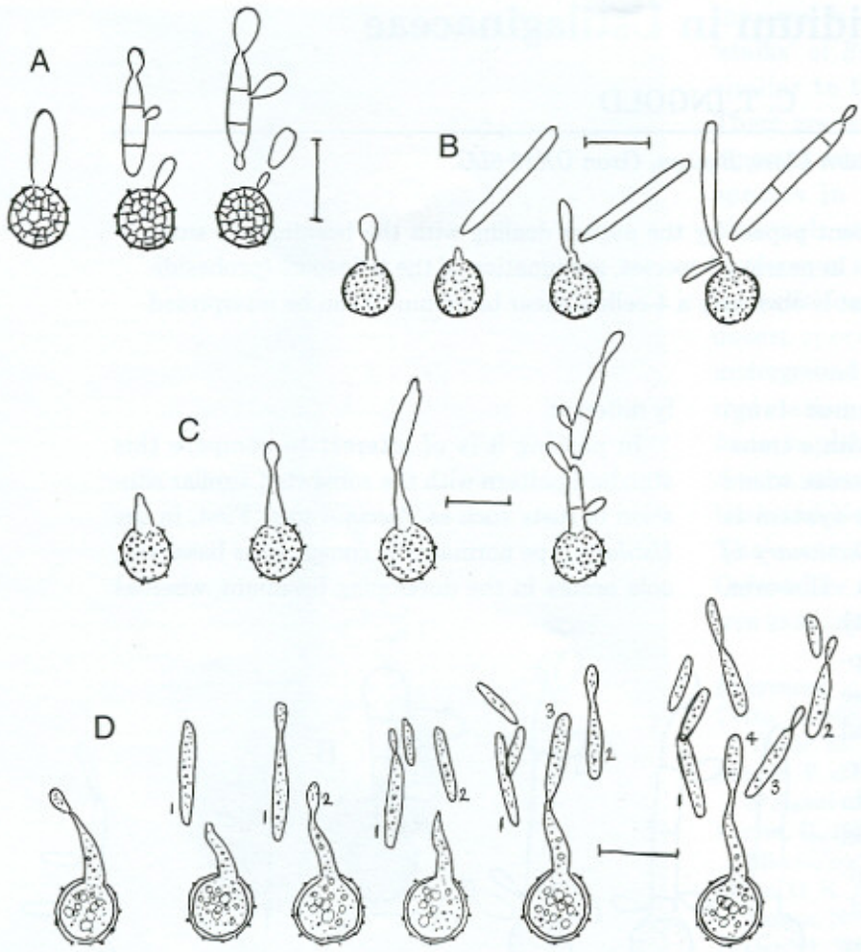

Fig 2 Stages in development of basidia in some species of *Ustilago*. A, *U. violacea*; B, *U. vaillantii*; C, *U. zeae*; D, *U. crus-gallii*. Bars = 10 μm.

in *Puccinia* such a one arises and, enlarging, drives the cytoplasm into a promycelium that becomes relatively long with a stalk region devoid of visible contents. This positions the fertile part in an appropriate posture for liberation of ballistosporic basidiospores. Secondly, each cell of the basidium uses up all its visible cytoplasm in the production of a single basidiospore which, unlike that of *Ustilago*, springs into the air.

In smuts of the *Ustilago*-type a particular cell of the 4-celled basidium may, according to conditions, behave in three ways. It may produce a basidiospore (sporidium), or a hypha, or conjugate with a compatible sister cell. Further, two types of outgrowth may occur from a teliospore, either broadly-based and hyphal in nature, or sporidial with a very narrow base and usually followed by detachment.

What happens in *Ustilago avenae* (Pers.) Rostr. (Ingold, 1983) is a convenient starting point from which to explore the range of the basidium in Ustilaginaceae. In this species there are two patterns (Fig 1, A). For most germinating teliospores three septa of the developing basidium are visible and the connexion of each sporidium with its parent cell is evident. However, sometimes only two cross-walls are to be seen, the third being hidden, apparently, by the opaque wall of the teliospore, and it is through this that the basidiospore emerges from the lowermost cell of the basidium.

The first of these two patterns seems to be the regular situation in many species, for example in *Bauhinus bistortarum* (DC) Denchev (Ingold, 1988) (Fig 1, B), *U. tragopogonis-pratensis* (Pres.) R. T. Moore (Ingold, 1985) (Fig 1, C), *B. kuehneanus* (Wolff) Denchev (Ingold, 1989b) (Fig 1, D) and in certain isolates of *U. trichophora* (Link) Körn. (Ingold, 1996) (Fig 1, E). However, the second pattern is characteristic of a number of species e.g. *Sporisorium tricholaenae* (Henn.) Vánky (Ingold, 1994) (Fig 1, G) and *Bauhinus vinosus* Tul. (Ingold, 1983) (Fig 1, H).

A slight variant is regularly found in *U. scitaminea* Sydow. The lowest cell of the basidium is completely enclosed by the teliospore wall which seems to be too tough to allow the emergence of sporidia so the basidium is 3-spored (Fig 1, F). The 4-celled nature of the basidium is revealed when, instead of sporidial production, conjugation occurs between sister cells (Ingold, 1988).

In a very few smuts each cell of the basidium habitually gives rise to a hypha from which, however, sporidia are soon produced. A well-known example is *U. hypodytes* (Schlecht.) Fr. (Ingold, 1983) (Fig 1, I).

In some species the basidium separates into two or more pieces before basidiospores are produced. In *Microbotryum violaceum* (Pers.) Fuckel that part of the young basidium outside the teliospore soon breaks free. Its subsequent division into three cells suggests that it is the upper three quarters of the basidium, leaving the remaining quarter surrounded by the wall of the

teliospore. All four cells produce sporidia (Ingold, 1983) (Fig 2, A).

There are a number of species in which a short germ-tube from the teliospore soon takes the form of a pointed sterigma from which a conidium-like structure is produced. In some further development indicates that this represents three quarters or a half of the basidium. An example of the former condition is seen in *U. vaillantii* Tul. (Ingold, 1984) (Fig 2, B) and of the latter in *U. zeae* (Bechman) Unger (Ingold, 1983) (Fig 2, C) and also in *Sporisorium formosanum* (Sawada) Vánky in which the two cells of the liberated 'conidium' may either produce sporidia or conjugate (Ingold, 1997a). Further in a few species the 'conidium' remains unicellular and is followed in succession by similar bodies from the same sterigma. This happens in *U. crus-gallii* Tracy & Earle (Ingold, 1987a) (Fig 2, D). There is no septation. It is just possible to regard these 'conidia' as basidiospores formed from a unicellular basidium, but obviously one quite unlike that of tilletiaceous smuts in which the basidiospores are generated simultaneously on an aerial basidium (Ingold, 1997b).

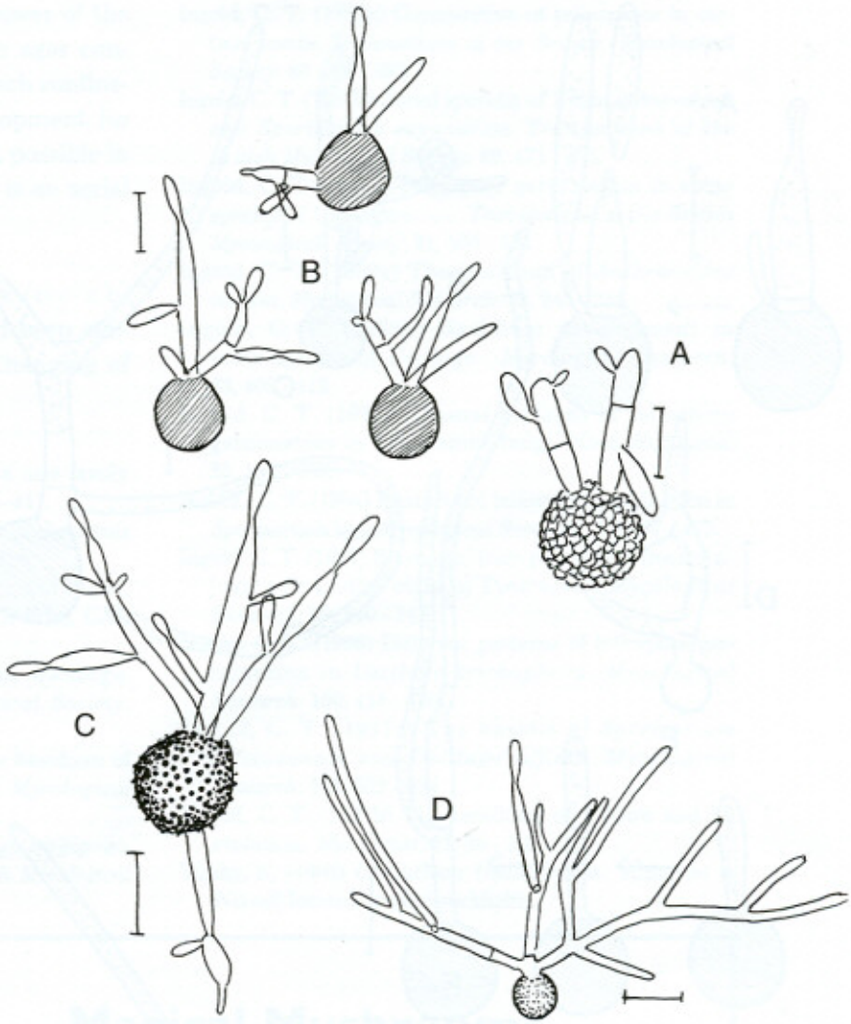

Fig 3 Germinated teliospores in some species of Ustilaginaceae. A, *Bauhinus succisa*; B, *U. aschersoniana*; C, *U. pamirica*; D, *Sporisorium puellare*. Bars = 10 μm.

Occasionally the axis of the basidium branches. This is sometimes to be seen in *Bauhinus succisa* Magn. (Ingold, 1983) (Fig 3, A) in which two uniseptate axes may develop from the teliospore each producing sporidia. However, basidia of the standard form are more usual. In *U. aschersoniana* Fischer v. Waldh. (Ingold, 1989b) (Fig 3,B) regularly three axes grow out in succession. The first has a median septum and seems to correspond with the top half of the basidium, the bottom half being represented by the two non-septate axes. Finally, four successive unicellular hyphae may emerge from the teliospore. This occurs in *U. pamirica* Golovin (Ingold, 1992) (Fig 3, C). It would appear that the basidium is unicellular, but 4-pronged.

In many smuts of the *Ustilago* type, conjugation occurs between sister cells of the basidium. If these are immediate neighbours the conjugation tube is inconspicuous, but otherwise it may be a striking feature (Fig 4, F).

In some smuts no basidiospores are produced by the basidium and only conjugation occurs. This is so in *U.tritici* (Pers.) Rostr. (Ingold, 1983) (Fig 4, D), *U. scorbiculata* Liro (Ingold, 1989b) and *Cintractia* spp. (Ingold, 1995) (Fig 4, F), but in others both types of behaviour are found often depending on the conditions during teliospore germination. Occasionally both occur in a single basidium (Fig 4, B).

From a conjugated pair of basidial cells, a hypha, presumably dikaryotic, grows out leaving the two parental cells devoid of visible contents. However, in *Cintractia* spp. (Fig 4, F), and occasionally in *Ustilago serena* Sydow, a relatively large conidium, developed from a short sterigma, is formed instead of a hypha.

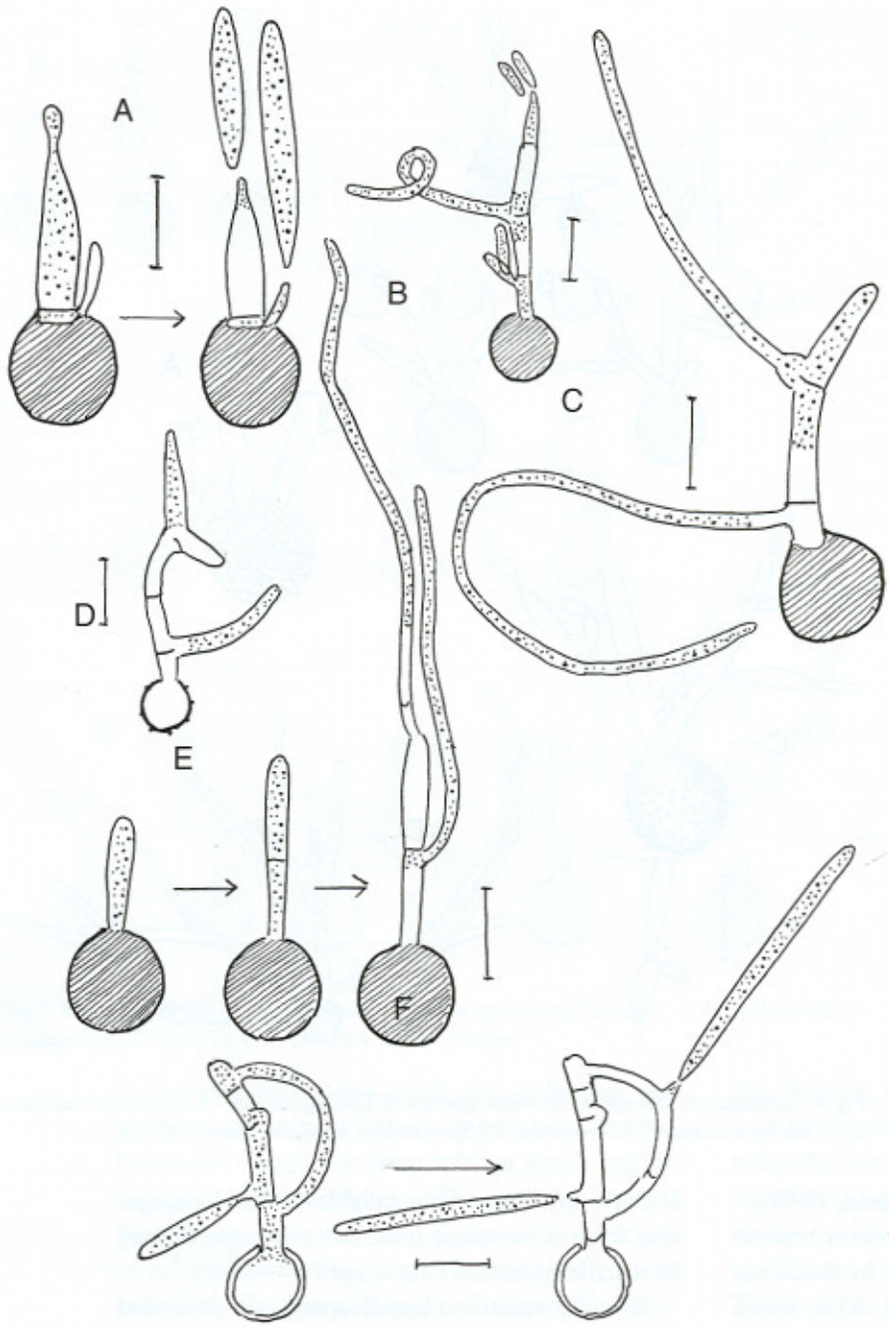

Fig 4 Germinated teliospores in some species of Ustilaginaceae. A, *Ustacystis waldsteiniae*; B, *Sporisorium tricholaenae*; C, *S. aegypticum*; D, *Ustilago tritici*; E, *U. commelinae*; F, *Cintractia peribebyensis*. Bars = 10 μm.

In spite of the 4-celled basidium being the standard pattern in Ustilaginaceae, in a few species it is clearly 3-celled, for example in *Sporisorium aegypticum* (Fischer v. Waldh.) Vánky (Ingold, 1992) (Fig 4, C). In this the two upper cells of the basidium invariably conjugate, indicating that they are always compatible no doubt because the mating-type gene is close to the centromere of the chromosome. From the conjugated pair the usual dikaryotic hypha grows out. However, a similar one emerges from the single basal cell which seems to have developed a short-cut to the production of a dikaryotic hypha by dispensing with septation at the second division of meiosis in the lower half of the basidium.

It is but a short step from this condition to that in *Ustilago commelina* (Komarov) Zundel (Ingold, 1989b) (Fig 4, E) in which the basidium is 1-septate each of the two cells producing a dikaryotic hypha. A 2-celled basidium is also a feature of *Ustacystis waldsteiniae* (Peck) Zundel (Ingold, 1992) (Fig 4, A) where from both cells a large basidiospore develops, the terminal one being consistently shorter than that in a lateral position.

Clearly, both the 3-celled and the 2-celled basidia can be regarded as derived from the 4-celled state. Indeed, only rarely have I studied an ustilaginaceous smut in which derivation from the standard type cannot be envisaged. However, this is so in *Sporisorium puellare* (Sydow) Deml (Ingold, 1988) (Fig 2, D). The initial stage of germination of the teliospore is conventional, but then a branch-system is formed which seems to bear no relationship to a basdium and no sporidia are formed.

At the start of this essay, it was emphasized that the basidium of *Ustilago* and its relatives is prostrate on the substratum, as are sporidia derived directly from it. These sporidia most usually increase by budding, but in some species there is soon a change to hyphal growth from which systems of aerial sporidia, of the *Cladosporium* type, may develop (Ingold, 1987b).

In conclusion I would emphasize that in a number of ustilaginaceous smuts interpretation of structure depends on following the course of germination of individual teliospores. In these particular smut fungi this is easy because the

process can be watched under high power of the light microscope with teliospores on agar confined under a coverglass. Strangely such confinement does not seem to affect development for many hours. Such an approach is not possible in tilletiatous smuts since the basidium is an aerial structure.

Postscript: the papers by Denchev (1997a,b) became available after this essay had been submitted for publication, hence the changing of some species of *Ustilago* to *Bauhinus*.

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