

The Ustilagineae, or "Smuts," of New Zealand.

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Plates 44-47.

THIS group of fungi is characterized by the production of masses of dark-coloured spores in or on the leaves, stems, or inflorescences of Phanerogams. On account of the dark colour and usually powdery nature of the spore-masses, members of this suborder are popularly termed "smuts." Many are of considerable economic importance, for, where preventive methods are not practised, certain species cause a heavy annual loss to those engaged in the culture of cereals and grasses. On this account they have for the past half-century been the subject of considerable investigation by mycologists, with the result that in most cases their structure and life-history are well known.

The spore-mass, or sorus, consists of numerous spores which at maturity may be free and one-celled, or may be aggregated into spore-balls; in certain genera many of the spore-balls are surrounded completely or in part by sterile cells. Various names have been applied to the spores by different workers (e.g., "chlamydospores," "teleutospores," "brand-spores," "pseudospores," "resting-spores"), but in this paper they will be termed simply "spores." The spore, on germination, usually produces a structure bearing lateral or terminal conidia. This body has been variously named (e.g., "promycelium," "germinal tube," "hemibasidium," "probasidium," "basidium"), but in accordance with its significance in classification it should more properly be termed a "basidium." Unfortunately, its behaviour is so varied in different genera and species as to make it impracticable to apply this term (see under *Ustilago*); to avoid confusion the term "probasidium" is used in this paper, for this implies that it is the fore-runner of the basidium, an opinion held by many modern taxonomists. In the majority of cases the probasidium gives rise to hyaline continuous spores (variously termed "sporidia," "sporidiola," "promycelial spores," "conidia"), to which in this paper the term "conidia" will be applied. A conidium, on germination, produces a hypha (infection hypha) which penetrates the host-tissues, where under favourable conditions it gives rise to a mycelium, from which eventually the spores develop.

All species undergo this cycle, but, as might be expected, the details vary considerably in different genera, and even in different species in the same genus. These differences, in so far as they concern New Zealand species, are dealt with under the respective species in which they occur.

Members of the Ustilagineae are usually considered to be obligate parasites. Strictly this is not the case, for Kniep (1921) has successfully grown *Urocystis Anemones* Wint. on culture media, the full cycle being completed thereon. Many species may be grown on media, where they produce abundant mycelium, but this is the first recorded instance in which spore-formation occurred. Then, too, at one stage in the cycle every species is saprophytic, producing probasidia and conidia (when these occur in the cycle) in the soil.

MORPHOLOGY.

MYCELIUM.

When a conidium germinates it produces a small infection hypha, which, if conditions are favourable, penetrates the tissues of the host. There it branches repeatedly to form a mycelium, the hyphae of which derive their necessary food substances from the host-cells. The hyphae ramify between and send into the host-cells minute botryoidal or irregular haustoria; occasionally the hyphae have been found to penetrate into the cells.

Infection may occur when the host is in the seedling stage (as in *Ustilago Avenae*, *U. levis*, *Tilletia Tritici*), at the time of flowering, through the stigma (*Ustilago Tritici*), or locally through the stem or leaf (*Urocystis Anemones*). Further particulars are given under the respective species.

The mycelium is difficult to detect in the host, partly owing to the minute size of the hyphae, and partly owing to the fact that at the time of spore-formation the hyphae commonly undergo gelatinization; but they may generally be observed in the vicinity of the developing sori. They are usually much septate, narrow, being only 2 or 3 micromillimetres thick, and have comparatively thick hyaline walls. The mycelium often persists in the perennial parts of the host, and in the spring grows into and infects the developing leaf and shoot. The hyphae may stimulate the host-cells to excessive division; consequently, with certain species, large galls are formed in the vicinity of the sorus (e.g., *Ustilago Zeae* Ung.).

SPORES.

These develop directly from the mycelium. They are usually produced in the inflorescences, replacing the ovules, but may also be formed within the tissues of the leaves and stems. From the vegetative mycelium, in certain restricted areas, special short hyphae are produced which are cut off by septa from the vegetative mycelium; they then become somewhat rounded, and the outer walls become partly gelatinized. Within these gelatinized walls, in the lumen of the cell, the spore develops, first appearing as an undifferentiated mass of protoplasm, which later becomes surrounded by a two-layered wall. As details of development differ in the different genera, they are more suitably dealt with under each genus. The spore at maturity consists of a two-layered wall—a hyaline, rather delicate endospore, and a well-defined, coloured episporium—enclosing the protoplasm, which is colourless, contains numerous oil-globules, and a single nucleus in which is a large nucleolus. The episporium may be smooth, finely or coarsely verruculose, or reticulate.

GERMINATION.

Spores may germinate as soon as mature, or may require a more or less protracted period of rest. The method of germination differs considerably in different genera, and even in different species in the same genus. These differences are more conveniently discussed under each genus and species. In general, however, there are two methods of germination, and upon them is based the separation of the two families—Ustilaginaceae and Tilletiaceae—of which the suborder is usually constituted. A short probasidium is produced; on it are borne either lateral and terminal conidia (Ustilaginaceae), or else one or many terminal conidia, which, if numerous, are arranged in a whorl (Tilletiaceae). Exceptions occur, such

as when a probasidium is produced which develops directly into an infection hypha, conidia being absent. In such a case the species is placed in one or other family on account of the possession of certain other characters. (See under "Taxonomy.")

In water the conidia produce short infection hyphae, seldom secondary conidia, but in nutrient solution they often give rise to secondary or tertiary conidia by a process of budding.

CYTOLOGY.

The vegetative mycelium (prior to the formation of spores) is invariably binucleate until shortly after gelatinization of the walls of the sporogenous hyphae, when the two nuclei fuse, the mature spore being uninucleate. When the spore germinates the protoplasm passes into the probasidium, but the nucleus usually remains within the spore and there divides, the daughter nucleus passing into the probasidium.

In *Ustilago* this probasidial nucleus and the one within the spore again divide, and all then migrate into the probasidium, where each takes up such a position that when the probasidium becomes septate each cell contains one nucleus. As each conidium is formed, one of the probasidial nuclei divides and the daughter nucleus migrates into the conidium. In those members of this family in which conidia are produced the conidia often conjugate, a short conjugation-tube passing from a conidium to one adjacent, with which it fuses, or both may produce tubes which meet and fuse. Through the tube the nucleus of one conidium passes to the other, where it remains, but does not fuse with its fellow. When this binucleate conidium germinates it produces an infection hypha, the cells of which are binucleate owing to simultaneous division of the two nuclei. This binucleate condition persists until spore-formation.

In *Tilletia* the probasidium is at first non-septate, and the spore nucleus divides until the number of daughter nuclei corresponds with the number of terminal conidia produced, into which they pass. In *Tilletia* conjugation occurs whilst the conidia are still attached to the probasidium. Here a short conjugation-tube is produced; this fuses with a contiguous conidium (or conidial tube), and the nucleus of the one migrates to the other. As in nutrient solution these conidia may produce an aerial mycelium from which secondary conidia arise, it follows that this mycelium, together with the secondary conidia, is binucleate.

In those species of either genus in which no conidia are produced conjugation is effected between neighbouring hyphae derived from the probasidium. Short lateral outgrowths are produced; these fuse, and the nucleus of one migrates into the cell of the other. In this manner the mycelium becomes binucleate. Exceptions occur, however, for Rawitscher (1912) has shown that with *Ustilago Maydis* Cda. (= *U. Zeae* Ung.) the conidia do not conjugate, the mycelium remaining uninucleate throughout its vegetative existence until the period of spore-formation, when during the formation of the sporiferous hyphae the ends of adjacent cells come in contact, their walls break down, and two nuclei come together in the swollen terminal region so produced. These nuclei fuse almost immediately, so that the developing spores are uninucleate as in normal plants.

This matter cannot here be discussed at greater length; further particulars may be obtained from the papers of Dangeard (1894), Harper (1899), Lutman (1911), Rawitscher (1914), Kniep (1921).

REMEDIAL TREATMENT.

Owing to the economic importance of these fungi, mycologists in various parts of the world have carried out considerable work on their control. According to the methods of infection, this remedial treatment may be classed under the two heads—(i) Destruction of seed-borne spores by steeping in some fungicide; (ii) destruction of perennating mycelium in the seed.

(i.) Many species are perpetuated by spores carried on the seed; these germinate and infect the host in the seedling stage (e.g., *Ustilago Avenae*, *U. levis*, *U. bromivora*, *U. Jensenii*, *Tilletia levis*, and *T. Triticici*); in fact, the majority of the species of economic importance are included in this group.

The treatment recommended is to steep the seed in some fungicide which destroys the spores without materially affecting the germination of the seed. Of the many solutions tried, formalin and copper-sulphate have been most widely used; unfortunately, both, though effective as fungicides, impair the germinating-vitality of the seed.

Successful trials have recently been made with other fungicides, one of the most promising being powdered copper-carbonate, first recommended by Darnell-Smith (1917; 1921). For particulars as to the methods of treatment, and a *résumé* of the effect of these three substances on the germination of wheat, see Neill (1923), who also gives a bibliography of recent experimental work in this connection.

German chemists have since 1914 been experimenting with considerable success with various organic and inorganic compounds in connection with smut-control, excellent results being claimed for certain mercury-chlorine-phenol derivatives sold under the trade names of "Uspulun," "Germisan," &c. Samples of some of these compounds are now available, and will be tried out in this laboratory with a view to ascertaining whether they are applicable under New Zealand conditions.

(ii.) Other species are perpetuated by means of hibernating mycelium in the ovule (e.g., *Ustilago striaeformis*, *U. Triticici*). This mycelium remains quiescent until the seed germinates, when it grows with the growing-point of the host until the formation of the inflorescence, eventually replacing the ovule by a mass of spores. Needless to say, external treatment with a fungicide is useless as a control in this case, since it cannot reach and destroy the internal mycelium.

Jensen (1888; 1889A) demonstrated by numerous experiments that if the seed were soaked for a few hours in cold water, then for a few minutes in hot water (53° C.); infection by *Ustilago Avenae* and "*U. nuda*" was prevented. Freeman and Johnson (1909) found by experimenting with Jensen's modified hot-water treatment that "*Ustilago nuda*" and *U. Triticici* could be entirely held in check. Their methods are summarized below:—

For barley, soak in cold water for five hours; follow by soaking in hot water at a temperature of 52° C. for fifteen minutes. For wheat, soak in cold water for five hours; follow by soaking in hot water at 54° C. for ten minutes. The seed may afterwards be stored for some time without detriment. Germination is but slightly affected if the treatment is carefully carried out.

Osner (1916) has shown that the hot-water treatment is also an efficient controllant of *Ustilago striaeformis*. It could also be used for all the cereal smuts, but the work entailed is such that most growers prefer the simpler chemical steeps.

A third method of combating these diseases is that of the production of resistant strains of the hosts. Unfortunately, little work in this connection has as yet been attempted on an extensive scale. That such strains do exist is readily demonstrable. For example, Mr. S. Hill, of Auckland, has selected a strain of *Bromus unioloides* (a plant that in New Zealand is invariably infected with *Ustilago bromivora*) which, although constantly grown side by side with infected plants, yet remains free from smut. I understand Mr. Hill intends to place seed from this smut-resistant strain on the market.

TAXONOMY.

The earlier systematists of last century had apparently vague ideas as to the position this suborder should occupy, for they usually included it as a subgenus of the genus *Uredo*. This close association with the rusts continued until the appearance of a paper by the brothers Tulasne (1847). In this paper, as a result of germination experiments, they separated the family Tilletiaceae from the Ustilaginaceae. They also discussed the position that they believed the suborder should occupy, comparing and contrasting it with the rusts. In a later work (1854) L. R. Tulasne sketched out the position he believed these two groups should occupy, suggesting their affinities; it is interesting to note that this work has largely been confirmed by modern workers.

Brefeld (1883) placed the suborder in the Hemibasidii, for he considered its members to be intermediate in position between the Basidiomycetes and the Phycomycetes, having arisen from the latter. He considered the probasidia to be of the nature of a basidium, and considered that the presence of this structure showed the group to be more closely related to the Basidiomycetes. He believed those Basidiomycetes with septate basidia to have arisen from the Ustilaginaceae, those with simple basidia to have arisen from the Tilletiaceae, for he believed the former to possess septate, the latter continuous basidia. As will be shown below, species and genera placed by him in the Tilletiaceae also possess septate probasidia.

Moeller (1895) erected for the Ustilagineae the order Protobasidiomycetes; this he divided into six families, all with septate basidia. He considered *Tilletia* to be the progenitor of those families possessing cruciate basidia, and *Ustilago* to have given rise to those with transversely septate basidia.

Patoulliard (1900) has arranged the classification of the Basidiomycetes in such a manner as to show the affinities of each order; his arrangement is such a convenient one that it will in part be followed in this paper in so far as the position of the Ustilagineae is concerned.

He divides the Basidiomycetes into two subclasses, Homobasidiae and Heterobasidiae, the latter being characterized by the septate or simple basidia, spores on germination producing conidia which form a mycelium reproducing the fructification. The Heterobasidiae he divides into four orders—Auriculariales, Tremellales, Tulasnellales, and Calocerales; in the first (characterized by the transversely-septate basidia) are included five suborders, of which the Ustilagineae is one. It is characterized by the probasidia being multiseptate, and the cells pleurosporous.

The suborder is usually divided into the two following families:—

- | | |
|-------------------|--|
| USTILAGINACEAE .. | Probasidium usually with lateral and terminal conidia. |
| TILLETIACEAE .. | Probasidium usually with terminal conidia. |

If the two methods of germination set out above are considered to be of sufficient importance to warrant the maintenance of two families, then, logically, a third family must be erected to contain those species (occurring in both the Ustilaginaceae and Tilletiaceae) the spores of which on germination give rise directly to an infection mycelium, a true probasidium being absent. This has not been done, however, and when these species have been encountered by workers they have been placed in one or other family on account of the possession of certain other characters. For example, it is often claimed—first by Brefeld (1883)—that the probasidia of the Ustilaginaceae are invariably transversely septate, those of the Tilletiaceae being continuous; but careful examination of mature cultures of members of the Tilletiaceae shows that the probasidia in this family also are transversely septate.

A third method of differentiation considered to be of value is that of spore-formation, for it is claimed that it is intercalary in the Ustilaginaceae, acrogenous in the Tilletiaceae. This character holds in so far as *Ustilago* and *Tilletia* are concerned, but when the development of the spores of those genera in which spore-balls occur is considered, as in *Sorosporium* and *Urocystis*, it is seen that in essentials the method of development is identical in each.

It is thus obvious to the systematist that the characters upon which the two families have been erected are not sufficiently distinct to warrant their retention; consequently the two should be merged in one, the Ustilaginaceae (the older name). This merging of the two families is by no means a new idea, for it has already been effected by several writers, among whom may be mentioned van Tieghem (1893), and Tubeuf and Smith (1897).

The suborder is poorly represented in New Zealand, for only twenty-three species are here recorded, included in seven genera. This is in marked contrast to the rusts, of which some 124 species have been collected and recorded. It is probable that many additional species will be added to the New Zealand records in the future; as specimens come to hand they will be dealt with in subsequent papers.

The writer believes that the object of any taxonomic paper is to present in such a manner as to enable any one to determine with a reasonable degree of accuracy the species discussed therein; consequently in this paper only species possessing distinct morphological characters are considered, those that have been separated on biologic grounds being relegated to the waste-paper basket of synonymy. For if biologic races are considered as species (necessitating germination experiments, cultural experiments, &c., to prove their identity), then the work entailed in their determination would defeat the object of the paper.

All descriptions are original, and unless otherwise stated are drawn up from material in the herbarium of the writer. All drawings have been made with the aid of a camera lucida, from spores mounted in 50 per cent. lactic-acid solution. Only mature spores have been drawn and measured; these have been obtained by shaking the specimen over a sheet of clean notepaper.

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USTILAGINACEAE.

Endophytic fungi parasitic upon Phanerogams. Mycelium either localized or widely dispersed, of hyaline septate hyphae. Spores arising in compacted masses of sporiferous hyphae, modified from the vegetative mycelium. Sori evident, forming compact or pulverulent spore-masses in definite areas on the host, or more rarely permanently embedded within the host-tissues. Spores coloured, smooth or variously sculptured, occurring singly or aggregated into spore-balls, the latter often partially or wholly enclosed within a membrane of sterile cells. Germination by means of a probasidium on which are usually produced lateral or terminal conidia.

In the family Ustilaginaceae (including the Tilletiaceae) are included twenty-one genera, seven of which have been collected in New Zealand. Among the various mycologists who have worked with the suborder, opinions are divided as to the number of genera that should be retained. For example, Clinton (1906) includes under the Ustilaginaceae (excl. Tilletiaceae) the following eleven genera: (1) *Ustilago*, (2) *Sphacelotheca*, (3) *Melanopsichium*, (4) *Cintractia*, (5) *Schizonella*, (6) *Mykosyrinx*, (7) *Sorosporium*, (8) *Thecaphora*, (9) *Tolysporella*, (10) *Tolyposporium*, and (11) *Testicularia*. Under the Tilletiaceae he includes (1) *Tilletia*, (2) *Neovossia*, (3) *Tuburcinia*, (4) *Urocystis*, (5) *Entyloma*, (6) *Burrillia*, (7) *Doassansia*, and (8) *Tracya*. Of these, Dietel (1900) includes *Cintractia* and *Sphacelotheca* under *Ustilago*, and lists in addition the two genera *Anthracoidea* Bref. and *Poikilosporium* Dietel. *Anthracoidea* is now considered to be a synonym (and in this paper listed as such) of *Cintractia*; the second, according to Clinton, is a synonym of *Thecaphora*. To those listed by Clinton may be added *Melanotaenium* De By. and *Elateromyces* Bubak, the latter of recent origin. Of those other genera that have been proposed from time to time, *Rhamphospora* D. D. Cunn. is placed by Clinton under *Entyloma*; *Doassansiopsis* Setch. is placed by the same author under *Doassansia*; *Cornuella* Setch. is placed by Sydow (1901) under the genus *Tracya*; *Graphiola* Poit. is no longer considered to belong to this suborder; and *Cerebella* Ces. is considered by Saccardo (1886) to be an Hyphomycete.

KEY TO GENERA.

Spores single, not in balls.		
Sori pulverulent at maturity.		
Sori naked at maturity.		
Elaters absent from the sori.		
Probasidia usually with lateral conidia	..	1. <i>Ustilago</i> .*
Probasidia usually with terminal conidia	..	5. <i>Tilletia</i> .*
Elaters present in the sori	..	2. <i>Elateromyces</i> .
Sori enclosed within a definite fungous membrane	..	4. <i>Sphacelotheca</i> .
Sori compact.		
Central columella of host-tissue present in the sorus	..	3. <i>Cintractia</i> .
Central columella absent	5. <i>Tilletia</i> .*
Spores aggregated into balls.		
Sterile cells present	7. <i>Urocystis</i> .
Sterile cells absent	6. <i>Sorosporium</i> .

* There is really no satisfactory key character upon which to separate these two genera; for the characters upon which separation is based, see under the respective genera.

1. USTILAGO (Persoon) Roussel.

Roussl., *Flora Calvados*, ed. 2, p. 47, 1806.

Uredo § *Ustilago* Pers., *Syn. Fung.*, p. 224, 1801. *Ustilagidium* Herzb., in Zopf, *Beitr. Phys. Morph. Org.*, vol. 5, p. 7, 1895.

Sori forming dark-coloured pulverulent spore-masses in various parts of the host, usually in the inflorescences.

Spores single, globose or angular; episporium coloured, smooth or variously sculptured; germinating by a short septate probasidium, which either produces conidia laterally and terminally, or develops directly into an infection hypha.

Distribution: World-wide.

New Zealand species nine, of which three are indigenous and six introduced. The genus is a large one, and contains more species than any other genus in the suborder, for Clinton (1906) records seventy-two for North America. McAlpine (1910) lists nineteen for Australia.

The pulverulent naked sori and single spores serve to separate this from any other genus, with the exception of *Tilletia*. The production of probasidia bearing lateral conidia serves to separate those species of *Ustilago* possessing this character from those of *Tilletia*, which produce probasidia bearing terminal conidia. But in both genera occur certain species in which the method of germination differs in that no conidia are produced, the probasidium developing directly into an infection hypha. With such species it is necessary to seek some other character in order to place them in one or other of these two genera, unless one follows Herzberg and places them in his genus *Ustilagidium*, separated from *Ustilago* on this account. Other characters serving to separate the two genera are spore-size, it being claimed that the spores of *Tilletia* are relatively larger than those of *Ustilago*, and method of spore-formation, those species in which the spores are produced acrogenously being placed in *Tilletia*; if intercalary, in *Ustilago*. The matter would be simplified if the genus *Ustilagidium* were erected to contain those forms in which no conidia are present; but this would necessitate, in order to maintain consistency, the erection of another genus to contain such species as *Ustilago bromivora*, where the method of germination departs considerably from the normal.

In New Zealand, members of this genus have been found only on the Gramineae, but elsewhere they have been recorded on the following additional families: Cyperaceae, Liliaceae, Polygonaceae, Portulacaceae, Caryophyllaceae, Oxalidaceae, and Onagraceae.

Spore-formation.—This was first worked out by Fischer von Waldheim (1869). Following their differentiation, gelatinization of the sporiferous hyphae commences, and continues until the lumen of each hypha is almost obliterated, when the hyphae become compacted together and the gelatinized portions fuse, so that a complex gelatinous mass is formed in which it is difficult to discern individual hyphae. These hyphae become divided by transverse septa into short-celled lengths, and in the cells thus formed the spores commence their development, those near the periphery of the mass first attaining to maturity. The gelatinous envelope surrounds the spore during its development, but gradually becomes less conspicuous until at maturity it has entirely disappeared.

Germination.—In the genus three methods may be observed: in *Ustilago Avenae* the probasidium becomes transversely septate, and from it arise numerous lateral and one terminal conidia; in *U. bromivora* the

probasidium is short and usually continuous—although it sometimes becomes two-celled—and on this structure is produced a terminal conidium which on germination (in nutrient solution) again produces a probasidium, which in turn gives rise to a conidium; in *U. Tritici* and *U. striaeformis* the probasidium gives rise directly to an infection hypha, conidia being absent.

KEY TO SPECIES OF USTILAGO.

Spores smooth.					
Spores under 6 mmm.* long	<i>U. comburens.</i>
Spores over 6 mmm.					
Sori compact, covered with a membrane	3. <i>U. Jensenii.</i>
Sori pulverulent, without a membrane	2. <i>U. levis.</i>
Spores rough; granular, verruculose, or verrucose.					
Spores somewhat coarsely verrucose.					
Sori principally in the leaves	5. <i>U. striaeformis.</i>
Sori principally in inflorescences.					
Sori semi-compact	7. <i>U. bullata.</i>
Sori pulverulent	6. <i>U. bromivora.</i>
Spores minutely verruculose.					
Spores over 10 mmm.	9. <i>U. Readeri.</i>
Spores under 10 mmm.					
Sori destroying entire inflorescences	4. <i>U. Tritici.</i>
Sori semi-compact, only partially destroying spikelets					1. <i>U. Avenae.</i>

1. *Ustilago Avenae* Jensen. (Text-fig. 2, and Plate 41, fig. 2.)

Gramineae.

Jens., *Charb. Cereales*, p. 4, 1889.

U. perennans Rostr., *Overs. K. Danske Vid. Selsk. Forh.* 1890, p. 15, 1890.
Contractia Avenae Ell. et Tr., *Jour. Myc.*, vol. 6, p. 77, 1890.

Sori in spikelets, seldom in the leaves, usually completely destroying the floral parts, forming a pulverulent, olivaceous spore-mass, which eventually falls away, leaving only the bare axis of the inflorescence.

Spores globose or subglobose, 5–9 mmm. diam.; epispore distinctly but finely verruculose, pallid olive, more lightly coloured on one side, 0.5–0.75 mmm. thick.

Host: *Arrhenatherum elatius* (L.) Beauv. In inflorescences. Herb. No. 1247. Plimmerton (Wellington), sea-coast, *E. Bruce Levy!* 22 Dec., 1920. *E. H. Atkinson!* 1 Dec., 1921. Ashburton (Canterbury), 70 m., *H. H. Allan!* 15 Dec., 1921. Crookston; Dunrobin (Otago), *J. C. Neill!* *G. H. C.* 7 Feb., 1924. †

Distribution: World-wide.

The form on *Arrhenatherum elatius* was separated as a distinct species on account of the presence of perennating mycelium in the perennial parts of the host; it is identical morphologically with the form on the oat, so that it cannot be considered as more than a biologic race.

Germination.—In water the spores commence to germinate in from twelve hours (fresh material) to three days (old material). A long and slender probasidium (occasionally two) is produced; into this the protoplasm of the spore penetrates, and after the probasidium has attained a length several times that of the diameter of the spore several (3–5) transverse septa appear. On or near these septa several elliptical, hyaline, minute, continuous conidia appear. When detached these may in turn germinate and produce long and narrow infection hyphae. In nutrient solution, according to Brefeld (1883), the conidia do not produce hyphae, but produce secondary or tertiary conidia by a process of budding.

* In this article the contraction "mmm." is used for micromillimetres.

† A few localities obtained between the dates of reading the paper and publication have been inserted.

Infection.—This was first studied by Brefeld, who found infection occurred only in the seedling stage of the host. He sprayed budding conidia on to the seedling leaves at different stages of growth; those plants which had attained a development of the leaf beyond the sheathing-leaf were found to be immune. The conidia germinated and produced an infection hypha which penetrated the cuticle and entered the parenchyma, where it produced numerous colourless branched hyphae. As the plant increased in size he found the hyphae increasingly difficult to trace, until at maturity he was able to locate them only in the nodes, where they appeared to be fragmentary and much broken up. Apparently only those hyphae situated in or near the growing-point are able to infect the ovules in the developing inflorescence.

Thus the fungus is transmitted by spores lodged on the seed, between the glume and the pale. When the seed is sown the spores germinate and infect the emerging cotyledon, as described above.

Von Liebenberg (1879) has shown that the spores, if kept under dry conditions, may remain viable for seven years; so that seed stored for several years, if sown without preventive treatment, may bear spores capable of infecting the young plants as they emerge. A second method of infection is known—that of infection from spores remaining in the soil from a previously infected crop. This source is scarcely likely to be troublesome here, for, judging from the readiness with which spores germinate in water, it is probable that with our rainfall such spores would have germinated long ere the seed-bed was prepared for a second crop.

Zade (1922) found that if spores were applied to the inflorescences at the time of flowering, all that fell on the stigmas germinated, producing long probasidia, which in turn produced abundant conidia. When the conidia germinated they produced infection hyphae which gave rise to a mycelium in the peripheral parenchyma of the glumes, the embryo remaining unaffected. He believes this mycelium, and the secondary conidia produced from the hyphae on the inner surface of the glumes, to form the most important source of infection. If this regularly occurs, then dipping of the seed in some fungicide prior to sowing would be useless as a controllant, for the solution used would be unable to penetrate into the glumes to destroy the perennating mycelium therein. In such a case the modified hot-water treatment alone would be of use (see p. 400).

2. *Ustilago levis* Magnus. (Text-fig. 1, and Plate 41, fig. 1.)

Magn. *Abh. Bot. Ver. Prov. Brand.*, vol. 37, p. 69, 1896.

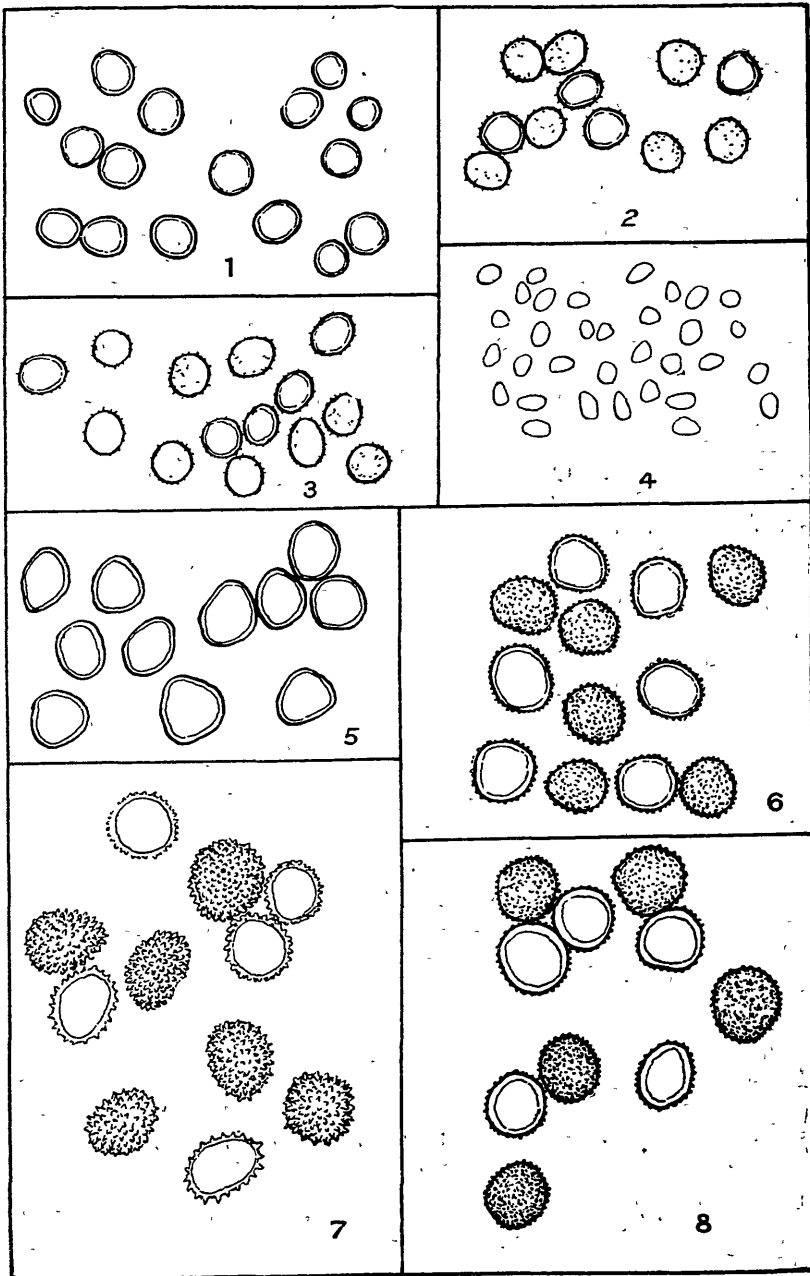
U. Avenae var. *levis* Kell. et Sw., *Ann. Rep. Kansas Exp. Stn.*, 2nd Rep., p. 259, 1890.

Sori in spikelets, destroying the inner parts, partially concealed within the glumes, forming a semi-compact, dark-brown, almost black spore-mass.

Spores subglobose, 5–9 mmm.; epispore smooth, dark chestnut-brown, more lightly coloured on one side, 0.75 mmm. thick.

Host: *Avena sativa* L. In inflorescences. Herb. Nos. 195, 304. Weraroa (Wellington), 80 m., *E. Bruce Levy!* 12 Jan., 1920. Ruakura (Auckland), 120 m., *A. H. Cockayne!* 27 Jan., 1921. Lincoln (Canterbury), 30 m., *F. E. Ward!* 18 Feb., 1921.

Distribution: Probably world-wide, but recorded only from North America and Europe.



TEXT-FIG. 1.—*Ustilago levis* Magn., from *Avena sativa* L.
 TEXT-FIG. 2.—*U. Avenae* Jens., from *Arrhenatherum elatius* (L.) Beauv.
 TEXT-FIG. 3.—*U. Tritici* Jens., from *Triticum vulgare* Vill.
 TEXT-FIG. 4.—*U. comburens* Ludw., from *Danthonia Buchanani* Hook. f.
 TEXT-FIG. 5.—*U. Jensenii* Rostr., from *Hordeum vulgare* L.
 TEXT-FIG. 6.—*U. bullata* Berk., from *Agropyron scabrum* Beauv.
 TEXT-FIG. 7.—*U. striaeformis* (Westnd.) Niessl, from *Holcus lanatus* L.
 TEXT-FIG. 8.—*U. bromivora* (Tul.) Fisch. v. Waldh., from *Bromus unioloides* H. B. K.

All $\times 1,000$.

This species is abundant throughout New Zealand. It is separated from the preceding on account of the smooth epispores of the spores. The sori also differ somewhat in their being more compact.

Germination, life-history, and control are the same as in *U. Avenae*.

3. *Ustilago Jensenii* Rostrup. (Text-fig. 5, and Plate 42, fig. 2.)

Rostr., *Overs. K. Danske Vid. Selsk. Forh.* 1890, p. 12, 1890.

Uredo Hordei var. *tecta* Jens., *Charb. Cereales*, p. 4, 1889. *Ustilago Hordei* Kell. et Sw., *Ann. Rep. Kansas Agr. Exp. Stn., 2nd Rep.*, p. 268, 1890.

Sori in spikelets, forming a semi-compact black mass, long covered by the transparent basal parts of the glumes.

Spores globose to shortly elliptical, $7-11 \times 5-8$ mmm.; epispore smooth, olivaceous or sepia-brown, more lightly coloured on one side, $0.75-1$ mmm. thick.

Host: *Hordeum vulgare* L. In inflorescences. Herb. Nos. 298, 1253. Ruakura (Auckland), 120 m., *A. H. Cockayne!* 25 Jan., 1921. Blenheim (Marlborough), 50 m., *J. Scott!* 28 Feb., 1921. Winton (Otago), *J. C. Neill!* 14 Feb., 1924.

Distribution: Australia; North America; Europe.

This is known as the "covered smut of barley," on account of the manner in which the sori are covered by the basal portions of the glumes. It is common on this host throughout New Zealand.

This species, together with *U. Avenae*, *U. levis*, and *U. Tritici*, were at one time included under the collective species *U. segetum* Dittm. Jensen (1889A), as the result of numerous infection experiments, split *U. segetum* into three races, as follows: (1) *U. segetum* var. *Avenae*; (2) *U. segetum* var. *Tritici*; (3) *U. segetum* var. *Hordei*. The variety *Hordei* he further divided into the two forms: *U. segetum* var. *Hordei* forma *nuda*; *U. segetum* var. *Hordei* forma *tecta*.

Brefeld (1888) considered the forms on barley and on wheat to be distinct, for he found the probasidium did not produce conidia, but gave rise directly to an infection hypha. He found also that these races would not infect oats; consequently he considered them to be distinct from the form on oats, and included them under the name of *U. Hordei* Bref. In his species are included *U. segetum* var. *Tritici* Jens. and *U. segetum* var. *Hordei* Jens. (including the two forms *nuda* and *tecta*).

Kellerman and Swingle (1890) raised to specific rank the two forms on barley—*nuda* and *tecta*—naming them respectively *U. nuda* (Jens.) Kell. et Sw., and *U. Hordei* (Pers.) Kell. et Sw. Thus Brefeld's *U. Hordei* was split by them into three species—(1) *U. Tritici* (Jens.) Kell. et Sw.; (2) *U. Hordei* (Pers.) Kell. et Sw.; (3) *U. nuda* (Jens.) Kell. et Sw.

Now, as the name *Hordei* was previously used by Brefeld, it cannot again be applied to a species; as *U. Hordei* of Kellerman and Swingle was named *U. Jensenii* by Rostrup the same year, this name should be used for this species. The matter is further complicated in that although the forms *tecta* and *nuda* are morphologically separable, and may therefore be considered as distinct species, the form *nuda* (*U. nuda* Kell. et Sw.) is identical morphologically with *U. Tritici* Jens., for both possess pulverulent sori, echinulate spores of the same size and colour, and the same method of germination. After extended and critical examination of these two so-called species I am unable to indicate a single morphological character by which they may be separated. True, in certain collections the spore-mass is slightly darker in colour on wheat than on barley, but this character is not distinct in all collections.

I am of the opinion, therefore, that *U. Tritici* Jens. and *U. nuda* Kell. et Sw. must be reunited under one name. As to the selection of this name: *U. segetum* cannot, of course, be used, nor can *U. Hordei* Bref., for this included the recognized species *U. Jensenii* Rostr. and the one under discussion. *U. Tritici* Jens. was by Kellerman and Swingle described on page 262; *U. nuda* Kell. et Sw. on page 277: since the former has page priority, it is the one to be used.

Clinton (1906) gives the citation of this species as *U. Tritici* (Pers.) Rostr., but the specific name used by Rostrup is taken from *Uredo segetum* var. *Tritici* Persoon, in *Tent. Disp. Fung.*, p. 57, 1797, a publication which antedates the starting-point of modern nomenclature.

The four species under discussion may then be separated by the following characters:—

Probasidium producing conidia.					
Sori pulverulent.					
Spores echinulate	<i>U. Avenae</i> Jens.
Spores smooth	<i>U. levis</i> Magn.
Sori compact	<i>U. Jensenii</i> Rostr.
Probasidium producing an infection hypha, conidia being absent					<i>U. Tritici</i> Jens.

Germination and infection (of *U. Jensenii*) are similar to the preceding two species.

4. *Ustilago Tritici* Jensen. (Text-fig. 3, and Plate 42, fig. 1.)

Jens.: Kell. et Sw., in *Ann. Rep. Kansas Agr. Exp. Stn.*,
2nd Rep., p. 622, 1890.

Ustilago segetum var. *Tritici* Jens., *Om. Korn. Brandp.*, p. 61, 1888. *U. segetum* var. *Hordei* forma *nuda* Jens., *Jour. Roy. Agr. Soc.*, vol. 24, p. 4, 1889. *U. Hordei* var. *nuda* Jens., *Charb. Cereales*, p. 4, 1889. *U. nuda* (Jens.) Kell. et Sw., *Ann. Rep. Kansas Agr. Exp. Stn.*, 2nd Rep., p. 277, 1890. *U. Tritici* (Pers.) Rostr., *Overs. K. Danske Vid. Selsk. Forh.* 1890, p. 15, 1890. *U. Hordei* Rostr., l.c., p. 10. *U. Tritici* forma *foliicola* P. Henn., *Zeitschr. Pflanzenkr.*, vol. 4, p. 139, 1894. *Ustilagidium Hordei* Herzb., in *Zopf, Beitr. Phys. Morph. Ora.*, vol. 5, p. 7, 1895. *U. Tritici* Herzb., l.c.

Sori in spikelets, destroying ovaries and glumes, forming olivaceous or almost black spore-masses, finally falling away and leaving the bare axis of the inflorescence.

Spores globose to shortly elliptical, 5–8 × 4–5 mmm.; epispore minutely but distinctly verruculose, pallid to dark olive, with a lighter-coloured zone on one side, 0.5–0.75 mmm. thick.

Hosts:—

Triticum vulgare Vill. In inflorescences. Herb. No. 407. Lincoln, Canterbury, 30 m., *F. E. Ward!* 5 March, 1921.

Hordeum vulgare L. In inflorescences. Herb. No. 46. Weraroa, (Wellington), 120 m., *G. H. C.* 11 Nov., 1919.

Distribution: World-wide.

The form on wheat is commonly known as "naked smut on wheat," that on barley as "naked smut of barley." As has been pointed out (under *U. Jensenii*), the two forms differ only in that each is confined to its host, but as they are identical in morphological characters they must be considered as the same species.

The two species on barley may be separated on account of the following differences:—

Sori compact; spores smooth	<i>U. Jensenii</i> .
Sori pulverulent; spores verruculose	<i>U. Tritici</i> .

Germination.—In water a probasidium is produced which gives rise directly to an infection hypha; this may branch and form a mycelium, but does not at any time produce conidia.

Infection.—With the race on barley it was first suggested by Jensen (1889B), and later independently confirmed by Hecke (1905), that infection occurs through the flower. With the race on wheat Maddox (1897) first demonstrated that infection occurred through the flower; his work was later confirmed by Brefeld (1903). The spores are deposited by wind on the stigmas at the time of pollination, where they germinate and produce a probasidium, which develops immediately into an infection hypha; this penetrates the style and enters the cells of the developing ovary, where a mycelium is formed. As the embryo commences to develop, hyphae pass into it and form a resting mycelium, which remains latent until such time as the grains germinate. When germination commences these hyphae grow out with the cotyledon, keeping pace with the growing-point until the formation of the inflorescence, when they penetrate to the developing ovaries. There they convert—together with the developing ovules—into a mass of mycelium, which later produces the spores.

The significance of this life-history, from the viewpoint of the farmer, is that the resting mycelium is embedded in the tissues of the grain, where it cannot be reached by fungicides; consequently the disease cannot be controlled by the usual steeping methods. Freeman and Johnson (1909) claim to have successfully combated this smut by means of Jensen's modified hot-water treatment (see p. 400).

5. *Ustilago striaeformis* (Westendorp) Niessl. (Text-fig. 7, and Plate 46, fig. 2.)

Niessl, *Hedw.*, vol. 15, p. 1, 1876.

Uredo striaeformis Westnd., *Acad. Roy. Belgique, Bull.* 18, ser. 2, p. 406, 1852.
Tilletia De Baryana Fisch. v. Waldh., in Rabh. *Fungi Eur.*, No. 1097, 1866.
T. Milii Fel., *Symb. Myc.*, vol. 1, p. 40, 1869. *T. striaeformis* Oud., *Bot. Zig.*, vol. 36, p. 440, 1878. *T. alopecurivora* Ule, *Bot. Ver. Prov. Brandenburg*, vol. 25, p. 214, 1884. *T. Brzuae* Ule, l.c. *Ustilago Poarum* McAlp., *Proc. Roy. Soc. Vic.*, n.s., vol. 7, p. 220, 1894. *U. washingtoniana* Ell. et Ev., *Bull. Torrey Cl.*, vol. 22, p. 57, 1895. *Tilletia Atrac-caespitosae* Lindr., *Soc. pro Fauna et Flora Fennica*, vol. 26, p. 15, 1904.

Sori rarely in the inflorescences, commonly in the leaves and leaf-sheaths, forming long striae often many centimetres in length, frequently converging to form irregular black areas, at first covered by the epidermis, becoming exposed and pulverulent, finally in old specimens the leaves becoming shredded; in inflorescences the sori are frequently hidden within the glumes, but eventually become pulverulent and partially exposed.

Spores globose to shortly elliptical, often somewhat angular, 10–17 × 8–12 mmm.; epispore moderately and somewhat coarsely verrucose, olive-brown, 1–1.5 mmm. thick.

Hosts:—

Dactylis glomerata L. In leaves and sheaths. Herb. No. 265.

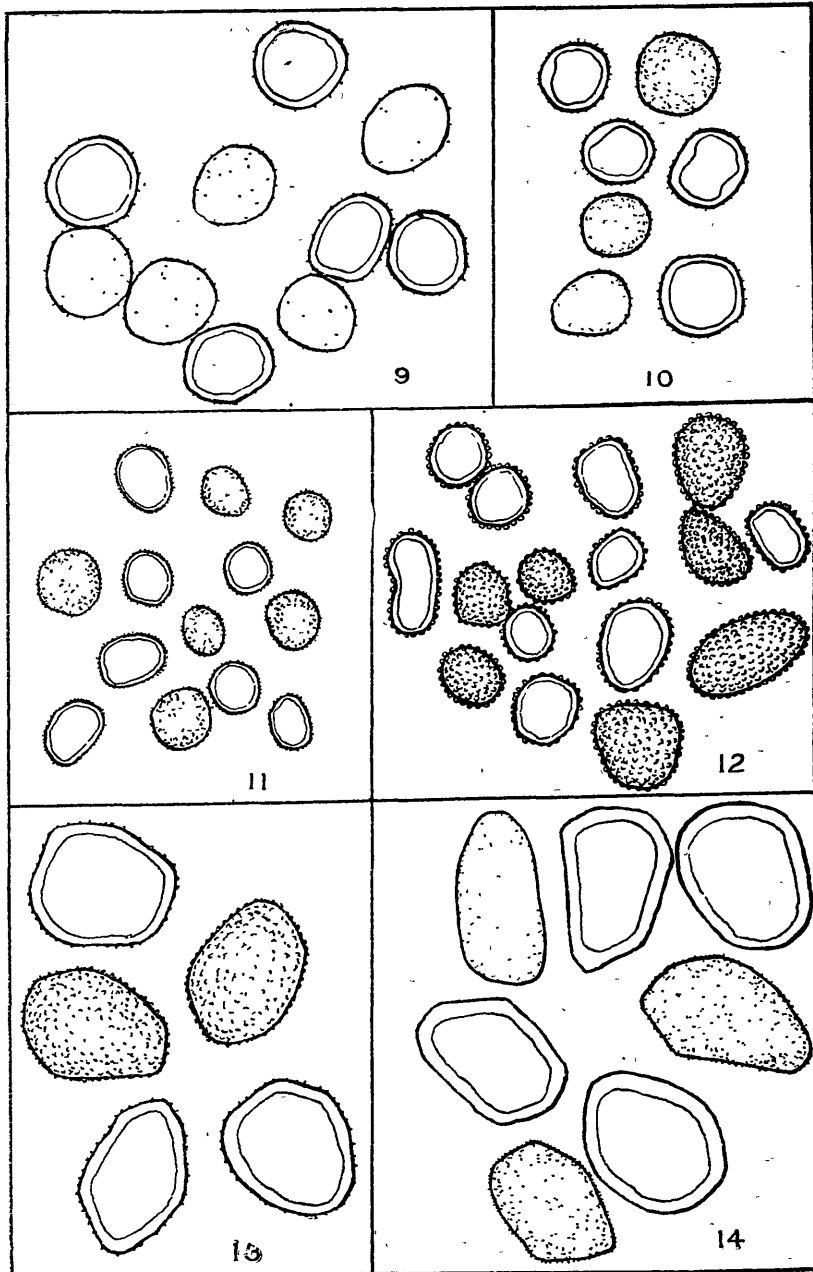
Cluny, Turakina (Wellington), 210 m., *G. H. C.* 2 Jan., 1921.

Holcus lanatus L. In leaves. Herb. No. 1276. Ettrick (Otago), 300 m., *R. B. Tenment!* 10 Feb., 1921. Karori (Wellington), 200 m., *R. Waters!* 6 Dec., 1923.

Distribution: World-wide.

This species is readily recognized by the manner in which the infected leaves become shredded, tearing occurring along the linear sori. Infected plants are usually stunted, and not infrequently killed outright.

Germination.—Osner (1916) has well illustrated the method of germination. A short probasidium is produced, and this grows directly into an infection hypha; no conidia are produced.



TEXT-FIG. 9.—*Ustilago Readeri* Syd., from *Danthonia pilosa* R. Br.
 TEXT-FIG. 10.—*Sphacelotheca Hydropiperis* (Schum.) De Bary, from *Polygonum* sp.
 TEXT-FIG. 11.—*Elateromyces niger* G. H. Cunn., from *Carex dipsacea* Berggr.
 TEXT-FIG. 12.—*E. olivaceus* (DC.) Bubak, from *Carex virgata* Sol.
 TEXT-FIG. 13.—*Cintractia sclerotiformis* (C. & M.) G. H. Cunn., from *Uncinia riparia*
 R. Br.
 TEXT-FIG. 14.—*C. Caricis* (Pers.) Magn., from *Carex ternaria* Forst. f.

All $\times 1,000$.

Infection.—According to Osner, healthy plants become infected through the flowers, as is the case with wheat or barley infected with *U. Tritici*. Following infection the hyphae remain quiescent in the seed until they germinate, when they grow out with the developing leaves and stems. These hyphae give rise to the linear sori; those that grow with the growing-point of shoots producing inflorescences infect the ovaries as they are formed. The mycelium also hibernates in the roots of perennial plants, and infects developing shoots as they emerge in the spring. Osner points out that the disease may be combated by means of the modified hot-water treatment (p. 400), but this would prevent only young plants (seedlings) from becoming infected, for, since he has shown the mycelium to be perennial in perennial plants, it follows that once such a plant has become infected nothing in the way of remedial treatment can be attempted.

The species is placed by the majority of systematists in the genus *Tilletia*, largely on account of the work of Fischer von Waldheim (1869), who claimed the method of spore-formation was that of this genus. Osner, however, has shown that spore-formation is intercalary in the spore-forming hyphae, and that this "adds weight to the contention that the organism is a species of *Ustilago* rather than of *Tilletia*." He mentions the appearance of transverse septa in the probasidium as another character in support of placing the species in *Ustilago*. This, however, is of little significance, since these septa also appear in the probasidia of *Tilletia*.

6. *Ustilago bromivora* (Tulasne) Fischer von Waldheim. (Text-fig. 8, and Plate 43, fig. 1.)

F. v. Waldh., *Bull. Soc. Nat. Mosc.*, vol. 40, p. 252, 1867.

Ustilago Carbo var. *vulgaris* d. *bromivora* Tul., *Ann. Sci. Nat.*, ser. 3, vol. 7, p. 81, 1847. *Cintractia patagonica* Cke. et Mass., *Grev.*, vol. 18, p. 34, 1889.

Sori in spikelets, often hidden within the glumes, sometimes destroying them at the base, at first bullate and somewhat compacted, becoming pulverulent, black.

Spores globose to shortly elliptical, often polygonal, 8–11 × 7–10 mmm; epispore minutely but densely verrucose, olivaceous or dark reddish-brown, 1 mmm. thick.

Hosts:—

Bromus hordeaceus L. In panicles. Herb. No. 442. Blenheim (Marlborough), 30 m., *F. Sisson!* 12 Nov., 1920.

Bromus unioloides H. B. K. Herb. No. 47. Weraroa (Wellington), 120 m., *G. H. C.* 11 Dec., 1919. Omaha, Thames Valley (Auckland), *W. G. Goodwin!* 22 Nov., 1921. Blenheim (Marlborough), 30 m., *R. Waters!* 27 Nov., 1923. Lincoln (Canterbury), 30 m., *F. E. Ward!* 3 Dec., 1923.

Distribution: World-wide.

The species is fairly abundant on prairie-grass throughout New Zealand. In many cases only occasional spikelets may be infected, but as a rule all on a panicle are attacked.

Germination.—In water the spores readily germinate, producing a small probasidium, on the apex of which is produced a single elliptical conidium. In nutrient solution, according to Brefeld (1883), a two-celled probasidium is formed; this produces conidia, which in turn develop a probasidium again producing conidia.

Infection occurs in a manner similar to *U. Avenae*. McAlpine (1910) states that treating the seed with formalin or copper-sulphate effectively controls this smut.

7. *Ustilago bullata* Berkeley. (Text-fig. 6, and Plate 42, fig. 3.)

Berk., *Fl. N.Z.*, vol. 2, p. 196, 1855.

Sori in inflorescences, at first enclosed in a lead-coloured membrane, when semi-compact, becoming exposed, when pulverulent, black.

Spores globose to shortly elliptical, $8-12 \times 7-8$ mmm.; episore closely and finely verrucose, olivaceous, 1 mmm. thick.

Host: *Agropyron scabrum* (Lab.) Beauv. In inflorescences. North Island, W. Colenso. 1849. (Type in Herb. Kew.)

Distribution: Australia.

The host is indigenous and widespread; it occurs also in Australia (Cheeseman, 1906, p. 923).

This species was described by Berkeley from material forwarded by Colenso to Kew. I have no New Zealand material in the herbarium, the above description being drawn up from Australian material kindly forwarded by Mr. C. C. Brittlebank, Plant Pathologist, Department of Agriculture, Melbourne.

Germination.—McAlpine (1910, p. 152) has successfully germinated the spores of this species. He found that in water the probasidium became three-celled, the proximal cell eventually developing into a well-developed infection hypha; no conidia were produced, but in nutrient solution a probasidium was produced, which gave rise to numerous conidia.

8. *Ustilago comburens* Ludwig. (Text-fig. 4, and Plate 41, fig. 3.)

Ludw., *Zeitschr. Pflanzenkr.*, vol. 3, p. 139, 1893.

Ustilago microspora Mass. et Rodw., *Kew Bull.*, p. 160, 1901. *U. exigua* Syd., *Ann. Myc.*, vol. 1, p. 177, 1903.

Sori in spikelets and stems, at first compact, bullate, and covered with a lead-coloured membrane, later destroying the entire panicle and becoming exposed on the rachis as a dense bronze pulverulent mass, eventually falling away, leaving the naked axis.

Spores globose to shortly elliptical, $3-5 \times 2-3$ mmm.; episore smooth, tinted olive, 0.5 mmm. or less in thickness.

Host: *Danthonia Buchananii* Hook. f. In panicles. Herb. No. 497. Dunstan Mountains (Otago), 350 m., W. D. Reid! 6 Dec., 1921.

Distribution: Australia.

The host is endemic, and is confined to the mountain regions of the South Island (Cheeseman, 1906, p. 891).

The species is characterized by the exceedingly minute size of the spores. It was first recorded on a species of *Stipa*, but McAlpine (1910, p. 154), who has examined portion of the type material, states that the host in question is a species of *Danthonia*.

I have been unable to germinate the spores.

9. *Ustilago Readeri* Sydow. (Text-figs. 9, 27, and Plate 43, figs. 2, 3.)

Syd. *in letter*; McAlp., *Smuts. Austr.*, p. 159, 1910.

Ustilago Agropyri McAlp., *Ag. Gaz. N.S.W.*, vol. 7, p. 154, 1896.

Sori in spikelets, stems, and leaves, commonly destroying the entire inflorescence. On stems and leaves forming conspicuous striae; in inflorescences, at first enclosed within the leaf-sheath, becoming exposed and appearing in the form of semi-compact masses covered with the remnants of the glumes, when greyish in colour, at length naked, pulverulent, black, finally falling away leaving the bare axis.

Spores globose to shortly elliptical, 11–14 × 8–12 mmm.; epispore minutely and closely verruculose, dark brown, 1–1.5 mmm. thick.

Hosts :—

Danthonia pilosa R. Br. In panicles, stems, and leaves. Herb. Nos. 782, 1267. Mount Hector, Tararua Mountains (Wellington), 1,600 m., *E. H. Atkinson!* 21 Dec., 1919. Plimmerton (Wellington), sea-shore, *E. H. Atkinson!* 1 Dec., 1921. Kelburn (Wellington), 120 m., *G. H. C.* 23 Nov., 1922; 4 Dec., 1923.

Danthonia semiannularis R. Br. Herb. No. 200. Whitianga (Hawke's Bay), *Shelford-Bidwell!* 18 Dec., 1920. Otane (Auckland), *H. F. Nunn!* 3 Mar., 1922. Botanical Gardens (Wellington), 80 m., *G. H. C.* 19 Jan., 1921. *J. C. Neill!* *G. H. C.* 4 Dec., 1923.

Anthoxanthum odoratum L. Herb. No. 1248. Wallaceville (Wellington), 30 m., *F. E. Ward!* 5 Dec., 1920.

Distribution : Australia.

Both species of *Danthonia* are indigenous and abundant throughout; they occur also in Australia (Cheeseman, 1906, p. 890). This smut has hitherto been recorded only on *Danthonia*, *Anthoxanthum* being an additional host.

This is the most abundant of all species of the Ustilaginaceae occurring in New Zealand, and appears season after season in the same locality. *U. Agropyri* McAlp. was based on a mixture of material of *Agropyron* and *Danthonia*, which was afterwards separated out.

Germination.—In water germination occurs within twenty-four hours, probasidia bearing abundant conidia being produced; frequently the conidia are borne on short sterigmata. In nutrient solution the conidia produce secondary conidia by budding.

2. ELATEROMYCES Bubak.

Bubak, *Archiv. pro Prirrodovedecky Vyzkum Cech*, [dil. 15, C. 3, p. 32, 1912.

Sori semi-compact, dark-coloured, usually confined to the inflorescences.

Spores single, globose to angular, smooth or verruculose, mixed with numerous coloured filaments (elaters) formed of numerous hyphae arranged in parallel fashion; germination by means of an elliptical probasidium, which becomes detached as a conidium.

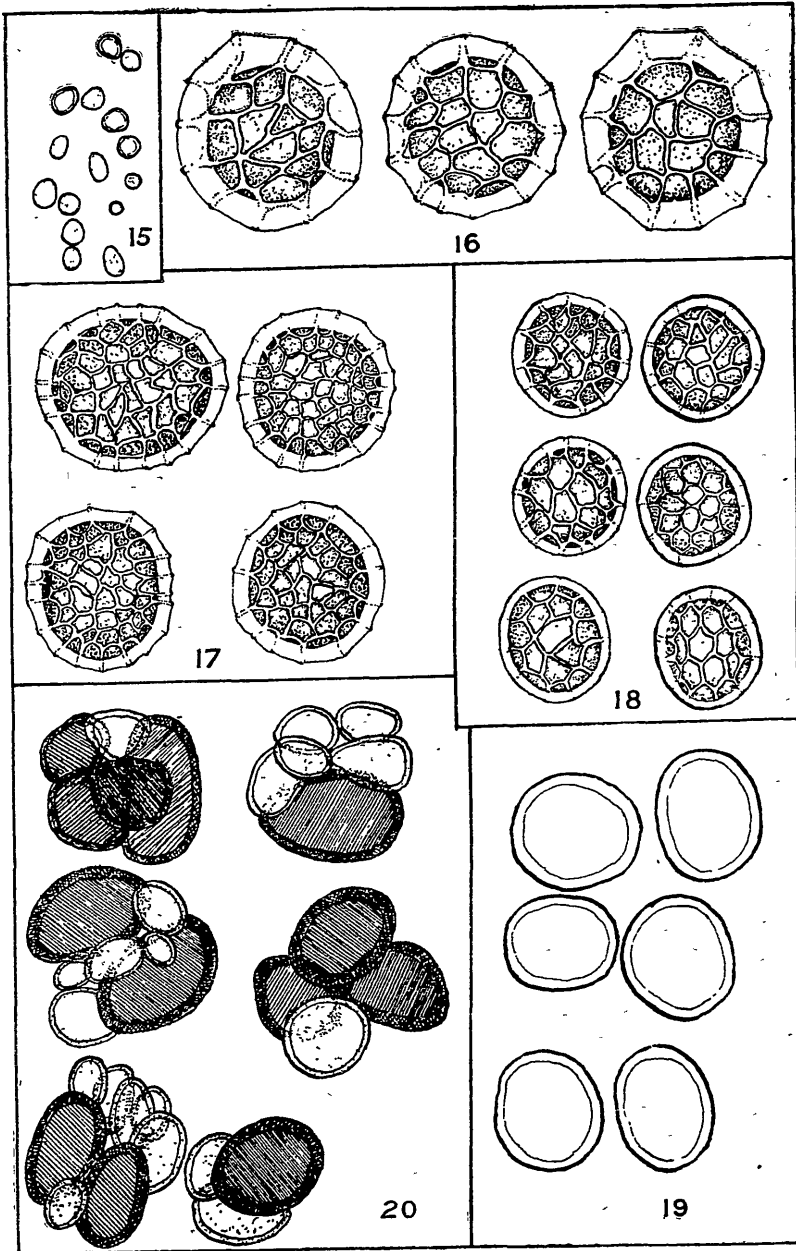
Distribution : World-wide.

Of the three New Zealand species, two are endemic, and the third is indigenous, being widely distributed elsewhere.

This genus was erected by Bubak on account of the presence in the sori of numerous peculiar filaments, or "elaters," as he has termed them. These elaters consist of numerous coloured hyphae arranged in a parallel manner. The hyphae are septate, and are 5–8 mmm. in thickness; the elaters may attain a length of 22 mm., but usually they are much shorter than this, being on an average 8–10 mm. long; in thickness they vary from 40 to 120 mmm. or even more. They are so characteristic that I have no hesitation in following Bubak and placing those New Zealand species possessing these structures in this genus. Their function is unknown, but they are supposed to assist in spore-distribution.

The method of germination is discussed under *E. olivaceus* and *E. niger*.

The three New Zealand species are confined to the Cyperaceae, two being parasitic on *Carex*, the third on *Gahnia*. Bubak records another species in addition to *E. olivaceus*—*E. Treubii* (Solms.) Bubak (= *Ustilago*



TEXT-FIG. 15.—*Cintractia Spinifexis* (Ludw.) McAlp., from *Spinifex hirsutus* Lab.

TEXT-FIG. 16.—*Tilletia Holci* (Westnd.) Rostr., from *Holcus lanatus* L.

TEXT-FIG. 17.—*T. decipiens* (Pers.) Koern, from *Agrostis vulgaris* With.

TEXT-FIG. 18.—*T. Tritici* Wint., from *Triticum vulgare* Vill.

TEXT-FIG. 19.—*T. levis* Kuehn, from *Triticum vulgare* Vill.

TEXT-FIG. 20.—*Urocystis Anemones* Wint., from *Ranunculus insignis* Hook. f.

All $\times 1,000$.

Treubii Solms.), on *Polygonum cinense* from Java; but his combination cannot be accepted, for *U. Treubii* is a synonym of *U. emodensis* Berk., according to Masee (1899). I cannot say whether it should be placed in *Elateromyces*, for I have not examined specimens.

KEY TO SPECIES.

Sori olivaceous	3. <i>E. olivaceus</i> .
Sori black, or nearly so.	
On <i>Gahnia</i>	1. <i>E. endotrichus</i> .
On <i>Carex</i>	2. <i>E. niger</i> .

1. *Elateromyces endotrichus* (Berkeley) n. comb.

Ustilago endotricha Berk., *Fl. N.Z.*, vol. 2, p. 196, 1855.

Sori in inflorescences, elliptical, black, pulverulent, intermixed with numerous long coloured elaters.

Spores globose, 5-7 mmm. diam., episporium minutely and closely verruculose, blackish olive.

Host: *Gahnia* sp. In inflorescences. North Island, *Sinclair*. (Type in Herb. Kew.)

Distribution: New Zealand.

Only the single collection now at Kew (as *Ustilago*) has been made of this species. It is closely related to the following, which may possibly turn out to be the same; I have separated *E. niger* principally on account of the larger spores, and especially the very numerous black elaters.

E. endotrichus has been recorded from Ceylon, but Petch (1912)—to whose paper I am indebted for the description of the spores, given above—states the Ceylon species is *E. (Ustilago) olivaceus*.

The method of germination is unknown.

2. *Elateromyces niger* n. sp. (Text-figs. 11, 28, and Plate 44, fig. 1.)

Sori in occasional ovaries, at first compact and partially concealed within the perigynium, becoming exposed when semi-pulverulent, black, elliptical, and up to 6 mm. in length; intermixed with very numerous conspicuous elaters, black in mass, blackish-olive individually, which may attain a length of 15 mm. but are commonly less, averaging 10 mm.

Spores globose to shortly elliptical, 6-9 × 5-7 mmm.; episporium minutely and moderately verruculose, dark olive, 0.75 mmm. thick.

Host: *Carex dipsacea* Berggr. In panicles. Herb. No. 311. Pen-carrow (Wellington), sea-coast, *E. H. Atkinson!* 10 Feb., 1921. (Type.)

The host is an endemic species, occurring throughout the lowland areas of both Islands (Cheeseman, 1906, p. 822).

This is separated from the following species on account of the smaller and more regular spores, black colour of the sori, elaters, and spores, and the conspicuous elaters. These latter are so numerous as to give the sori a woolly appearance, as if a small tuft of hair had been caught and held in the position occupied by the sorus.

Germination.—In water, after three days, a few spores germinated after the material had been kept in the herbarium for twenty-one months. The method of germination is similar to *E. olivaceus*, a small probasidium being produced. This is elliptical in shape, and about the same length as the spore. Shortly after its formation it becomes detached and functions as a conidium. The spores did not germinate when placed in nutrient solution (soil extract).



FIG. 1.—*Ustilago levis* Magn., on *Avena sativa* L.

FIG. 2.—*U. Avenae* Jens., on *Arrhenatherum elatius* (L.) Beauv. Healthy plant on left, smutted plants on right.

FIG. 3.—*U. comburens* Ludw., on *Danthonia Buchanani* Hook. f. Diseased plants in centre: note how completely the inflorescences are destroyed.

Photos by H. Drake. All natural size.



FIG. 1.—*Ustilago Tritici* Jens., on *Triticum vulgare* Vill. Note (in centre) that inflorescence is completely destroyed before it is free from the shot-blade (the latter dissected away to show apical portion of the smutted inflorescence).

FIG. 2.—*U. Jensenii* Rostr., on *Hordeum vulgare* L. Note compact nature of sori, and fact that the inflorescence is destroyed ere it has emerged from the shot-blade (on left).

FIG. 3.—*U. bullata* Berk., on *Agropyron scabrum* Beauv. Normal inflorescence on right. Note bullate nature of the sori.

Photos by H. Drake. All $\frac{3}{4}$ natural size.



FIG. 1.—*Ustilago bromivora* (Tul.) F. v. Waldh., on *Bromus unioloides* H. B. K. Normal inflorescence on the right.
FIG. 2.—*U. Readeri* Syd., on *Anthoxanthum odoratum* L. Normal inflorescence in the centre.
FIG. 3.—*U. Readeri* Syd., on *Danthonia pilosa* R. Br.

Photos by H. Drake. All $\frac{3}{4}$ natural size.



FIG. 1.—*Elatерomyces niger* G. H. Cunn., on *Carex dipsacea* Berggr. Reduced to $\frac{1}{4}$.
 FIG. 2.—*Cintractia Caricis* (Pers.) Magn., on *Carex* spp. Infected specimen of *Carex Gaudichaudiana* Kunth. on left: note the almost spherical nature of the sori. Infected specimens of *Carex ternaria* Forst. f. on the right: note the fusoid nature of the sori, an unusual condition possibly meriting a varietal name. $\frac{2}{3}$ natural size.

Photos by H. Drake.



FIG. 1.—*Cintractia Spinificis* (Ludw.) McAlp., on male (left) and female (right) inflorescences of *Spinefex hirsutus* Lab.

FIG. 2.—*Urocystis Anemones* Wint., on leaf of *Ranunculus insignis* Hook. f.

Photos by H. Drake. Both reduced to $\frac{1}{3}$.



FIG. 1.—*Sorosporium Neillii* G. H. Cunn., in inflorescences of *Scirpus nodosus* Rottb. Slightly infected specimens in the centre.
FIG. 2.—*Ustilago striaeformis* (Westnd.) Niessl, in leaves of *Holcus lanatus* L. Note linear arrangement of sori.

Photos by H. Drake. All natural size.

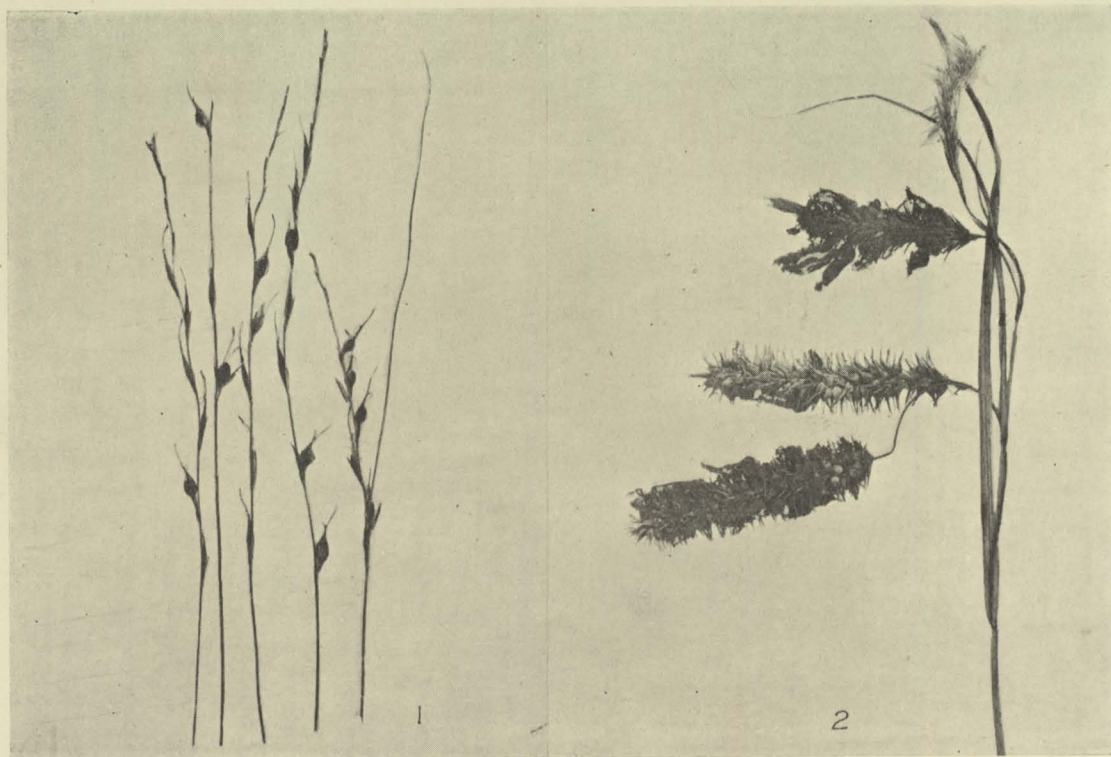
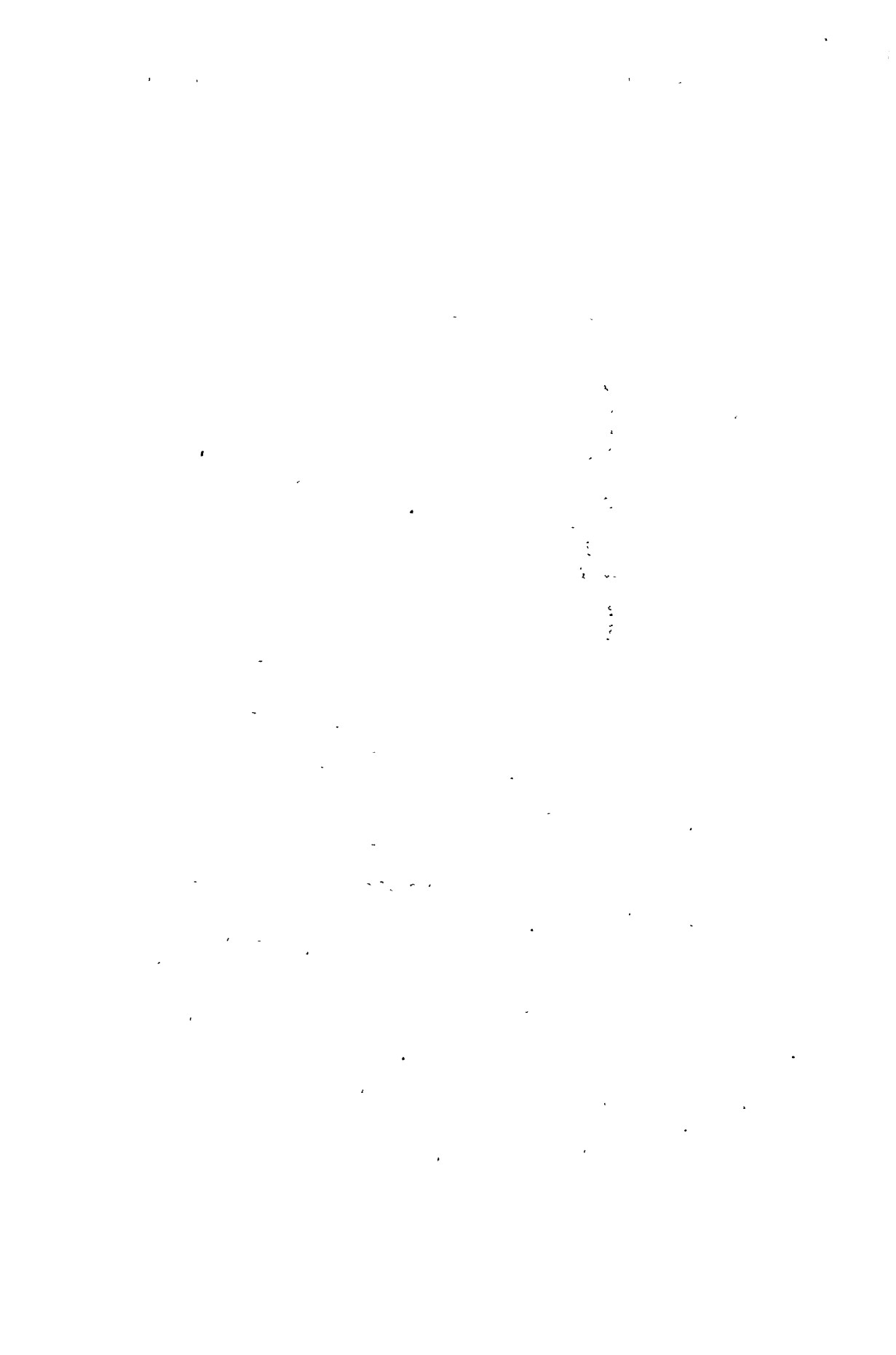


FIG. 1.—*Cintractia sclerotiformis* (C. & M.) G. H. Cunn., in the ovaries of *Uncinia riparia* R. Br. $\frac{3}{4}$ natural size.
 FIG. 2.—*Elateromyces olivaceus* (DC.) Bubak, on *Carex dipsacea* Berggr. Specimen shows abnormal development of elaters. $\frac{3}{4}$ natural size.

Photos by H. Drake.



[*Latin diagnosis.*]

Elateromyces niger sp. nov.

Soris ad ovaria destruentibus, semi-pulverulentis, atris, ellipticis, ad 6 mm. longis. Fibra intermixto, copioso, atro, 8–15 mm. longo.

Sporis globosulis v. breviter ellipticis, 6–9 × 5–7 mmm.; episporio subtilissime verruculoso, olivaceo, 0.75 mmm. crasso.

Hab.: In ovariiis *Carex dipsaceae* Berggr. Pencarrow (Wellington, N.Z.), sea-coast, *E. H. Atkinson!*

3. *Elateromyces olivaceus* (De Candolle) Bubak. (Text-fig. 29, and Plate 47, fig. 2.)

Bubak, *Archiv pro Prirod. Vyzk. Cech*, dil. 15, C. 3, p. 33, 1912.

Uredo olivacea DC., *Fl. Fr.*, vol. 6, p. 78, 1815. *Ustilago olivacea* (DC.) Tul., *Ann. Sci. Nat.*, ser. 3, vol. 7, p. 88, 1847. *U. caricicola* Tracy and Earle, *Bull. Torrey Cl.*, vol. 26, p. 493, 1899. *U. catenata* Ludw., *Zeitschr. Pflanzenkr.*, vol. 3, p. 139, 1893.

Sori in occasional ovaries, at first compact and partially concealed within the perigynium, becoming pulverulent, olive-brown, up to 5 mm. long, intermixed with numerous conspicuous yellowish elaters, which attain a length of 22 mm. but are usually much less, averaging 5–8 mm.

Spores globose to shortly elliptical, frequently irregular, often arranged in chains, 7–14 × 4–7 mmm.; episporium closely and finely verrucose, pallid olive, 0.5–1 mmm. thick.

Hosts:—

Carex virgata Sol. In inflorescences. Herb. Nos. 499, 1249. Pencarrow (Wellington), sea-coast, *E. H. Atkinson!* 10 Feb., 1921.

Carex dipsacea Berggr. In inflorescences. Herb. No. 1250. Tapuwai, Hokianga (Auckland), 12 m., *E. H. Atkinson!* 18 Dec., 1923.

Distribution: World-wide.

Both hosts are endemic, and are widely distributed throughout the lowland areas of both Islands (Cheeseman, 1906, pp. 814–822).

The olive colour of the sori, and especially the straw colour of the elaters, together with the larger and more irregular spores, separate this from the two preceding species. The markings on the episporium are also characteristic, for they are more of the nature of warts, appearing flattened and closely crowded together.

Ustilago catenata Ludw. was based on a specimen of a host supposed to be a species of *Cyperus*, but McAlpine (1910, p. 158) states that he had portion of the type examined by Mr. L. Rodway, Government Botanist, Hobart, who pronounced it to be *Carex pseudo-cyperus* L.

Germination.—In water this commences within a few hours, a fine probasidium being produced. This elongates but does not become septate, and is then detached as a conidium. In the case of the larger spores a second conidium may be produced, depending on the quantity of the protoplasm contained within the spore. In nutrient solution, according to Brefeld (1883), budding occurs to a slight extent. When this process of germination is compared with such a species as *Ustilago Avenae*, in which a definite septate probasidium is produced, it appears rather a stretch of imagination to term the germination product a probasidium; rather should it be considered a conidium, for it behaves in a similar manner, and is about the same size and shape.

3. CINTRACTIA CORNU.

Cornu, *Ann. Sci. Nat.*, ser 4, vol. 15, p. 279, 1883.

Anthracoidea Bref., *Unters. Gesammt. Myk.*, vol. 12, p. 144, 1895.

Sori in the form of a firmly compacted black spore-mass, usually surrounding a central columella of host-tissue, situated in various parts of the host, usually in the inflorescence.

Spores single, globose or more commonly angular, episporic coloured, smooth or verruculose, germination as in *Ustilago* or slightly modified.

Distribution: World-wide.

Of the three species that have been collected in New Zealand, one is endemic, the others indigenous. Eleven species are recorded by McAlpine (1906) for Australia, and thirteen for North America by Clinton (1906).

Members of the genus occur on the families Gramineae, Cyperaceae, and Juncaceae.

The genus is characterized by the (usually) compact sori, central columella of host-tissue, and centripetal manner of spore-formation.

Germination occurs as in *Ustilago*, but in one species, *C. Caricis*, the apical cell of the probasidium becomes longitudinally septate, each cell producing a conidium. On this character Brefeld erected the genus *Anthracoidea*.

Spore-formation has been studied by Cornu (*l.c.*, p. 269). In the position of the future sorus the mycelium penetrates into and becomes aggregated around a central columella of host-tissue; in this the mycelium persists. On the periphery of this columella the sporiferous hyphae develop; they soon become gelatinized, when the whole mass appears as a gelatinous cylinder applied to the central columella. These hyphae become septate, and the spores commence their development within the lumen of the cells thus formed. Development proceeds from the periphery of the mass inwards, so that mature spores appear first at the periphery. A section through a sorus shows mature spores on the outside, and increasingly immature spores as the columella is approached, until near this axis the spores are seen to be little more than gelatinous masses. As the spores near maturity the hyaline envelopes surrounding them become absorbed; the spores become exposed and assume a dark colour, but remain firmly agglutinated together, probably adhering by remnants of the gelatinous hyphae, for when placed in water the sori readily break up. In several species all the sporogenous hyphae do not develop spores, but many remain sterile, and may be seen projecting between rows of the spores.

KEY TO THE SPECIES.

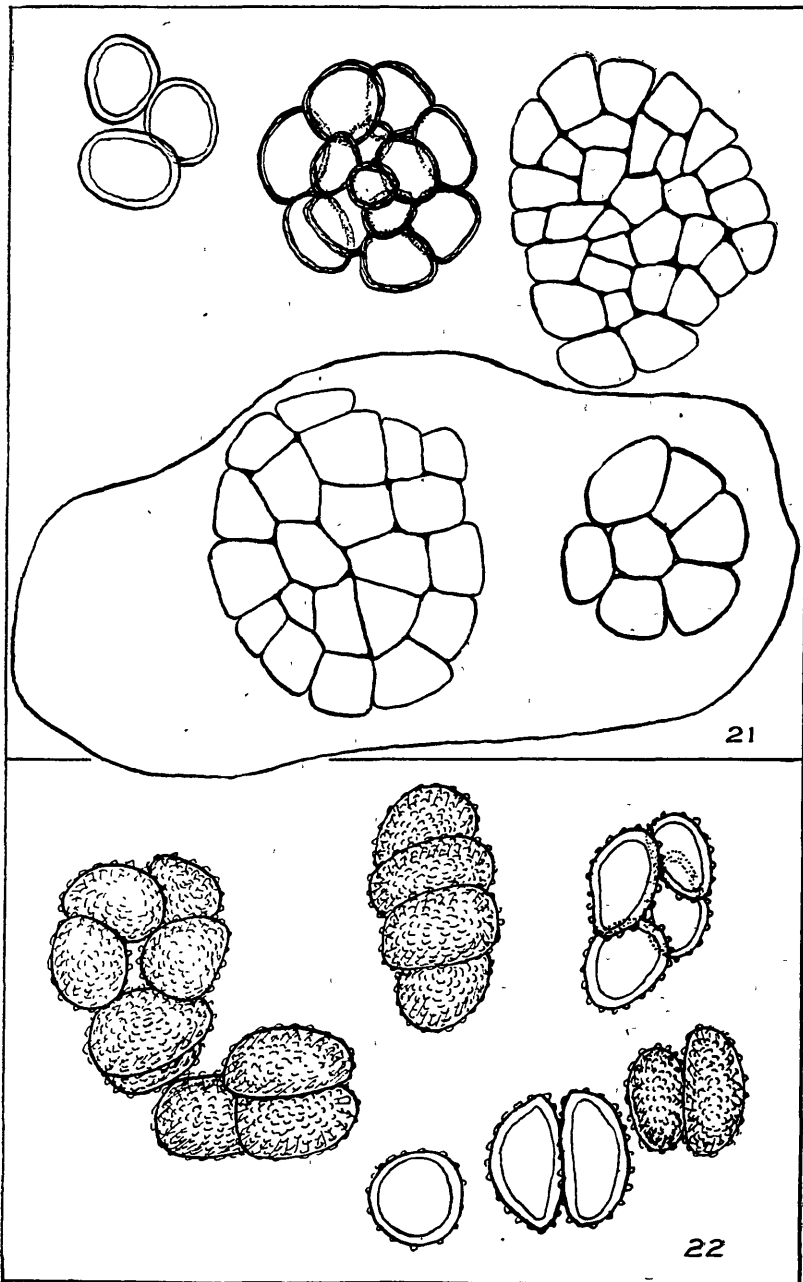
Spores minute, under 6 mmm. long	1. <i>C. Spinificis</i> .
Spores large, over 10 mmm.			
On <i>Carex</i>	2. <i>C. Caricis</i> .
On <i>Ucinia</i>	3. <i>C. sclerotiformis</i> .

1. *Cintractia Spinificis* (Ludwig) McAlpine. (Text-fig. 15, and Plate 45, fig. 1.)

McAlp., *Smuts Austr.*, p. 174, 1910.

Ustilago Spinificis Lüd., *Zeitschr. Pflanzenker.*, vol. 3, p. 138, 1893.

Sori in spikelets, frequently concealed within the glumes, destroying the ovaries and forming in their stead a compact cylindrical olive-black spore-mass, which may attain a length of 7 mm.



TEXT-FIG. 21.—*Sorosporium solidum* (Berk.) McAlp., from *Schoenus Carsei* Cheesem.

TEXT-FIG. 22.—*S. Neillii* G. H. Cunn., from *Scirpus nodosus* Rottb.

× 1,000.

Spores globose to shortly elliptical, $3-5 \times 2-3$ mm.; episporium very delicately but distinctly verruculose, pallid olive, with a lighter-coloured zone on one side, 0.5 mm. thick.

Host: *Spinifex hirsutus* Lab. In male and female spikelets. Herb. Nos. 309, 1259. Pencarrow (Wellington), sea-coast, *E. H. Atkinson!* 10 Feb., 1921.

Distribution: Australia.

The host is indigenous and widely distributed along the coast: it occurs also in Australia and New Caledonia (Cheeseman, 1906, p. 850).

Osborn (1922) has recorded the pathological changes this species effects in the host. The inflorescences, both male and female, become considerably modified, the anthers become sterile, and the filaments do not elongate, and the various organs are modified in number, structure, and position.

Germination, according to McAlpine (*l.c.*, p. 174), does not occur in water, but takes place readily in nutrient solution. A four-celled probasidium is produced, and on this are borne the conidia. These multiply by budding, but before the solution is exhausted the conidia may produce hyphae which, if they reach the air, form abundant aerial conidia.

I have failed to germinate the spores either in water or nutrient solution, but the material was probably too old, for it has been kept in the herbarium for twenty-one months.

2. *Cintractia Caricis* (Persoon) Magnus. (Text-fig. 14, and Plate 44, fig. 2.)

Magn., *Abh. Bot. Ver. Prov. Brand.*, vol. 37, p. 79, 1896.

Uredo Caricis Pers., *Syn. Fung.*, p. 225, 1801. *Ustilago Caricis* Ung., *Enstl. Bodens.*, p. 211, 1836. *U. urceolorum* Tul., *Ann. Sci. Nat.*, ser. 3, vol. 7, p. 86, 1847. *U. Scirpi* Kuehn. *Hedw.*, vol. 12, p. 150, 1873. *Anthracoidea Caricis* Bref., *Unters. Gesamt. Myk.*, vol. 12, p. 144, 1895.

Sori in occasional ovaries, at first partially concealed within the perigynium, becoming exposed when subglobose or elliptical, 3-7 mm. long, at first covered by an evanescent white membrane of semi-gelatinized hyphae which later falls away, exposing the black, firmly agglutinated spore-mass.

Spores irregular, subglobose or more frequently polygonal, $16-27 \times 9-15$ mm.; episporium minutely and densely verruculose, frequently obscurely pitted, sepia-coloured, 1.5-2 mm. thick.

Hosts:—

Carex Gaudichaudiana Kunth. In inflorescences. Herb. No. 1261.

Lake Wakatipu (Otago), 340 m., *L. Cockayne!* 1909.

Carex subdola Boott. Herb. No. 1263. Lake Wakatipu (Otago), *L. Cockayne!* 1909.

Carex ternaria Forst. f. Herb. Nos. 295, 1260, 1262, 1264. Peel Forest (Canterbury), 120 m., *H. H. Allan!* 5 April, 1919. Tasman (Nelson), 10 m., *G. H. C.* 4 Feb., 1920. Seatoun (Wellington), sea-shore, *E. H. Atkinson!* *G. H. C.* 25 Jan., 1921. *J. C. Neill!* *G. H. C.* 6 Dec., 1923.

Carex sp. Herb. No. 45. Southern Alps, Canterbury, *T. Kirk!* 1883.

Distribution: World-wide.

Of the hosts, two of the named species are endemic; the third, *C. Gaudichaudiana*, is indigenous, occurring also in Australia (Cheeseman, 1906, pp. 818-20).

In certain specimens the sori project beyond the perigynium for several millimetres, giving to infected plants a very conspicuous appearance. Sori may be confined to occasional ovaries, or every ovary in the inflorescence may be infected.

Germination.—In water a probasidium is produced which becomes septate in the normal manner save that in addition the terminal cell becomes longitudinally septate. From each of the two cells thus formed a conidium is produced, as well as numerous lateral conidia. The conidia produce infection hyphae in the normal manner. It is claimed that germination does not occur until the spores are twelve months old.

3. *Cintractia sclerotiformis* (Cooke and Massee) n. comb. (Text-fig. 13, and Plate 47, fig. 1.)

Ustilago sclerotiformis Cke. et Mass., *Grev.*, vol. 17, p. 8, 1888.

Sori in occasional ovaries, sometimes in all, at first partially concealed within the perigynium, becoming exposed when compact, black, elliptical, up to 6 mm. long.

Spores subglobose to elliptical, commonly polygonal, 16–22 × 11–18 mmm.; epispor closely and minutely verruculose, dark brown, 1.5 mmm. thick.

Hosts :—

Uncinia caespitosa Boott. In inflorescences. Taheraiti, *T. Kirk.*
(Type in Herb. Kew.)

Uncinia leptostachya Raoul. Herb. No. 20. Peel Forest (Canterbury),
120 m., *H. H. Allan!* Feb., 1920.

Uncinia riparia R. Br. Herb. No. 1257. Peel Forest (Canterbury),
120 m., *H. H. Allan!* 5 April, 1919. Mount Peel (Canterbury),
700 m., *H. H. Allan!* 6 Mar., 1921. Botanical Gardens, Wellington,
80 m., *E. H. Atkinson!* *G. H. C.* 19 Jan., 1921. *J. C. Neill!*
G. H. C. 4 Dec., 1923.

Distribution: New Zealand.

The first two hosts are endemic, the third occurs also in Australia; all are widely distributed throughout New Zealand (Cheeseman, 1906, pp. 801–3).

This is a true *Cintractia*, for a transverse section shows that it possesses all the characters of this genus. The species is closely related to the preceding, but is separated by the comparatively broader and smaller spores, more conspicuous markings, and thinner nature of the epispor.

I have been unable to germinate the spores.

4. *SPHACELOTHECA* de Bary.

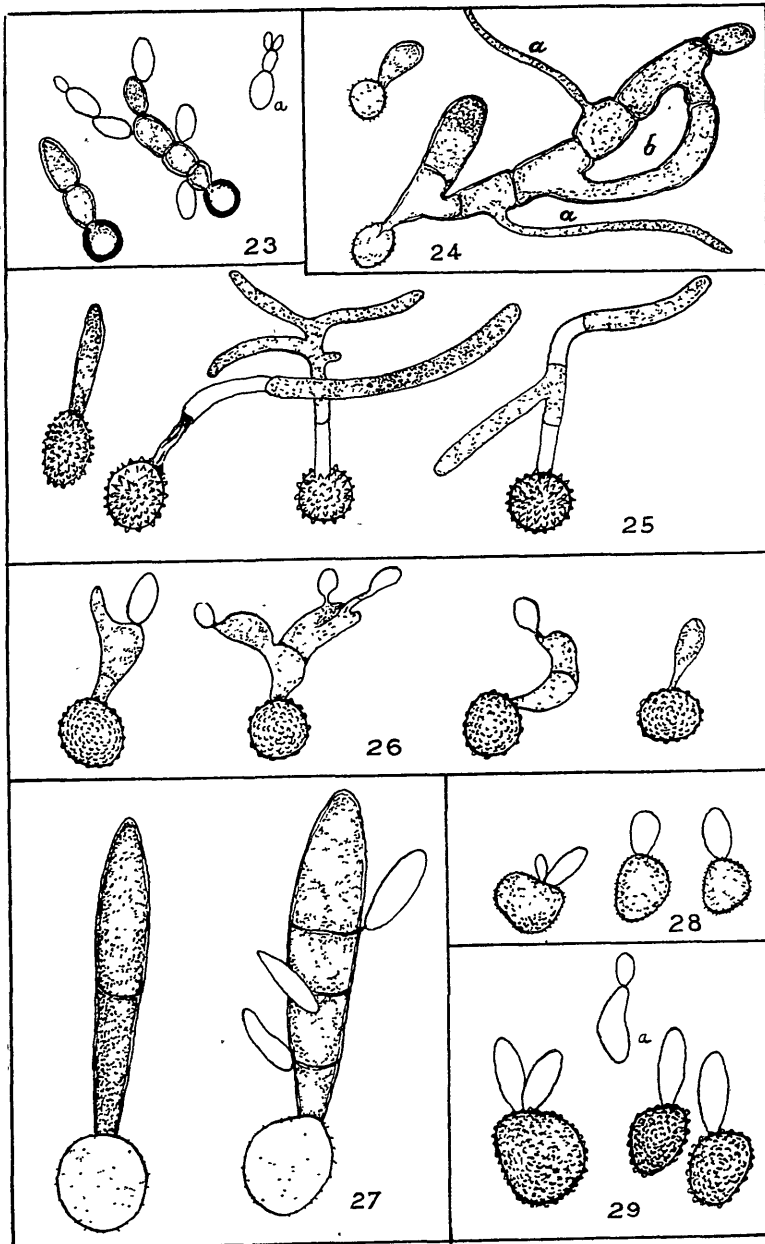
De By., *Verg. Morph. Biol. Pilze*, p. 187, 1884.

Endothlaspis Sor., *Rev. Myc.*, vol. 12, p. 4, 1890.

Sori in the form of a pulverulent spore-mass, surrounding a central columella of host and fungous tissues, enclosed within a more or less permanent false membrane of fungous tissue, becoming exposed either by apical or irregular rupture of this membrane.

Spores single, epispor coloured, smooth or variously sculptured; germination as in *Ustilago*.

Distribution: World-wide.



SPORES GERMINATING IN WATER: SHOWING THE DIFFERENT METHODS.

TEXT-FIG. 23.—*Ustilago levis* Magn.: a, conidium producing secondary conidia by budding.

TEXT-FIG. 24.—*U. Tritici* Jens.: a, infection hyphae produced from cells of the probasidium; b, conjugating hyphae.

TEXT-FIG. 25.—*U. striaeformis* (Westnd.) Niessl (modified from Osner).

TEXT-FIG. 26.—*U. bromivora* (Tul.) F. v. Waldh. Two-celled probasidia producing conidia.

TEXT-FIG. 27.—*U. Readeri* Syd.

TEXT-FIG. 28.—*Elateromyces niger* G. H. Cunn. Spores producing conidia, probasidia being absent.

TEXT-FIG. 29.—*E. olivaceus* (DC.) Bubak. Spores producing conidia.

All $\times 1,000$.

Only a single indigenous species has as yet been collected in New Zealand. In North America Clinton (1906) records sixteen species, all, with one exception, confined to the Gramineae; the exception occurs on the Polygonaceae.

The method of development, structure, and nature of the columella and enclosing membrane—structures on which the genus is separated from *Ustilago*—are dealt with under the species.

Spore-formation.—This is similar to *Ustilago* save that the process is confined to a definite region of the sporiferous hyphae; the columella and receptacle, although formed from potentially sporogenous tissue, remaining sterile.

The genus is separated from *Ustilago* on account of the presence of a definite false membrane of fungous tissue surrounding the sorus. This membrane is somewhat urn-shaped, and encloses a cavity in which are situated the pulverulent mass of spores arranged around a central columella of combined host and fungous tissue.

1. *Sphacelotheca Hydropiperis* (Schumacher) de Bary. (Text-fig. 10.)
Polygonaceae.

Uredo Hydropiperis Schum., *Enum. Pl. Saell.*, vol. 2, p. 234, 1803. *Ustilago Candollei* Tul., *Ann. Sci. Nat.*, ser. 3, vol. 7, p. 93, 1847. *U. hydropiperis* Schroet., *Beitr. Biol. Pfl.*, vol. 2, p. 355, 1877.

Sori in the ovaries, up to 5 mm. long, consisting of an outer urn-shaped receptacle composed of fungous cells, opening at the apex by a reflexed margin, enclosing the dark-purple spore-mass, which in turn surrounds the more or less evident columella.

Spores subglobose to shortly elliptical, 10–17 × 11–13 mmm.; episore minutely and closely verruculose, dark purple, 1 mmm. thick.

Hosts:—

Polygonum serrulatum Lag. (= *P. prostratum* A. Rich.). In inflorescences. North Island, W. Colenso.

Polygonum sp. Herb. No. 1272. Kaitaia, North Auckland, E. H. Atkinson! 16 Dec., 1923.

Distribution: World-wide.

The former host is indigenous and widespread; it occurs also in Australia, Europe, Asia, &c. (Cheeseman, 1906, p. 590).

The species was first recorded by Berkeley (1855) for New Zealand from specimens collected by Colenso; he determined the species as *Ustilago Candollei* var. *a* Tul.

Infection occurs in the seedling stage, according to De Bary (1887), the hyphae growing with the growing-point until the ovaries are formed. When the ovule is formed the hyphae pass into it through the funiculus, completely replacing it and forming in its stead a compact hyphal mass. This mass later becomes differentiated into an outer sterile layer enclosing a central columella; between these two structures the spores are formed. The whole of this tissue is at first enclosed within the ovary-wall, but, owing to continuous development of these structures by formation of fresh hyphae at their base, the spore-receptacle with its enclosed structures soon outgrows and ruptures the ovary, which may sometimes fall away.

Germination is effected by the production of a probasidium, which produces lateral conidia, as does *Ustilago Avenae*.

5. TILLETIA Tulasne.

Tul., *Ann. Sci. Nat.*, ser. 3, vol. 7, p. 112, 1847.

Sori in the form of a black spore-mass in various parts of the host, usually in the ovaries, frequently fetid, pulverulent or not.

Spores single, epispore coloured, smooth or variously sculptured; germination by means of a short probasidium producing a terminal whorl of elongate conidia, which often give rise to secondary conidia on germination.

Distribution: World-wide.

The four species that have been collected in New Zealand are all introduced. McAlpine (1906) records five species for Australia; Clinton (1906) twenty-two for North America.

The genus is separated from *Ustilago* mainly on account of the methods of germination and spore-formation. When these characters are unknown the species may be placed in either genus, but the large-spored forms are usually considered to belong to *Tilletia*.

Spore-formation.—According to Fischer von Waldheim (1869), prior to spore-formation the sporogenous hyphae produce in succession numerous lateral pyriform branches. These increase in diameter at their apices, finally appearing as globular bodies surrounded by a gelatinous membrane and attached to the main hyphae by slender stalks. Within the gelatinous walls the spores develop, and as they approach maturity the gelatinous membrane gradually becomes absorbed. Thus in this genus spore-formation is acrogenous, differing in this respect from *Ustilago*, in which the method of spore-formation is intercalary.

The genus is confined to the Gramineae, although it has been recorded (doubtfully) as occurring on *Sphagnum* (Musci).

KEY TO SPECIES.				
Spores smooth 2. <i>T. levis</i> .
Spores reticulate.				
On <i>Agrostis</i> 1. <i>T. decipiens</i> .
On <i>Holcus</i> 4. <i>T. Holci</i> .
On <i>Triticum</i> 3. <i>T. Tritici</i> .

1. *Tilletia decipiens* (Persoon) Koernicke. (Text-fig. 17.) Gramineae.

Koern., in Wint. *Die Pilze*, vol. 1, p. 110, 1884.

Uredo segetum var. *decipiens* Pers., *Syn. Fung.*, p. 225, 1801. *Tilletia sphaerococca* F. v. Waldh., *Bull. Soc. Nat. Mosc.*, vol. 1, p. 14, 1867.

Sori in ovaries, concealed within the glumes, black, compact, fetid.

Spores globose or subglobose, 24–30 × 22–26 mmm.; epispore covered with a network of raised reticulations 2.5 mmm. high, surrounding polygonal depressions 3–5 mmm. wide, pallid brown.

Host: *Agrostis vulgaris* With. In inflorescences. Herb. No. 176. Wyndham (Southland) *E. Bruce Levy!* 1 Mar., 1920. Khandallah (Wellington), 200 m., *E. Bruce Levy!* 5 April, 1922. Tapanui (Otago), *J. C. Neill!* *G. H. C.* 2 Feb., 1924.

Distribution: Europe.

The host is an introduced species, abundant throughout. The fungus exerts a stunting effect on the host; its presence may be noted on this account and also because infected plants are of a more pallid colour than the normal. Fresh specimens are slightly fetid when crushed.

The mycelium perennates in the perennial parts of the host.

Germination.—In nutrient solution a probasidium bearing a terminal whorl of fusiform septate conidia is produced. The conidia may produce sickle-shaped secondary conidia whilst still attached to the probasidium.

2. *Tilletia levis* Kuehn. (Text-figs. 19, 30.)

Kuehn, *Hedw.*, vol. 12, p. 152, 1873.

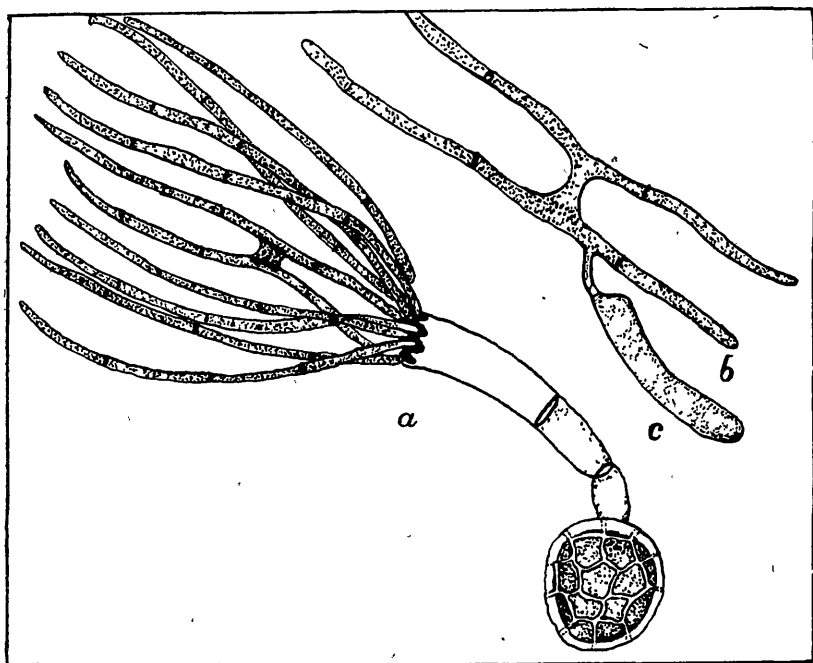
Ustilago foetens Berk. et Curt., *Grev.*, vol. 3, p. 59, 1874. *Tilletia foetens* (B. & C.) Trel., *Parasit. Fung. Wis.*, p. 35, 1884.

Sori in ovaries, concealed within the glumes, ovate or elliptical, 5–8 mm. long, dark brown, fetid.

Spores globose to shortly elliptical, $17\text{--}25 \times 15\text{--}17$ mmm.; epispore smooth, pallid brown, 1.5–2 mmm. thick.

Host: *Triticum vulgare* Vill. In inflorescences. Herb. Nos. 401, 1266. Ashburton (Canterbury), 30 m., *H. H. Allan!* 21 March, 1921. Lincoln (Canterbury), 80 m., *F. E. Ward!* 27 Jan., 1922.

Distribution: World-wide.



TEXT-FIG. 30.—*Tilletia levis* Kuehn. *a*, septate probasidium with a terminal whorl of conidia; *b*, conjugating conidia, producing secondary conidia, *c*.

This, together with the following species, is known as “stinking-smut” of wheat, on account of the fetid smell the spore-mass emits when crushed.

The stinking-smuts are the two most important smuts attacking this host, for not only do they destroy the inflorescences, but their presence, even in small quantities, renders the grain unfit for milling, partly on account of the musty smell such grain possesses, partly because the flour is supposed to have a toxic effect when consumed. It is further claimed that if such grain be fed to poultry disastrous results may follow. For example, McAlpine (1910, p. 81) records the effect upon the egg-laying propensities of 650 fowls fed with smutted wheat: the egg-yield dropped from a daily average of 100 to 16. Other authors record detrimental effects to stock, such as staggering, inflammation, and even occasional abortion.

On the other hand, some workers consider that these reports are much exaggerated, and record experiments in which no detrimental results followed. Baudys (1921) experimented with animals, and also upon himself, without any ill effects. Poultry, mice, and rabbits were fed on smutted grain (*T. Tritici*) and actually increased in weight; he himself was not affected in any way.

When threshed the infected grains, which are hard and compact, may pass through the machine and be distributed in this manner, when they are usually termed "smut-balls." It has been shown by von Liebenberg (1879) that the spores may retain their viability up to eight years, if kept in a dry place.

Infection occurs in the seedling stage, as in *Ustilago Avenae*. Germination has been worked out and figured by numerous authors, being first recorded by Berkeley (1847).

In water a probasidium is produced, and on the end of this is borne a whorl of slender sickle-shaped conidia. The conidia may in turn produce either stout allantoid secondary conidia, or else directly produce infection hyphae.

This and the following species are readily controlled by steeping the grain prior to sowing in some suitable fungicide. For this purpose copper-sulphate solution, formalin, and, as a dry treatment, copper-carbonate, are usually recommended.

3. *Tilletia Tritici* Winter. (Text-fig. 18.)

Wint., in Rabh. *Krypt. Fl.*, vol. 1, p. 110, 1881.

Uredo Caries DC., *Fl. Fr.*, vol. 6, p. 78, 1815. *Tilletia Caries* Tul., *Ann. Sci. Nat.*, ser. 3, vol. 7, p. 113, 1847. *T. Secalis* (Cda.) Kuehn, in F. v. Waldh., *Apercu Syst. Ust.*, p. 50, 1877.

Sori in ovaries, concealed within the glumes, shortly elliptical, 4-6 mm. long, dark brown, fetid.

Spores globose or subglobose, 16-24 mmm. diam.; episporium with a network of raised reticulations about 1 mmm. high, surrounding polygonal depressions 2-4 mmm. wide, pallid brown.

Host: *Triticum vulgare* Vill. In inflorescences. Herb. No. 599. Lincoln (Canterbury), 80 m., *F. E. Ward!* 27 Jan., 1922.

Distribution: World-wide.

This is separated from the preceding species on account of the reticulate spores. Both species occur on the same host, frequently in the same spike.

Gaines and Stevenson (1923) give as a synonym *Tilletia Secalis* Kuehn., for they have shown the form on rye to be identical with the above, differing only in that it is found on a different host.

Potter and Coons (1918) claim that this species may be separated from the preceding in the field on account of the following differences:—

<i>Tilletia Tritici.</i>	<i>Tilletia levis.</i>
Considerably stunts the host.	Has little stunting effect.
Causes infected grains to become much inflated, and consequently shorter in length.	Has little effect upon the shape of the grain, merely causing it to shrivel slightly.
Spore mass more powdery, friable, or even granular.	Spore-mass inclined to be unctuous.

Germination and method of infection are similar to the preceding.

4. *Tilletia Holci* (Westendorp) Rostrup. (Text-fig. 16.)

Rostr., *Ust. Daniae*, p. 156, 1890.

Polycystis Holci Westnd., *Bull. Acad. Belg.*, ser. 2, vol. 11, p. 660, 1860. *Tilletia Rauwenhoffii* F. v. Waldh., *Apercu Syst. Ust.*, p. 50, 1877.

Sori in ovaries, partially concealed within the glumes, elliptical, 1–2 mm. long, compact, black, slightly fetid.

Spores globose or subglobose, 22–32 × 24–28 μmm.; episporium covered with a network of raised reticulations 3–4.5 μmm. high, surrounding polygonal depressions 4–7 μmm. wide, chestnut-brown.

Host: *Holcus lanatus* L. In inflorescences. Herb. No. 500. Ettrick (Otago), 300 m., *R. B. Tenment!* 10 Feb., 1921.

Distribution: Europe; North America.

I have a collection of *Holcus lanatus* L. with this species in the ovaries and *Ustilago striaeformis* in the leaves.

The three species possessing reticulate spores may readily be separated if the following differences are noted:—

Spores under 25 μmm.	<i>T. Tritici.</i>
Spores over 25 μmm.						
Reticulations 2–2.5 μmm. high			<i>T. decipiens.</i>
Reticulations 3–4.5 μmm. high			<i>T. Holci.</i>

Furthermore, the reticulations of *T. Holci* are coarse, and separated by large polygonal interspaces; those of *T. decipiens* are closely compacted, being separated by much smaller areas; whilst those of *T. Tritici* are intermediate in size.

I have been unable to germinate the spores of *T. Holci*.

6. *SOROSPORIUM* Rudolphi.

Rud., *Linnaea*, vol. 4, p. 116, 1829.

Sori in the form of dark-coloured pulverulent spore-masses in various parts of the host, chiefly in the inflorescences, formed of numerous spore-balls, consisting of few or many spores, at first somewhat loosely united, but at maturity completely separating; sterile cells absent.

Spores coloured some shade of brown, globose to angular, smooth or verruculose; germination similar to that of *Ustilago*.

Distribution: World-wide.

New Zealand species two—one endemic, the other indigenous; both are confined to the Cyperaceae. Members of the genus have elsewhere been recorded on the following families: Gramineae, Cyperaceae, Juncaceae, Portulacaceae, and Caryophyllaceae. McAlpine (1910) records thirteen species for Australia.

The genus is characterized by the rather temporary nature of the spore-balls, for these generally break up at maturity, when species cannot be distinguished from *Ustilago*. In one or two species the balls remain somewhat firmly united, when they are liable to be confused with the allied genera *Thecaphora* and *Tolyposporium*. The former may be separated by the pallid colour of the spore-balls, and the fact that the spores are variously marked on their free, but smooth on their united surfaces (seen when the spores are separated), the latter by the individual spores being firmly united in the ball by ridged folds of their episporia.

Spore-formation has been investigated by Fischer von Waldheim (1869) in the type species, *S. Saponariae* Rud. The mycelium in the infected region

changes somewhat rapidly to sporiferous hyphae, which soon become gelatinized. At various points several of these hyphae become twisted into small masses, become gelatinized, and lose their outlines. They then become enclosed by other hyphae from the adjoining mycelium. These hyphae also become gelatinized, and in consequence their outlines are indistinct. In the centre of these masses spore-differentiation commences: the spores are at first clear, but quickly change colour, becoming brown. At this stage they are few in number and immature. They then divide until the number of the mature ball is arrived at, the gelatinous outer zone of hyphae gradually disappearing until at maturity practically no trace remains.

KEY TO SPECIES.

Spore-balls of 2-6 spores	1. <i>S. Neillii</i> .
Spore-balls of 15-50 spores	2. <i>S. solidum</i> .

1. *Sorosporium Neillii* n. sp. (Text-fig. 22, and Plate 46, fig. 1.)

Cyperaceae.

Sori in occasional ovaries, frequently in all, at first enclosed within the perigynium, becoming exposed when black, compact, globose or elliptical, 3-4 mm. long. Spore-balls of 2-6 spores, irregularly elliptical, dark chestnut-brown, up to 50 mmm. long, readily breaking up at maturity.

Spores irregular, angular, subglobose or elliptical, frequently flattened on one side, 12-20 × 9-15 mmm.; episporio coarsely and densely verrucose, chestnut-brown, 1.5-2 mmm. thick.

Host: *Scirpus nodosus* Rottb. In inflorescences! Herb. Nos. 1279, 1285. Bluff (Southland), seashore, *W. D. Reid!* 26 May, 1922. Seatoun (Wellington), seashore, *J. C. Neill!* *G. H. C.* 6 Dec., 1923.

Distribution: Australia.

The host is indigenous and abundant throughout; it occurs also in Australia, South Africa, and South America (Cheeseman, 1906, p. 776).

Germination.—In water germination commenced in three days; a short and slender probasidium is produced, and on this, both laterally and terminally, conidia are produced. In certain specimens the terminal conidium is formed before the probasidium becomes septate, but as a rule septation precedes the production of conidia.

This species differs from *S. piluliformis* (Berk.) McAlp., on *Scirpus prolifer* Rottb., in that the spore-balls are less than half the size, are lighter in colour, and break up readily; the spores are larger, and possess more verrucose, not tuberculate, episporio.

[*Latin diagnosis.*]

Sorosporium Neillii.

Soris ad ovaria pauca destruentibus; atris, compactis, globosis vel ellipticis, 3-4 mm. longis. Spororum pilis sporis 2-6; inaequaliter ellipticis, atro-castaneis, ad 50 mmm. longis; facile disruptis maturitate.

Sporis inaequaliter angulatis, subglobosis vel ellipticis, 12-20 × 9-15 mmm.; episporio crasse denseque verruculoso, castaneo, 1.5-2 mmm. crasso.

Hab.: In ovariiis *Scirpi nodosi* Rottb. Bluff (Southland, N.Z.), *W. D. Reid!* Seatoun (Wellington, N.Z.), *J. C. Neill!*

2. *Sorosporium solidum* (Berkeley) McAlpine. (Text-fig. 21.)

McAlp., *Smuts Austr.*, p. 183, 1910.

Ustilago solida Berk., *Fl. Tas.*, vol. 2, p. 270, 1860. *Urocystis solida* F. v. Waldh., *Apercu Syst. Ust.*, p. 38, 1877.

Sori in occasional spikelets, partly enclosed within the glumes, at first compact, becoming pulverulent, black, elliptical, 3–4 mm. long. Spore-balls subglobose to elliptical, often irregular, composed of from 15 to 50 or more similarly coloured spores somewhat firmly united, attaining a size of 115×50 mmm., although commonly much less, averaging about 50 mmm.

Spores subglobose or somewhat angular, $12-18 \times 10-15$ mmm.; epispore smooth, dark chestnut-brown, 1 mmm. thick.

Host: *Schoenus Carsei* Cheesem. In spikelets. Herb. No. 423. Auckland, T. Patterson! Oct., 1921.

Distribution: Australia.

The host is confined to the swamps of the Auckland and Taranaki Provinces (Cheeseman, 1906, p. 781).

The New Zealand form differs from the description given by McAlpine in that the sori are (when mature) pulverulent, the spore-balls larger, and the spores slightly smaller (McAlp., 20–24 mmm. long.).

I have been unable to germinate the spores.

7. *UROCYSTIS* Rabenhorst.

Rabenh., Klotsch, in *Herb. Viv. Myc.*, ed. 2, No. 393, 1856.

Polycystis Lev., *Ann. Sci. Nat.*, ser. 3, vol. 5, p. 269, 1846.

Sori in the form of dark-coloured pulverulent masses of spore-balls, usually in the leaves and stems of the host, occasionally in the inflorescences. Spore-balls compact, permanent, of one or many fertile cells, enclosed within an envelope of few or many tinted sterile cells.

Spores dark-coloured, irregular in shape; epispore smooth or variously sculptured; germination by means of a short probasidium, producing terminally one or a whorl of elliptical conidia, which on germination produce either secondary conidia or infection hyphae.

Distribution: World-wide.

The following species is the sole representative of the genus that has been as yet collected in New Zealand.

Members of the genus have been found on the following host families: Gramineae, Cyperaceae, Juncaceae, Liliaceae, Amaryllidaceae, Ranunculaceae, Rosaceae, and Violaceae.

The genus is characterized by the permanent spore-balls, which consist of one or several dark-coloured spores surrounded wholly or in part by an envelope of sterile cells. The phyllogenous habit, and tendency to gall-formation, are also characteristic.

Spore-formation has been worked out by De Bary (1887). His work has since been supplemented by numerous other workers. The sporiferous hyphae branch, become gelatinized, somewhat swollen, then twined into an indistinguishable semi-gelatinous mass. In the central portions of this mass the spores become differentiated; the outer layer of the mass consists of slender branches derived from the gelatinous mass of hyphae. These become divided by transverse septa into numerous short cells; several persist as the sterile envelope so characteristic of the genus, the remainder become absorbed as the spores mature.

1. *Urocystis Anemones* Winter. (Text-fig. 20, and Plate 45, fig. 2.)

Ranunculaceae.

Wint. in Rabb. *Krypt. Fl.*, vol. 1, p. 123, 1881.

Sori in leaves (when chiefly epiphyllous), petioles, and stems, forming irregular swellings, at first covered by the epidermis, becoming exposed when appearing as a pulverulent black mass. Spore-balls irregular, from 15 to 30 mmm. in length, composed of from one to five spores, partially surrounded by more numerous and smaller sterile cells.

Spores subglobose to polygonal, 10-15 × 8-14 mmm.; epispore smooth, or sometimes delicately verruculose, dark brown, 1 mmm. thick; sterile cells subglobose to polygonal, pallid brown, smooth, often reduced or wanting.

Host: *Ranunculus insignis* Hook. f. On leaves and petioles. Herb. No. 503. Mount Dennan, Tararua Mountains (Wellington), 1,500 m., E. H. Atkinson! 7 Jan., 1922.

Distribution: World-wide.

The host is endemic, and confined to the mountain-ranges of both Islands (Cheeseman, 1906, p. 10).

Infection experiments were carried out by Plowright (1889, p. 94). He applied conidia to the foliage of *Ranunculus repens*, and two months later, in the vicinity of the points of inoculation, he observed signs of the formation of the spore-beds. He found the mycelium to be localized, infection occurring wherever the infection hyphae penetrated.

Germination has been observed and figured by numerous workers. In water, after forty-eight hours, a probasidium is produced, on the apex of which a whorl of three or four conidia is formed.

Brefeld (1895) found that the spores would germinate only after six months' rest in damp earth; but Kniep (1921) found that forms from different hosts differed, in that some required this period of rest, whilst others germinated as soon as they were mature. He considered the species to be in reality an aggregate one, thus explaining the differences in germination as recorded by various workers.

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COMBINED HOST AND FUNGUS INDEX.

All synonyms are in italics. Page numbers of synonyms and of incidental references are in ordinary type; those under which are to be found descriptions of species, genera, or families, or hosts of these species, are in italics. An asterisk preceding a page number indicates that an illustration of the species in question will be found on that page.

This index gives only those synonyms that have been used in recent literature, or are some guide to the species in question.

	Pages		Pages
Agropyron	413	Elateromyces <i>Bubak</i>	403, 414
<i>scabrum</i> (<i>Lab.</i>) <i>Beauv.</i>	.. 413	<i>endotrichus</i> (<i>Berk.</i>) <i>G. H. Cunn.</i>	.. 416
Agrostis		<i>niger</i> <i>G. H. Cunn.</i>	*411, 416, *422
<i>vulgaris</i> <i>With.</i>	.. 424	<i>olivaceus</i> (<i>DC.</i>) <i>Bubak</i>	*411, 417, *422
Anthoxanthum		<i>Treubii</i> (<i>Solms.</i>) <i>Bubak</i>	.. 414
<i>odoratum</i> <i>L.</i>	.. 414	<i>Endothlaspis</i> <i>Sor.</i>	.. 421
<i>Anthracoidea</i> <i>Bref.</i>	.. 418		
<i>Caricis</i> <i>Bref.</i>	.. 420	Gahnia..	.. 414
Arrhenatherum		<i>sp.</i>	.. 416
<i>elatius</i> (<i>L.</i>) <i>Beauv.</i>	.. 405	GRAMINEAE	404, 418, 423, 424, 427, 429
Avena			
<i>sativa</i> <i>L.</i>	.. 406	Holcus	
		<i>lanatus</i> <i>L.</i>	.. 410, 427
Bromus		Hordeum	
<i>hordaceus</i> <i>L.</i>	.. 412	<i>vulgare</i> <i>L.</i>	.. 409
<i>unioloides</i> <i>H. B. K.</i>	401, 412	LILIACEAE	.. 404, 429
Carex ..	414, 420		
<i>dipsacea</i> <i>Berggr.</i>	.. 416, 417	ONAGRACEAE	.. 404
<i>Gaudichaudiana</i> <i>Kunth.</i>	.. 420	OXALIDACEAE	.. 404
<i>pseudo-cyperus</i> <i>L.</i>	.. 417		
<i>subdola</i> <i>Boott.</i>	.. 420	POLYGONACEAE	.. 404, 423
<i>ternaria</i> <i>Forst. f.</i>	.. 420	Polygonum	
<i>virgata</i> <i>Sol.</i>	.. 417	<i>cinense</i>	.. 416
CARYOPHYLLACEAE	404, 427	<i>prostratum</i> <i>A. Rich.</i>	.. 423
Cintractia <i>Cornu</i>	.. 403, 418	<i>serrulatum</i> <i>Lag.</i>	.. 423
<i>Avenae</i> <i>Ell. et Tr.</i>	.. 405	<i>sp.</i>	.. 423
<i>Caricis</i> (<i>Pers.</i>) <i>Magn.</i>	.. *411, 418, 420	PORTULACAEAE	.. 427
<i>patagonica</i> <i>Cke. et Mass.</i>	.. 412		
<i>sclerotiformis</i> (<i>Cke. et Mass.</i>) <i>G. H. Cunn.</i>	.. *411, 418, 421	RANUNCULACEAE	.. 429, 430
<i>Spinificis</i> (<i>Ludw.</i>) <i>McAlp.</i>	*415, 418	Ranunculus	
CYPERACEAE	404, 414, 418, 427, 429	<i>insignis</i> <i>Hook. f.</i>	.. 430
		<i>repens</i> <i>L.</i>	.. 430
Dactylis			
<i>glomerata</i> <i>L.</i>	.. 410	Schoenus	
Danthonia		<i>Carsei</i> <i>Cheesem.</i>	.. 429
<i>Buchanani</i> <i>Hook. f.</i>	.. 413	Scirpus	
<i>pilosa</i> <i>R. Br.</i>	.. 414	<i>nodosus</i> <i>Rottb.</i>	.. 428
<i>semiannularis</i> <i>R. Br.</i>	.. 414		

	Pages	Ustilago	Pages
Sorosporium <i>Rud.</i> ..	403, 427	<i>bromivora</i> (Tul.) F. v. Waldh.	400, 401, 404, 405, *407, 412, *422
Neillii G. H. Cunn. ..	*419, 428	<i>bullata</i> Berk. ..	405, *407, 413
piluliformis (Berk.) McAlp. 428	<i>Candollei</i> Tul. 423
Saponariae <i>Rud.</i> 427	<i>caricicola</i> Tr. et Earle 417
solidum (Berk.) McAlp. ..	*419, 429	<i>Caricis</i> Ung. 420
Sphacelotheca De Bary ..	403, 421	<i>catenata</i> Ludw. 417
Hydropiperis (Schum.) De Bary ..	*411, 423	<i>comburens</i> Ludw. ..	405, *407, 413
Spinifex		<i>emodensis</i> Berk. 416
<i>hirsutus</i> Lab. 420	<i>endotricha</i> Berk. 416
Tilletia Tul. ..	399, 403, 404, 424	<i>exigua</i> Syd. 413
<i>Airae-caespitosae</i> Lindr. 410	<i>foetens</i> Berk. et Curt. 425
<i>alopecurivora</i> Ule 410	<i>Hordei</i> Bref. 408
<i>Brizae</i> Ule 410	<i>Hordei</i> Jens. 408
<i>Caricis</i> Tul. 426	var. <i>nuda</i> Jens. 408
<i>De Baryana</i> F. v. Waldh. 410	var. <i>tecta</i> Jens. 408
<i>decipiens</i> (Pers.) Koern. ..	*415, 424	<i>Hordei</i> Kell. et Sw. 408
<i>foetens</i> (Berk. et Curt.) Trel. 425	<i>Hordei</i> Rostr. 409
<i>Holci</i> (Westnd.) Rostr. ..	*415, 424, 427	<i>Hydropiperis</i> Schroet. 423
<i>levis</i> Kuehn. ..	400, *415, 424, *425	<i>Jensenii</i> Rostr. ..	400, 405, *407, 408, 409
<i>Milii</i> Fel. 410	<i>levis</i> Magn. ..	398, 400, 405, 406, *407, 409, *422
<i>Rauwenhoffii</i> F. v. Waldh. 427	<i>Maydis</i> Cda. 399
<i>Secalis</i> Kuehn. 426	<i>microspora</i> Mass. et Rodw. 413
<i>sphaerococca</i> F. v. Waldh. 424	<i>nuda</i> Kell. et Sw. ..	400, 408, 409
<i>striaeformis</i> (Westnd.) Oud. 410	<i>olivacea</i> (DC.) Tul. 417
<i>Tritici</i> Wint. ..	398, 400, *415, 424, 426	<i>perennans</i> Rostr. 405
TILLETIACEAE 398, 401	<i>Poa</i> McAlp. 410
Triticum		<i>Readeri</i> Syd. ..	405, *411, 413, *422
<i>vulgare</i> Vill. 409, 425, 426	<i>Scirpi</i> Kuehn. 420
Uncinia		<i>sclerotiformis</i> Cke. et Mass. 421
<i>caespitosa</i> Boott. 421	<i>segetum</i> Dittm. 408
<i>leptostachya</i> Raoul 421	var. <i>Avenae</i> Jens. 408
<i>riparia</i> R. Br. 421	var. <i>Hordei</i> Jens. ..	408, 409
Urocystis <i>Rabenh.</i> ..	403, 429	var. <i>Tritici</i> Jens. ..	408, 409
<i>Anemones</i> Wint. ..	397, 398, *415, 430	<i>solida</i> Berk. 429
<i>solida</i> F. v. Waldh. 429	<i>Spinificis</i> Ludw. 418
<i>Ustilagidium</i> <i>Herzb.</i> 404	<i>striaeformis</i> (Westnd.) Niessl ..	400, 405, *407, 410, *422
<i>Hordei</i> <i>Herzb.</i> 409	<i>Treubii</i> Solms. 414
<i>Tritici</i> <i>Herzb.</i> 409	<i>Tritici</i> <i>Jens.</i> ..	398, 405, *407, 409, *422
USTILAGINACEAE ..	398, 401, 403	<i>Tritici</i> <i>Rostr.</i> 409
USTILAGINAE ..	397, 401	forma <i>follicola</i> P. Henn. 409
<i>Ustilago</i> (Pers.) <i>Rouss.</i> ..	399, 403, 404	<i>urceolorum</i> Tul. 420
<i>Agropyri</i> <i>McAlp.</i> 413	<i>washingtoniana</i> Ell. et Ev. 410
<i>Avenae</i> <i>Jens.</i> ..	398, 400, 405, *407, 409	<i>Zea</i> (Ing. ..	398, 399
var. <i>levis</i> <i>Kell. et Sw.</i> 406		