Craterellus Pers., Cantharellus Fr. and Pseudocraterellus gen. nov.

By E. J. H. Corner (Botany School, Cambridge, England).

With 7 Textfig.

Affinity between Craterellus and Cantharellus has long been supposed. They began as one in the history of nomenclature, but soon parted to the perplexity of systematists until most recently, when they have been re-united by Kühner and Romagnesi (1953). Their types indicate diversity. Craterellus cornucopioides is thelephoroid, Cantharellus cibarius agaricoid. Yet, between these extremes so many intermediates appeared, such as Craterellus cantharellus (Schw.) Fr., as well as Cantharellus infundibuliformis Fr. and Can. cinereus Fr., that the idea grew up of a primitive complex relating Aphyllophorales with Agaricales: and about this nucleus of humicolous fungi a taxonomic grade, Cantharellaceae, formed into which wandered lignicolous and epiphytic agarics which had lost their gills (Rimbachia, Trogia, Leptotus), obscurities (Nyctalis), and ochraceous spored genera (Gomphus). Here, as in many broad and tentative conceptions of mycology, is an artifical assemblage to be resolved by anatomical and biochemical analysis. It is my intention to show that Craterellus can be sharply distinguished from Cantharellus and that a third genus for Cantharellus (Craterellus) sinuosus Fr. must be separated. Of the fifty species attributed to Craterellus most must be transferred to Cantharellus. Craterellus may be related to some section of Stereum in its wide sense. Cantharellus is related to Clavariadelphus Donk, and Pseudocraterellus may be a derivative of Cantharellus.

Generic Resemblances.

The three genera agree in these points:

1. fruit-bodies gymnocarpic, short-lived, with inflating and, generally, thin-walled hyphae:

2. hymenium generally thickening through intercalary outgrowth of basidia; hymenial folds, when present, not formed by marginal outgrowth of hyphal tips, the edge blunt and fertile, without a trama of longitudinal hyphae:

3. basidia stichic; sterigmata 2-8, incurved:

- 4. spore-wall colourless, smooth, non-amyloid:
- 5. cystidia, gloeocystidia, dichophyses, etc., absent.

The thickening hymenium, as I have described for many *Clavariaceae* (C or n er 1950, p. 11), is the chief distinction from *Agaricales*, the hymenium of which is limited to a single layer of basidia (though these may project to different levels from a common sub-hymenium). The feature allies the genera with clavarioid and thele-phoroid fungi with plane hymenium; it appears as a lower state than the precise lamellate, or poroid, hymenophore which approximates the hymenial surfaces so closely and economically as to deny extension into the interstices. The stichic basidium appears, thus, as an adaptation of the meiotic sporangium to its own excressence from a congested surface, and not as a primitive mark.



Fig. 1. Cantharellus infundibuliformis Fr. A-F, early stages in the development of the fruit-body, $\times 5$: G, abortive primordia, $\times 5$: a-c, tangential sections of the pileus showing the development of the hymenial folds, $\times 10$.

Generic Distinctions.

Craterellus Pers.

Fruit-body erect, tubular-infundibuliform without a pileate limb, the conical primordium becoming hollow at an early stage, the inner surface of the fruit-body sterile and often corticate: stem as the sterile basal part: hymenium smooth or plicate-reticulate from the thickenings of the fruit-body medulla, not through foldings of the hymenium: hyphae without clamps, short-celled, not secondarily septate, walls often somewhat thickened.

Cantharellus Fr.

Fruit-body erect, pileate with horizontal limb developed epinastically, solid or secondarily tubiform through splitting of the medulla in the stem and centre of the pileus: stem as the sterile erect part of the fruit-body: hymenium smooth or plicate to sublamelliform through intercalary growth of the hymenium, the trama of the folds loose or disrupted: hyphae clamped, mostly long-celled, not secondarily septate.

Pseudocraterellus gen. nov.

Ut Cantharellus sed hyphis sine fibulis, ordine secundo septatis, cellulis brevibus non ramosis pluribus inter ramosas sistentibus: typus Cantharellus (Craterellus) sinuosus Fr.



Fig. 2. Can. infundibuliformis. Late stages in the development of the pileus, $\times 2$. A, perforation of the pileus beginning: B, perforation extending into the stem: C, tangential section of the pileus showing the deep hymenial folds.

As *Cantharellus*, but the hyphae secondarily septate without clamps, consisting of rows of short unbranched cells separating the branched cells.

Cantharellus.

Development. The fruit-body develops as a gymnocarpic agaric, the pileus forming through outgrowth of hyphae from the apex of the conical primordium and its margin becoming deflexed or incurved through epinastic growth. In Can. cibarius and its allies, the agaric form is readily distinguishable from that of *Craterellus*. In Can. infundibuliformis and its allies (sect. *Tubiformis* Smith and Morse, 1947), the appearance is deceptive. Their primordia are more slender and elongate and, as in slender agarics, the stem soon becomes hollow, but this hollow often extends to the centre of the pileus, making it pervious and the whole fruitbody tubiform, (Text-figs. 1, 2). The cavity is schizogenous, developing long after the pileus has formed, and its surface is lined by the



Fig. 3. Can. infundibuliformis. Diagram of the structure of a hymenial fold in section: a, the medulla of the pileus; b, the loose, disrupted trama of the fold; c, the disrupted subhymenium; d, the narrow, current subhymenium below the thickening hymenium.

medullary hyphae of the flesh: the resemblance to *Craterellus* is superficial. Can. cinereus Fr. comes between these two groups and in its colour and scaliness lends even more resemblance to *Craterellus cornucopioides*, but its pileate primordia, gill-folds, and clamped hyphae are typical of *Cantherellus*.

Hymenium. The hymenium is smooth for an appreciable distance behind the growing margin of the pileus. In some species it remains smooth; in others, folds arise through intercalary growth of the hymenium which loosens the subhymenial or tramal tissue. The folds are mainly radial following, that is, the medullary hyphae of the pileus, and they may bifurcate in conformation also, apparently, of the medullary construction. There is no outgrowth of hyphal tips along a radial line to form a gill and, therefore, the blunt edges of the folds are fertile and there is no trama of longitudinal hyphae. In some species, however, as Can. infundibuliformis, the folds develop strongly to form a system of primaries, up to 3 mm. deep, dichotomising and with secondaries towards the margin. It is tempting to invoke a special form-factor, as for the outgrowth of gills, yet it can be seen in section that, as the folds deepen, their internal tissue loosens and breaks down, and no other process seems to take place than buckling of the surface along the main lines of growth of the pileus. A truly lamellate hymenium does not occur. Finally, subordinate reticulations, resembling the Merulius-honeycomb, may develop between and on the sides of the folds. It is this massive intercalary growth of the thickening hymenium which dilates the stem apex and splits the centre of the pileus into the shape of Craterellus.

Sporing begins very early in the primordia, when the pileus is 1-2 mm. wide. Basidia mature et c. 300 μ from the developing edge of the hymenium.

Pseudocraterellus.

The fruit-body develops in the same way as in *Cantherellus*. The pileus may also become pervious into the hollow stem. The hyphal construction is strikingly different, resembling what I have described for *Clavaria* (Corner, 1950, p. 14). This character at once separates the species from *Cantherellus* and strengthens the definition of *Craterellus*.

Craterellus.

The development of the fruit-body can be likened to that of an unbranched *Clavaria* which, from a very early stage, becomes tubular, and would remain tubular if it were not for a multiplication of the medullary hyphae dilating the tube into a funnel. There is no outgrowth of a pileate limb with decurved margin: indeed, for a considerable time the fruit-body is vasiform and erect with a constricted orifice. I have followed the development in detail in the tropical form of Cr. cornucopioides, distinguishable by its 4-6-spored basidia (Corner 1948, p. 42, as the 'Malayan species'), and also in the Malayan Cr. verrucosus Mass.

The primordium is conical until 3-5 mm. high, when a hollow, which has appeared in the middle, extends to the apex. This is the

only schizogenous cavity in the fruit-body and it is soon obliterated. The peripheral hyphae of the apex continue to grow upwards and form the tubular fruit-body, both outer and inner surfaces of which



Fig. 4. Craterellus cornucopioides, tropical form. Longitudinal sections of a mature fruit-body $(\times 1)$ and of development stages $(\times 2)$.

are external surfaces developed behind the growing margin (textfigs. 4—7). The hymenium forms on the outside and a sterile cortex of excrescent hyphal ends on the inside, and in most cases both layers thicken throughout the life of the fruit-body. Thus, *Craterellus* is remarkable among Basidiomycetes for its tubular fruit-body, like and enormors *Solenia* upside down and inside out.

Faint ribs or reticulations occur on the hymenium. They begin as fine lines about 0.5—1 mm. behind the growing margin, and they thicken to 0.2—0.8 mm. high and wide. They fork distally or fan



Fig. 5. Cr. cornucopioides, tropical form. Diagrams of the structure of early stages in longitudinal section, $\times 20$, showing the origin of the cavity and the development of tubular growth; in the central figure the cavity is about to extend to the apex of the primordium.

upwards, much as the folds of *Cantherellus*, but their nature is different, for they are found on the stem where there is no hymenium and they occur in this tropical variety of *Cr. cornucopioides* in which the hymenium does not thicken. They are localised thickenings of the medulla, or flesh or trama of the fruit-body, where the hyphae have branched more freely to produce, as it were, cords immersed in the general tissue, much as a funiculose pattern can be seen in the fruit-bodies of *Cladoderris* and some polypores and in the mycelial excursions of some lignicolous fungi. The hymenium, developing on the outside of these thickenings, conforms to the pattern to which it has not contributed. No lines appear on the inner side of the fruit-body because the cortex obscures them. The scurfy squamules, formed by the cortex, do not arise from the disruption



Fig. 6. Cr. cornucopioides, tropical form. Above, diagram of the apex of a young fruit-body in longitudinal section, showing the manner of tubular growth, (compare fig. 7). Below, the wall of the fruit-body in transverse section, showing the ridges caused by thickening of the medulla; h, hymenium; c, cortex on the inside of the fruit-body; m, the medulla of longitudinal hyphae.

of a continuous cortex, as in most scaly surfaces in fungi, but from uneven excressence of the cortical hyphae in small patches 0.1— 0.5 mm. wide in the first place: even in this detail, *Craterellus* is peculiar and differs from *Cantharellus*.

The sides of the fruit-body become somewhat bullate, concavities on the one side corresponding with convexities on the other. This pattern is caused, presumably, by unequal enlargement of the medullary cells and tensions exerted by the hymenium on the thin tissue.

Affinities of the genera.

Cantharellus is connected with Clavariadelphus. The series Cl. pistillaris, Cl. truncatus (= Cr. pistillaris Fr.) and Cl. unicolor leads so gradually to Can. odoratus, or Can. cibarius var. cantharellus (Schw.) Heim, that it is difficult to know where to draw a distinction, (Heim, 1954). No truly pileate limb with inferior hymenium develops, apparently, in any of these species of Clavariadelphus, though the somewhat dilated apex is sterile in Cl. truncata and Cl. unicolor, and this pileate limb serves to distinguish Cantharellus. This alliance is one of the reasons for separating Clavariadelphus from Clavaria (Corner 1950, p. 45), just as the alliance of Gomphus is with Ramaria, and those who cannot follow the microscopic construction will have to unite Clavariaceae, Cantharellaceae and Thelephoraceae. On the other hand, the more slender species of the section Tubiformis seem related with Pseudocraterellus. The occurrence of secondary septation of the hyphae in the fruit-body deserves much greater attention; it can be found in the stems of slender fruitbodies of Coprinus and Mycena, as well as in the massive stems of some species of Tricholoma and Lepiota, and it permeates the energetically growing fruit-bodies of Clitocybe cyathiformis and its ally C. expallens. In contrast, it occurs in some species of the closely knit genus Clavulina and not in others. Donk (1953) placed Craterellus and Cantharellus near to Clavulina in his group Cantharelloideae, all three having stichic basidia. It seems that secondary septation has arisen independantly in Pseudocraterellus and Clavulina, for there is no pileate tendancy in Clavulina, such as there is Clavariadelphus with Cantharellus, and link to its basidia seem also analogous in form, rather than homologous, with the cantharelloid. The affinity of Clavulina seems to be with the chiastic Clavulinopsis, as the stichic Cantharellus is related to the chiastic Clavariadelphus.

This being so, the occurrence of stichic basidia in *Craterellus* is not in itself evidence of affinity with *Cantharellus*. I regard it, again, as an instance of parallel modification of the chiastic basidium in another alliance. So far as I have determined, *Craterellus* sensu stricto consists of two groups:

- 1. white or clear yellow fruit-bodies without a sterile cortex: hymenium smooth: Cr. aureus B. et C. (with Cr. diamesa Ricker as a synonym) and, possibly, Cr. laeta Pat. et Har.
- 2. grey, black, or fuliginous ochraceous fruit-bodies with scurfy squamulose cortex: hymenium rugulose: Cr. cornucopioides

Pers., C. verrucosus Mass., and possibly Cr. comperi Lév., Cr. dubius Peck, Cr. ocreatus Pers., Cr. orinocensis Pat., Cr. philippinensis Bres., Cr. violaceus Fr. and Cr. zelleri Burt.



Fig. 7. Cr. cornucopioides, tropical form. The margin of the fruit-body in longitudinal section, as shown in fig. 6; \times 500.

Now, there are in the tropics membranous-cartilaginous, mesopodal species of *Stereum* sensulato with the spore and hyphal characters of *Craterellus*, the alliance of which may well be with them. Certainly, it is well distinct from *Cantharellus*.

Summary.

Craterellus is distinguished by its tubiform, non-pileate fruitbody and hyphae without clamps. Cantharellus is pileate and may develop hymenial folds which are not present in Craterellus: its hyphae are clamped. Pseudocraterellus, with Cantherellus sinuosus Fr. as the type-species, differs from Cantharellus in the secondarily septate hyphae without clamps. The development of Cr. cornucopioides and Can. infundibuliformis is illustrated.

Cantharellus is related to Clavariadelphus, and Craterellus possibly to mesopodal Stereum. Pseudocraterellus seems to be a derivative of Cantharellus. There appear to be about twelve species in Craterellus sensu stricto.

References.

Corner, E. J. H. (1948). Studies in the basidium I. New Phytol. 47, 22-51.

Corner, E. J. H. (1950). Clavaria and allied genera. Ann. Bot. Mem. n. 1. Donk, M. A. (1933). Revision der niederländischen Homobasidiomycetes-Aphyllophoraceae, II. Med. bot. Mus. Rijkuniv. Utrecht, n. 9.

Donk, M. A. (1949). Nomina conservanda for *Basidiomycetes*. Bull. Jard. bot. Buitenz. ser. III, 18, p. 127.

Heim, R. (1954). A propos de trois Chanterelles américaines. Rev. Mycol. Paris 19, 46-56.

Kühner, R. and Romagnesi, H. (1953). Flore analytique des Champignons Supérieurs. Paris. (p. 47).

Singer, R. (1945). New genera of Fungi, II. Lloydia 8, 140-141.

Smith, A. H. and Elizabeth E. Morse. (1947). The genus Cantharellus in the Western United States. Mycologia 39, 497-534.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: Sydowia Beihefte

Jahr/Year: 1956

Band/Volume: 1

Autor(en)/Author(s): Corner E. J. H.

Artikel/Article: <u>Craterellus Pers., Cantharellus Fr. and</u> <u>Pseudocraterellus gen. nov. 266-276</u>