ROYAL GARDENS, KEW.

BULLETIN

OF

MISCELLANEOUS INFORMATION.

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DCLVI.—A REVISION OF THE GENUS TILLETIA.

(*With Plate.*)

GEO. MASSEE.

All species included in the genus, as at present defined, are endophytic obligate parasites, and out of a total of twenty-six species, all are parasitic on plants belonging to the Gramineæ, with the exception of *Tilletia arctica*, Rostr., and *T. Sphagni*, Nawaschin. The former of these is parasitic on *Carex festiva*, Dewey, and the latter in the capsules of *Sphagnum squarrosum*, Pers. The infested capsules are somewhat dwarfed, and formed what were known as microsporangia by bryologists, while the fungus spores they contained were called microspores.

In the Uredineæ what may be termed biological species have been proved to exist; that is to say, of a species one or more forms not morphologically distinct may exist, that are distinguishable only by the fact that they are confined to one particular host-plant.

Professor Eriksson, our best authority on grain-rusts, has the following remarks* on this phase of the subject:—"Between certain of these forms which constitute a species, for instance, the three forms of black rust—*Puccinia graminis*, Pers.—we have not succeeded in discovering, even with the aid of a microscope, any distinguishing difference, such as the size, colour, and distribution of the pustules, the shape and size of the spores, &c. However, there is a difference between them with regard to their inner nature that is of no little practical interest. The difference appears in that every form is almost exclusively confined to its particular cereal, and that consequently it is able to infect no cereal but that one."

* Eriksson in Bot. Gaz. xxv. (1898), p. 29.

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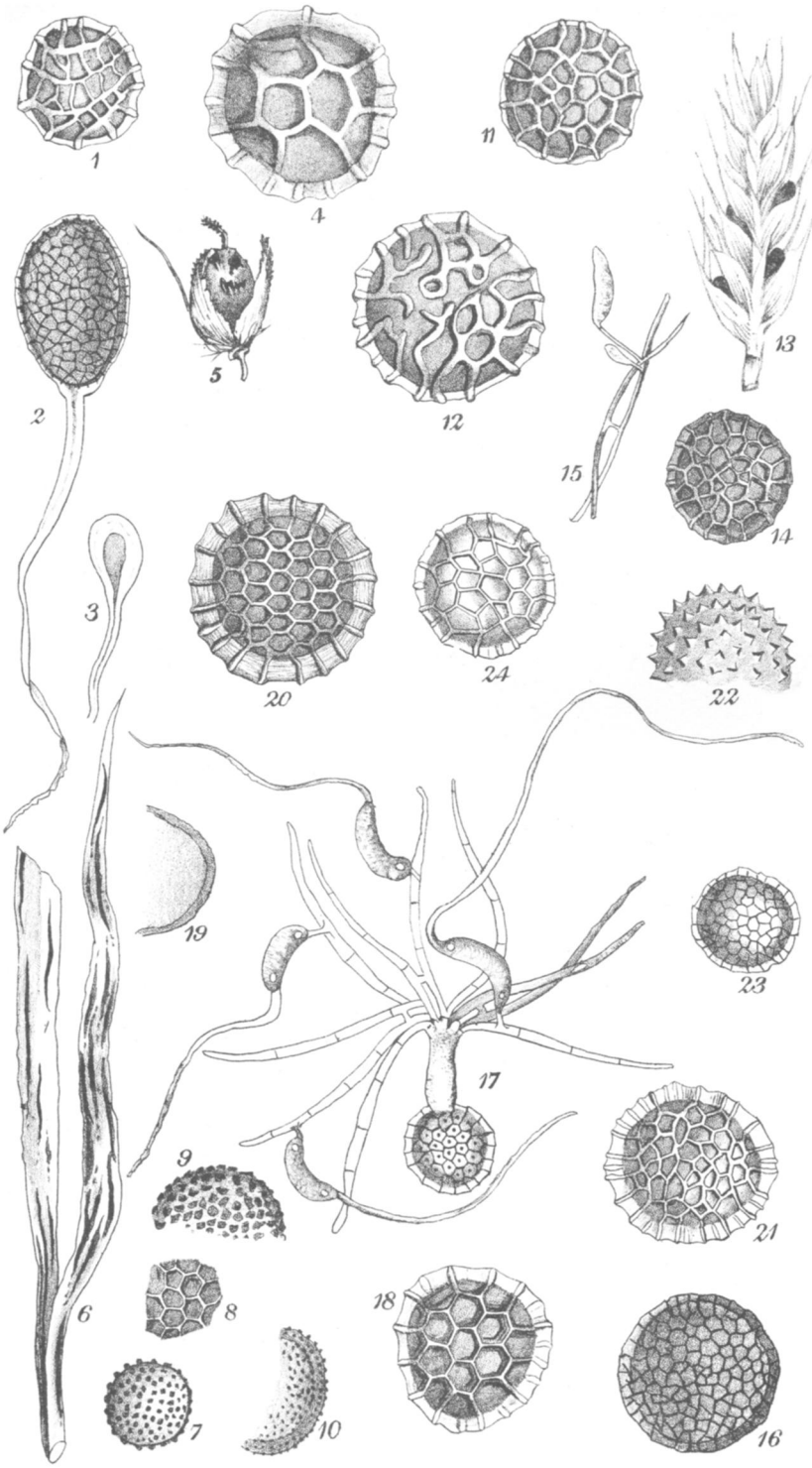

Spores of Tilletia.

E. Weller & Grahams Ltd Litho. London. 79/4. 7. 99

In the genus *Tilletia* the existence of such biological forms has not been demonstrated, but the species enumerated in the following pages are founded on morphological characters.

Examination of a large amount of material has led to the conclusion that the host-plant is absolutely worthless as a factor in the discrimination of morphologically defined species. For this reason the species as here understood, do not coincide with those of many previous workers, where the host was an important, and not infrequently the only feature relied upon for distinguishing between presumedly distinct but allied species.

With regard to geographical distribution, the genus is very widely distributed, whereas the species are restricted in their range, each being confined to a portion of one Continent, with the exception of those species that are parasitic on cultivated cereals, the explanation of which is obvious. Of these *Tilletia Caries* occurs in Europe, Africa, Australiâ, United States, South America; *T. levis* in Europe, Australia, United States; *T. Hordei* in Europe, Asia, Africa.

The following table shows the distribution of the species :—

Europe, 13 species.—*lævis*, *de Baryana*, *arctica*, *Lolii*, *controversa*, *separata*, *Caries*, *Rauwenhoffii*, *Hordei*, *endophylla*, *Sesleriæ*, *Berkeleyi*, *Sphagni*, (*Fischeri ?*).
Asia, 2 species.—*controversa*, *Hordei*, (*Vulpiæ ?*).
Africa, 3 species.—*verrucosa*, *Caries*, *Hordei*.
Mauritius, 1 species.—*Ayresii*.
Australia, 4 species.—*lævis*, *mixta*, *epiphylla*, *Caries*.
United States, 9 species.—*lævis*, *rotundata*, *mixta*, *rugispora*, *cerebrina*, *buchloeana*, *Caries*, *Elymi*, *fusca*.
Antilles, 1 species.—*magnusiana*.
South America, 3 species.—*hyalospora*, *Caries*, *zonata*.

TILLETIA, Tulasne in Ann. Sci. Nat., sér. 3, vol. vii., p. 112 (1847); Sacc., Syll. vii. (1888), p. 481.

Endophytic obligate parasites. Spore-mass pulverulent, black or blackish-olive at maturity, often fœtid, especially when moistened. Spores free, produced singly at the tips of somewhat gelatinous, swollen, fertile hyphæ, at first covered by the epidermis of the host, forming a blackish powdery mass at maturity. On germination, the spore gives origin to a promycelium, which bears a terminal whorl of slender, elongated secondary-spores at its apex. Secondary-spores usually conjugating in pairs, and on germination producing slender, elongated conidia.—*Ustilago*, Link, in Berl. Mag. der Gesellsch. der Nat. Freunde, iii. (1809); Lév., in Ann. Sci. Nat., sér. 2, xi. (1839), 116.

Tulasne separated the species included under *Tilletia*, from the heterogeneous assemblage of species previously included under *Ustilago*, *Uredo*, *Erysibe*, &c., of old authors, taking as his principal generic character, the peculiar mode of germination and production of secondary-spores as observed in *Tilletia Caries* (*T. Tritici*, Winter).

The principal distinctive features of *Tilletia*, as defined by the systematist are :—spores free (not aggregated in groups), forming

a dry pulverulent mass at maturity, and producing on germination a whorl or cluster of secondary-spores at the apex of the promycelium.

Entyloma agrees in the free spores, and in the mode of production of the secondary-spores, but differs in the spore-mass not being pulverulent at maturity.

Urocystis agrees with *Tilletia* in the spore-mass being dry and pulverulent when mature, also in the method of germination and formation of secondary-spores, but differs in the spores being produced in groups, the central ones of the group being fertile, the peripheral ones sterile.

The mode of spore-germination is up to the present unknown in more than half the accepted species, their claim to a position in the genus depending on the two remaining features indicated above—spores free, forming a pulverulent mass at maturity; now these characters are also common to the genus *Ustilago*, and the means of distinguishing between the two genera in the absence of evidence afforded by germination, and absence of knowledge as to the origin of the spores, turns on the relatively much larger spores in *Tilletia*, which (with one exception, *T. lævis*) have the epispore reticulated or warted.

Neovossia was originally separated from *Tilletia* on some slight difference in the structure of the epispore. It has recently been studied by Brefeld, and although the spore-structure does not indicate a generic distinction, this author retains the genus as valid; the distinction from *Tilletia* advanced being a negative character—the secondary spores are produced in a tuft at the apex of the promycelium, as in *Tilletia*, but do not conjugate in pairs as in the last-named genus. This attitude is somewhat surprising, remembering that Brefeld does not admit of any sexual significance in a junction by a transverse band of adjoining pairs of secondary-spores.

Key to the species.

Series A. Epispore smooth ... ... 1. *T. lævis.*
Series B. Epispore warted or echinulate.
Spores produced in the ovary.
Spores 20–25 μ; epispore with acute pyramidal warts ... 2. *T. verrucosa.*
Spores 20–25 μ; epispore densely covered with minute warts ... ... 3. *T. rotundata.*
Spores deep chestnut-brown under the microscope, 16–18 μ; epispore very minutely warted ... ... 4. *T. mixta.*
Spores straw-coloured under the microscope, 13–16 μ; epispore very minutely warted ... ... 5. *T. Ayresii.*
Spores yellow-brown under the microscope, 12–15 μ; epispore densely and minutely warted ... ... 6. *T. magnusiana*
Spores 16–22 μ, densely covered with minute, irregular, flat-topped, dark coloured warts, formed by the breaking up of the epispore, interstices paler ... ... 7. *T. rugispora.*
Spores produced in leaves and culm.
Spores 10–18 μ, densely covered with minute, dark, flat-topped warts formed by the breaking up of the epispore, interstices paler ... ... 8. *T. de Baryana.*
Spores blackish-brown under the microscope; epispore minutely papillose ... ... 9. *T. arctica.*
Spores 35–38 μ; epispore with scattered exceedingly minute warts ... ... 10. *T. epiphylla.*

Series C. Epispore reticulated.
- Spores produced in the ovary.
  - Spores sub-hyaline or very pale brown under the microscope.
    - Spores 20-24 μ, almost colourless; epispore with sub-concentric ribs united by transverse bars ... ... 11. *T. hyalospora.*
    - Spores 23–26 μ, pallid; epispore with a shallow, small-meshed network ... ... 12. *T. Lolii.*
    - Spores 18–25 μ, pale brown; epispore with a shallow, large-meshed network... ... ... 13. *T. controversa.*
  - Spores dark brown under the microscope.
    - Ridges on the epispore with numerous free ends, or more or less formed of coalesced warts.
      - Spores 23–28 μ; epispore with ridges forming a reticulation, but having many free ends... ... 14. *T. cerebrina.*
      - Spores 16–21 μ; ridges of the epispore forming the reticulation mainly formed of confluent warts or spines ... ... 15. *T. buchloeana.*
    - Reticulation of the epispore formed of plates or ridges without free ends.
      - Spore-mass foetid.
        - Spores 20-27 μ; network of epispore, large-meshed 16. *T. separata.*
        - Spores 17–22 μ; network of epispore, small-meshed 17. *T. Caries.*
      - Spore-mass not foetid.
        - Spores 24–28 μ, dark olive-brown; reticulation of epispore shallow and small-meshed ... ... 18. *T. Elymi.*
        - Spores dark brown, averaging 33 μ; ridges of epispore 4 μ high; meshes polygonal, large ... 19. *T. inolens.*
        - Spores 25–30 μ, olive-brown; reticulation of epispore rather deep, large-meshed ... ... 20. *T. Rauwenhoffii.*
        - Spores 16–25 μ, dark brown; reticulation of epispore large-meshed, mesh very irregular in form ... 21. *T. fusca.*
        - Spores 19–20 μ, brown; reticulation of epispore small meshed ... ... 22. *T. Hordei.*
        - Spores 15–18 μ, brown; reticulation of epispore small-meshed ... ... 23. *T. zonata.*
- Spores produced on the leaves or culm.
  - Spores 18–25 μ, brown, border similarly coloured; reticulation of the epispore small meshed... ... ... 24. *T. endophylla.*
  - Spores 25–28 μ, dark brown; reticulation of epispore shallow and small-meshed ... ... 25. *T. Sesleriæ.*
  - Spores 15-18 μ; reticulation of epispore very small-meshed 26. *T. Berkeleyi.*
- Spores produced in the capsules of Sphagnum ... ... 27. *T. Sphagni.*

1. **Tilletia lævis**, *Kühn in Rabenh. Fung. Eur.* (1873), 1697.—Spore-mass produced in the ovary, deep brown with an olive tinge, foetid; spores globose, angularly globose, elliptic, &c., very variable in form and size, averaging 17-21 μ, or 15–26 × 10–15 μ, wall about 2 μ thick, pale olive-brown or sometimes almost cream-colour, epispore perfectly smooth.—Fischer de Wald., Aperçu (1877), 47; Wint. in Rabenh. Krypt. Flora, Pilze, i. (1884), 109; Sacc., Syll. vii. (1888), no. 1776. *T. fœtens*, Arthur in Bull. Agric. Exper. Stat. Indiana, no. 28 (1889), ex Journ. Myc. v. 165. *Ustilago fœtens*, Berk. & Curt. in Grevillea, iii. (1874), 59.

HOST.—*Triticum vulgare*, Linn.

HAB.—England, France, Germany, Italy, Austria, Hungary, Russia, United States, Victoria.

Exsicc.—Rabenh. Fungi Eur. 1697; Roum. Fung. Sel. Exs., 5217; Sacc. Myc. Ven., 373; Ellis, N. Amer. Fungi, 1497; Rav. Fung. Carol., 100; Thümen, Myc. Univ., 1115; Flor. Exs. Austro-Hung. 352 (mixed with *T. Caries*); Thümen, Fung. Austr., 373.

The specimen in Rabenh. Fung. Eur., 1697, communicated by Kühn, and also Berkeley's type, examined.

Fig. 19, spore of *T. lævis*.

2. **Tilletia verrucosa,** *Cooke & Massee in Grevillea* xvii. (1888), 16.—Spores-mass occupying the ovary, pale brown, foetid. Spores globose or subglobose, pale yellowish brown, 20–25 μ diam., bristling with large, acute, pyramidal warts about 3 μ high. —Sacc. Syll. ix. (1891), no. 1177.

HOSTS.—*Panicum coloratum*, Linn.; *Ehrharta calycina*, Sm.

HAB.—Africa. Mozambique Distr., Portuguese East Africa, Lower Zambesi, between Lupata and Tete, *Kirk*. Cape Colony, in ovary of *Ehrharta* in herb. Thunberg.

Readily distinguished amongst species having warted spores by the pale yellowish brown or amber colour of the spores, and the large, pointed, pyramidal warts on the epispore. Type in herb. Kew.

Fig. 22, spore of *T. verrucosa*.

3. **Tilletia rotundata,** *Massee*.—Spore-mass occupying the ovary, dark brown; spores globose or angularly globose, 20–25 μ diam., yellowish-brown, translucent, wall thick, epispore densely covered with minute warts.—*Ustilago rotundata*, Arthur in Bull. Iowa Agric. Coll., 1884, 173.

HOST.—*Panicum virgatum*, Linn.

HAB.—United States; Connecticut, South Manchester.

Exsicc.—Ellis & Everh., N. Amer. Fung., ser. 2, 1894.

Lacking the evidence afforded by germination, it is impossible to assign, with certainty, the generic position of this species; morphologically the spore characters indicate *Tilletia*.

4. **Tilletia mixta,** *Massee*.—Spore mass blackish brown, formed in the ovary; spores globose, angularly globose, or broadly elliptic, averaging 16–18 μ diam., margin about 2 μ broad, deep chestnut brown, granulated or very minutely warted.—*T. fusca*, Ellis & Everh. in exsicc. not in Journ. Myc. iii. 55.

HOST.—*Eriochloa annulata*, Kunth; *Festuca microstachya*, Desv.

HAB.—Australia; Murrumbidgee, *Bennett*. United States; Idaho, Boise City, *Ellis & Everhart*.

Exsicc.—Ellis & Everh., N. Amer. Fung. ser. 2, 1895.

Allied to *Tilletia de Baryana* in spore-structure, but quite distinct in the rich chestnut colour of the spore, the much smaller warts or granulations on the epispore, and in being produced in the ovary.

Fig. 10, spore of *T. mixta*.

5. **Tilletia Ayresii**, *Berk., MS. in herb. Kew.*—Spore-mass buff, produced in the ovary; spores globose or broadly elliptic, 13–16 μ or 12–13 × 16 μ, border 1·5–2 μ broad, very pale straw-colour, densely covered with very minute warts.

HOST.—*Panicum maximum*, Nees.

HAB.—Mauritius; Hills above Port Louis, *Ayres*, 4754 in herb. Berkeley.

Readily recognised by the small, almost colourless, warted spores. Type in herb. Kew.

6. **Tilletia magnusiana**, *Fischer de Waldh., Aperçu* (1887), 47.—Spore-mass produced in the ovary, blackish; spores globose, ovoid, flattened or pointed, 10–14 μ diam., or up to 12 × 16 μ, clear yellow-brown, epispore very densely granulose or almost papillose.—Sacc. Syll. vii. (1883), no. 1777.

HOST.—*Panicum geniculatum*, Willd.

HAB.—Antilles.

Distinguished among species developing in the ovary of the host by the very finely papillose epispore. Not examined.

7. **Tilletia rugispora**, *Ellis in Journ. Myc.* vii. (1893), 275, figs. 8 and 9.—Spore-mass formed in the ovary, pale greyish brown; spores almost uniformly globose, pale brown, 16–22 μ diam., border 2–2·5 μ wide, not paler, epispore densely covered with small, flat-topped, irregularly shaped warts of a brown colour, formed by the cracking of the epispore during the growth of the spore, interstices paler.—Sacc. Syll. xi. (1895), no. 1337.

HOSTS.—*Paspalum undulatum*, Poir.

HAB.—United States, Brazos Co., Texas.

Exsicc.—Ellis & Everh. N. Amer. Fung., 2704.

The ornamentation of the epispore is described by Ellis as "tuberculose-reticulate, the reticulations about 1 μ high and 1·5 μ broad.

The surface of the epispore is cracked in a tesselated manner, the top of the warts being dark, and the cracks separating adjacent warts paler, presenting, on a surface view the appearance shown in fig. 8. Authentic specimen from Ellis, and also specimen in N. Amer. Fungi, 2704, examined.

Fig. 8, surface of spore; fig. 9, spore of *T. rugispora*.

8. **Tilletia de Baryana**, *Fischer de Waldh. in Bull. Soc. Imp. Nat. Moscow*, xl. (1867), 251.—Spore-mass blackish brown, forming elongated streaks on the leaves of the host plant; spores globose, rarely irregularly globose or broadly elliptic, brown, 10–18 μ diam., border not obvious, epispore densely covered with minute dark-topped warts formed by the breaking up of the epispore.—Fischer

de Waldh., Aperçu (1877), 48. *T. striæformis*, Wint. in Rabenh., Krypt. Flora, Pilze, i. (1884), 108.; Sacc., Syll. vii. (1888), no. 1774. *T. Milii*, Fuckel, Symb. Myc. (1869), 40; Fischer de Wald., Aperçu (1877), 48. *T. Calamagrostis*, Fuckel, Symb. Myc. (1869), 40; Fischer de Wald., Aperçu (1877), 49; Sacc., Syll. vii. (1888), no. 1775. *T. serpens*, Karsten, Fung. Fenn. (1883), no. 599, with description. *T. aculeata*, Ule in Verhandl. bot. Ver. Brandenburg, 1884, 213, and in Hedwigia, 1886, 112; Sacc., Syll. vii. (1888), no. 1785, under "species minus notæ." *T. alopecurivora*, Ule in Verhandl. bot. Ver. Brandenburg, 1884, 214, and in Hedwigia, 1886, 113; Sacc., Syll. vii. (1888), no. 1787, under "species minus notæ." *T. Brizæ*, Ule in Verhandl. bot. Ver. Brandenburg, 1884, 214, and in Hedwigia, 1886, 113; Sacc., Syll. vii. (1888), no. 1786, under "species minus notæ." *Uredo striæformis*, Westend. in Bull. Acad. Belg. 1851, 406. *Ustilago Salveii*, Berk. and Broome in Ann. Nat. Hist., ser. 2, v. (1850), 463. *Ustilago macrospora*, Desmaz., Crypt. France, sér. i. (1850), no. 2127.

Hosts.—A variety of grasses. Students of this genus have separated the forms chiefly by the hosts. There is no real difference, as far as I am aware; but for convenience of reference I class the hosts and forms together. As *T. de Baryana* (typical form), on *Anthoxanthum odoratum*, Linn., *Brachypodium pinnatum*, Beauv., *Festuca ovina*, Linn., *Holcus lanatus*, Linn., *H. mollis*, Linn, and *Lolium perenne*, Linn. As *T. striæformis*, on *Agrostis alba*, Linn., *A. vulgaris*, With., *Arrhenatherum avenaceum*, Beauv., *Briza media*, Linn., *Bromus inermis*, Leyss., *Dactylis glomerata*, Linn., *Deyeuxia halleriana*, Vaisey, *Festuca elatior*, Linn., *F. ovina*, Linn., *Holcus lanatus*, Linn., *H. mollis*, Linn., *Lolium perenne*, Linn., *Milium effusum*, Linn., *Phleum pratense*, Linn., *Poa pratensis*, Linn. As *U. Salveii*, on *Dactylis glomerata*, Linn., *Brachypodium pinnatum*, Beauv. and another grass. As *T. Milii*, on *Milium effusum*, Linn. As *T. Calamagrostis*, on *Agropyron repens*, Beauv., *Calamagrostis halleriana*, DC. and *C. lanceolata*, Roth. As *T. serpens*, on *Dactylis glomerata*, Linn. As *T. aculeata*, on *Agropyron repens*, Beauv. As *T. alopecurivora*, on *Alopecurus pratensis*, Linn. As *T. Brizæ*, on *Briza media*, Linn.

Hab.—Europe, except Russia and the Mediterranean region; United States.

Exsicc.—Under name of *Ustilago Salveii*, Cooke, Fung. Brit., 57; Westend., Herb. Crypt. Belg. 1164, Thümen, Fung. Aust., 840; Desmaz., Crypt. France, sér. 2, 1; Vize, Fung. Brit., 133. Under *Ustilago macrospora*, Desmaz., Crypt. France, sér. 1, 2127. Under *T. striæformis*, Rabenh.-Wint., Fung. Eur., 3503; Sydow, Myc. March., 1416, 1610, 2013, 2014, 3009; Ellis, N. Am. Fung., 1498. Under *T. de Baryana*, Rabenh., Fung. Eur., 1097, 2491, 3393; Westend., Crypt. Belg., 677; Thümen, Fung. Austr., 1230, and Fung. Univ., 1020; Sydow, Myc. March., 20, 26. As *T. Milii*, Fuckel, Fung. Rhen., 2410. As *T. Calamagrostis*, Fuckel, Fung. Rhen., 1925; Sydow, Myc. March., 2620; Zopf and Sydow, Myc. March, 10; Rabenh., Fung. Eur., 2694. As *T. aculeata*, Rabenh.-Wint., Fung. Eur., 3603. As *T. alopecurivora*, Sydow, Myc. March., 2120.

The types of most of these names have been seen. Berkeley's type is with his own specimens at Kew. . Specimens illustrative of Desmazière's, Westendorp's, Fischer de Waldheim's, Fuckel's, Ule's and Karsten's names authenticated by these writers have been seen. Sydow's Myc. March., 2120, if correctly named, determines *T. alopecurivora* to be a form of *T. de Baryana*. Lastly, Ule's very unsatisfactory account of *T. Brizæ* makes this appear another form of the same species.

Fig. 6, sori ; fig. 7, spore of *T. de Baryana*.

9. **Tilletia arctica,** *Rostr. in Bot. Tidssk.*, 1886, 230.—Spore-mass forming black, very long, parallel streaks on the leaves and culms ; spores globose or ovoid, blackish-brown, 13–19 μ diam., epispore very minutely papillose.—Sacc., Syll. vii. (1888), no. 1781.

HOST.—*Carex festiva*, Dewey.

HAB.—Finland.

Appears to be allied to *Tilletia de Baryana* : not examined.

10. **Tilletia epiphylla,** *Berk. & Broome in Trans. Linn. Soc.*, ser. 2, (Bot.) ii. (1882), 67. Spore-mass subpulverulent, brown, forming elongated pustules on the leaves of the host ; pustules gregarious, each seated on a small yellow spot, narrow, 1–2 mm. long ; spores globose, 35–38 μ diam. ; wall thin, pale brown, translucent ; epispore with exceedingly minute warts.—Sacc., Syll. vii. (1888), no. 1783.

HOST.—*Zea Mays*, Linn.

HAB.—Queensland, *Bailey*, 228.

Berkeley and Broome describe the spores as smooth, but when carefully examined under a magnification of 400 diameters, the epispore is seen to be studded at regular intervals with very minute warts. The gregarious, small, linear pustules resemble a *Puccinia* superficially. Type specimen examined.

11. **Tilletia hyalospora,** *Massee.*—Spore-mass pale wood-colour, occupying the ovary. Spores globose or subglobose, 20–24 μ diam., border 2–2·5 μ wide ; surface reticulated ; there are usually 3–5 more or less parallel, simple or forked prominent ridges, connected by thinner and lower transverse bars.

HOST.—*Piptochætium* sp.

HAB.—Bolivian Andes, near Sorata, about 11,500 ft. *Mandon*, 1275.

Characterised by the type of ornamentation of the epispore. A primary band appears as if wound in an oblique spiral round the spore, as in the carpogonium of a *Chara*, the more or less parallel lines formed by this band being connected by thinner,

transverse bars. The specimen occurred in the ovary of a species of *Piptochætium* in Mandon's Plantæ Andinæ Bolivianæ. Type in herb. Kew.

Fig. 1, spore of *T. hyalospora*.

12. **Tilletia Lolii**, *Auersw. in Klotzsch, Herb. Myc.* (1854), 1999. —Spore-mass formed in the ovary, pale dull brown, foetid ; spores globose or sometimes broadly elliptic, pallid, averaging 20–25 μ diam., border 2·5–3 μ wide ; epispore furnished with thin ridges combined to form a shallow, small-meshed reticulation ; mesh averaging about 2 μ diam.—Fischer de Waldh., Aperçu (1877), 50 ; Wint. in Rabenh., Krypt. Flora, Pilze, i. (1884), 109 ; Sacc., Syll. vii. (1888), no. 1764.

HOSTS.—*Lolium perenne*, Linn. ; *Lolium temulentum*, Linn.

HAB.—Germany.

Exsicc.—Klotzsch-Rabenh., Herb. Myc., 1999.

Distinguished by the pale colour of the spore-mass, and the pale ochraceous or almost colourless spores when viewed by transmitted light, the thin ridges, and small, shallow network. Specimen from quoted exsiccata examined.

Fig. 21, spore of *T. Lolii*.

13. **Tilletia controversa**, *Kühn in Rabenh. Fung. Eur.* (1874), no. 1896, with description. Spore-mass blackish, produced in the ovary, foetid ; spores almost uniformly globose, pale brown, 18–25 μ diam., margin 3 μ wide, not paler, epispore furnished with ridges anastomosing to form a rather large-meshed network, mesh averaging 3–3·5 μ diam. Mycelium perennial in the rhizome of the host-plant.—Fischer de Wald., Aperçu (1877), 49 ; Wint. in Rabenh., Krypt. Flora, Pilze, i. (1884), 110 ; Sacc., Syll. vii. (1888), no. 1765. *T. calospora*, Passerini in Grevillea, v. (1876), 47 ; Fischer de Waldh., Aperçu (1877), 48 ; Wint. in Rabenh., Krypt. Flora, Pilze, i. (1884) 110 ; Sacc., Syll. vii. (1888), no. 1767.

HOSTS.—*Agropyron repens*, Beauv. ; *Agropyron glaucum*, Roem. & Schult. ; *Alopecurus agrestis*, Linn. ; *Elymus aralensis*, Regel.

HAB.—Italy, Germany, Austria, Turkestan.

Exsicc.—Rabenh., Fung. Eur., 1896 ; Roum., Fung. Sel. Gall., 4624 ; Flor. Exs. Austro-Hung., 351 ; Kunze, Fung. Sel., 210 ; Thümen, Myc. Univ., 1217 ; Rabenh., Fung. Eur., 2492 ; Roum., Fung. Gall. 1699.

Differs from *Tilletia endophylla* and from *T. Caries*, in the larger reticulations. *T. Rauwenhoffii* differs, on the other hand, from the present species in the much larger reticulations, and in the broader and almost colourless border of the spore.

The specimen of *T. controversa* in Rabenh., Fung. Eur., 1896, is authentic material and was communicated by Kühn. An authentic specimen of *T. calospora*, Passer., from the author also examined.

Fig. 18, spore of *T. controversa*.

14. **Tilletia cerebrina**, *Ellis and Everh. in Journ. Myc.* iii. (1887), 56.—Spore-mass formed in the ovary, dark brown or blackish; spores globose or sub-globose 23–28 μ and up to 30 μ long when ellipsoid, dark brown, border about 2·5 μ thick, paler; epispore ornamented with thickish ridges which are more or less sinuous and branched, the branches not unfrequently combining here and there to form an irregular reticulation, but free ends of the ridges are usually present in considerable numbers; mesh varying from 2–5 μ diam.—Sacc., Syll. vii. (1888), no. 1768.

HOST.—*Deschampsia cæspitosa*, Beauv.

HAB.—United States; Rocky Mountain region.

Characterised by the bands on the epispore being irregularly branched and as a rule having numerous free ends, although in some spores the reticulation is fairly uniform and free ends rare or absent. Authentic specimen from Ellis examined.

Fig. 12, spore of *T. cerebrina*.

15. **Tilletia buchloeana**, *Keller & Swingle in Journ. Myc.* v. (1889), 11.—Spore-mass formed in the ovary, dirty brown; spores globose or very slightly oval, 16·5–18 × 20–21 μ, brownish; epispore marked with scattered regular spines or faint reticulations (formed by coalescence of the spines ·5–1·5 μ high, covered by the outer hyaline layer, which is 1·5–4 μ thick.—Sacc., Syll. ix. (1891), no. 1178.

HOST.—*Buchloe dactyloides*, Engelm.

HAB.—United States; Kansas.

The fungus is borne on the male plants. In its presence often all or nearly all the staminate spikelets produce the ovaries, all of which are infested. The few female plants collected in the same localities were free from the fungus (*Keller & Swingle*). Judging from the figures the spores are reticulated at maturity. Not examined.

16. **Tilletia separata**, *Kunze, in Josh. Kunze, Fung. Select. Exs.* (1874), 29.—Spore-mass formed in the ovary, blackish brown, foetid; spores globose, irregularly or angularly globose, or broadly elliptic, clear brown, 20–27 μ diam., border about 3 μ wide, not appreciably paler; epispore with raised ridges anastomosing to form an irregular, small-meshed network, mesh averaging 1·5–2·5 μ diameter.—Wint. in Rabenh., Krypt.-Flora, Pilze i. (1884), 111; Sacc., Syll. vii. (1888), no. 1766. *T. decipiens*, Wint. in Rabenh.,

Krypt. Flora, Pilze i. (1884), 111; Sacc., Syll. vii. (1888), no. 1762. *T. Secalis*, Kühn in Fischer de Waldh., Aperçu (1877), 50; Wint. in Rabenh., Krypt. Flora, Pilze i. (1884), 110; Sacc., Syll. vii. (1888), no. 1763. *Erysibe sphærococca* α *Agrostidis*, Wallr., Flora Germ. Crypt. iv. (1833), 213. *Uredo decipiens* α, Strauss in Wetterau Gesell. Ann. ii. (1810), 111. *Uredo Secalis*, Corda in Hlubek, Œconom. Neuigk, 1848, 9, t. i. *Uredo segetum var. decipiens*, Pers., Syn. Fung. (1801), 225. *Uredo* (*Ustilago*) *sphærococca*, Rabenh., Krypt. Flora, Pilze ii. (1846), 213.

HOSTS.—*Secale cereale*, Linn.; *Apera Spica-venti*, Beauv.; *Agrostis alba*, Linn.; *Agrostis vulgaris*, With. (*Agrostis pumila*, Linn., is a form of *A. vulgaris* dwarfed by the *Tilletia*).

HAB.—Britain, France, Germany, Switzerland, Russia.

Exsicc.—Rabenh., Fung. Eur., 2191; Zopf & Sydow, Myc. March. 19; Flor. Gall. et Germ. Exs., 786; Roum., Fung. Sel. Exs. 5,706; Josh. Kunze, Fung. Sel. Exs., 29.

Distinguished from *Tilletia Caries* by the wider border of the spore and the smaller reticulations. The spores of *Tilletia endophylla* resemble those of *T. separata*; the first named, however, differs in forming the spore-mass in the leaves and not the ovary of the host. Examination of material in the exsiccata quoted above has been made.

Figs. 17 and 20, spores of *T. separata*, in one case germinating.

17. **Tilletia Caries**, *Tul. in Ann. Sci. Nat.*, sér. 3, vii. (1847), 113, t. 5, figs. 1–16.—Spore-mass produced in the ovary, blackish, with an olive sheen, foetid; spores globose, brown, 17–22 μ diam., border 1–1·5 μ, not paler; epispore furnished with ridges anastomosing to form a rather large-meshed network; mesh often variable in size and form, averaging about 3–3·5 μ.—Fischer de Waldh., Aperçu (1877), 49. *T. Tritici*, Wint. in Rabenh., Krypt. Flora, Pilze, i. (1884), 110; Sacc., Syll., vii. (1888), no. 1760. *Lycoperdon Tritici*, Bjerk. in Act. Suec., 1775, 326; *Uredo Caries*, DC., Fl. France, vi. (1815), 78. *Uredo sitophila*, Ditm. in Sturm, Deutchl. Flora, Abt. 3, pt. 1 (1817), 69.

HOSTS. — *Triticum vulgare*, Vill.; *Triticum Spelta*, Linn.; *Triticum monococcum*, Linn.

HAB.—Britain, France, Germany, Austria, Italy, Belgium, Switzerland, Russia, Finland, Algeria, Queensland, Victoria, United States, Chile.

Exsicc.—Rabenh. Fung. Eur., 2395; Cooke, Brit. Fungi, 53; Cooke, Fung. Brit., ed. 2, 429; Briosi e Cavara, Fung. Parasit., 155 (with figs.); Ellis and Everh., N. Amer. Fungi, 3236; Roum., Fung. Gall. Exs., 1645; Fuckel, Fungi Rhen., 252; Thümen, Myc. Univ., 724; Sydow, Myc. March., 2621; Vize, Fung. Brit., 130; Berk., Brit. Fungi, 113; Desm., Crypt. France, sér. 1, 124; Thümen, Fung. Austr., 343; Zack, Leiner u. Sitzenb., Krypt. Badens, 401; Sacc., Myc. Ven., 1153 (mixed with *Tilletia lævis* Kühn); Holl, Schmidt und Kunze, Deutschl. Schwamme, 190.

Remarkable for the narrow coloured border of the spore. Somewhat resembling in spore-characters *Tilletia endophylla*. The spores of the latter are, however, larger, darker in colour, with a wider border, and altogether larger in size; moreover, *T. endophylla* forms elongated blackish streaks on leaves, and is not produced in the ovary.

Fig. 13, *T. Caries* in an ear of wheat; fig. 14, spore; fig. 15, two sporidia after conjugation.

18. **Tilletia Elymi**, *Dietel and Holway in Bot. Gaz.*, xix. (1894), 305.— Spore-masses black, destroying the ovaries; spores globose, dark olive brown, 24–28 μ diameter. Epispore reticulated with ridges 2·6–4 μ high and about 3 μ apart.—Sacc., Syll. xi. (1895), no. 1338.

HOST.—*Elymus* sp.

HAB.—United States; Skamania co., Washington State, *W. N. Suksdorf*.

Appears to be closely allied to *Tilletia controversa*, Kühn, which has also been recorded as occurring in the ovary of a species of *Elymus*. Not examined.

19. **Tilletia inolens**, *McAlpine in Agric. Gaz. of N. S. Wales*, vii. (1897), 154, figs. 30–33.—Produced in inflorescence and on upper leaves, black, powdery, without smell. Mycelium septate, hyaline, 4–5 μ thick. Spores globose, dark brown, 28–36 μ diam., average 33 μ; ridges of epispore 4 μ high, yellowish brown; meshes polygonal, about 4–5 μ diameter.

HOST.—*Deyeuxia Forsteri*, Kunth.

HAB.—Victoria, Ardmona.

Not examined. Appears to be most closely allied to *T. Rauwenhoffii*, Fischer de Waldh.

20. **Tilletia Rauwenhoffii**, *Fischer de Waldh., Aperçu* (1877), 50.— Spore-mass produced in the ovary, blackish; spores almost constantly globose, olive-brown, 25–30 μ diam.; border almost colourless, 3–4 μ wide; epispore ornamented with prominent ribs anastomosing to form a network of large irregularly hexagonal reticulations; mesh averaging 3·5–4 μ diameter.—Sacc., Syll. vii. (1888), no. 1769. *Polyactis Holci*, Westend. in Bull. Acad. Belg., sér. 2, xi. (1889) 660, fig. 1.

HOSTS.—*Holcus lanatus*, Linn., *Holcus mollis*, Linn.

HAB.—Belgium, England, Ireland.

Exsicc.—Rabenh.-Wint., Fung. Eur., 3104; Roum., Fung. Gall., 3509.

Readily distinguished by the very large size of the network on the epispore, usually only 4–6 areolæ being present on a

hemisphere ; also by the very wide, almost colourless, border. Authentic specimens from Westendorp and Fischer de Waldheim examined.

Fig. 4, spore of *T. Rauwenhoffii ;* fig. 5, the fungus on *Holcus mollis.*

21. **Tilletia fusca,** *Ellis & Everh. in Journ. Myc.* iii. (1887), 55.—Spore-mass occupying the ovary, dark olive-brown ; spores globose or sub-globose, 16-25 μ diam., brown border about 2 μ broad, paler ; the epispore ornamented with raised ridges anastomising to form an irregular network ; mesh averaging 3 μ diameter.—Sacc., Syll. vii. (1888), no. 1771. *T. asperifolia,* Ellis and Everh. in Journ. Myc. iii. (1887), 55 ; Sacc., Syll. vii. (1888), no. 1772. *T. montana,* Ellis and Everh. in Journ. Myc. iii. (1887), 55 ; Sacc. Syll. vii. (1888), no. 1773.

HOSTS.—*Festuca microstachya,* Desv. (?) ; *Sporobolus asperifolius,* Nees and Meyen ; *Sporobolus gracillimus,* Vasey.

HAB.—United States, Rocky Mountain region.

Allied to *Tilletia Caries,* but distinguished by the spore-mass not being foetid, the larger spores, larger and more irregular reticulations, and border paler than the remainder of the spore. Specimens illustrating the species and its two synonyms enumerated above were received from Ellis. The specimen from the author called *T. fusca,* agrees exactly with the original description of this species in *Journ. Myc.* iii. (1887), 55. On the other hand, further material issued under the name of *Tilletia fusca* (Ellis and Everh., N. Amer. Fung., ser. 2, 1895, in ovary of *Festuca microstachya,* from Boise City, Idaho) does not at all agree with the diagnosis of the species as quoted above, but has the epispore densely and minutely warted, and is identical with *Tilletia mixta,* Massee.

The priority of the specific name *fusca* turns on this name standing first in order on the same page where *montana* and *asperifolia* are also described.

Fig. 11, spore of *T. fusca.*

22. **Tilletia Hordei,** *Körn. in Hedwigia,* 1877, 30. Spore-mass formed in the ovary, blackish-brown ; spores globose or broadly elliptic, brown 19·5-20·5 μ diam., or 19 × 21 μ, border about 2·5 μ thick, epispore covered with a small-meshed network ; mesh averaging 2 μ diameter.—Sacc. Syll. vii. (1888), no. 1770. *T. Trabuti,* Jaczewski in Bull. Soc. Myc. France, ix. (1893), 50.

HOSTS.—*Hordeum fragile,* Boiss. ; *Hordeum murinum,* Linn.

HAB.—Turkey, Assyria, Algeria.

Closely resembling *Tilletia Caries* in spore-structure ; the border is a little wider in the present species. Specimen from Algiers examined.

Fig. 24, spore of *T. Hordei.*

23. **Tilletia zonata**, *Brefeld. Unters. Mykol.* xii. (1895), 161, t. x., figs. 3–7.—Spore-mass formed in the flower-bud, blackish; spores globose, 15-18 μ diam., with a thin external gelatinous layer; epispore brown, furnished with slightly raised ridges anastomosing to form a network.—Hedwigia, Beibl. (Elench. Fung. nov.), 1896, xxi.

HOST.—*Sporobolus ligularis*, Hackel.

HAB.—Ecuador.

The above is vaguely and briefly described by Brefeld in the work quoted; the mode of germination is however given in detail, and beautifully illustrated. Apparently closely allied to *Tilletia fusca*.

24. **Tilletia endophylla**, *de Bary in Rabenh., Herb. Myc.*, ed. 2, 500.—Spore-mass forming blackish-brown streaks on the leaves of the host 1–3 cm. long; spores globose, angularly globose, or broadly ellipsoid, 18–25 μ diam., border about 2 μ wide, altogether brown; epispore ornamented with a rather small-meshed reticulation, the walls of which are thickish; mesh averaging about 2 μ diameter.—Fischer de Waldh., Aperçu (1877), 49; *T. olida*, Wint. in Rabenh., Krypt. Flora, Pilze, i. (1881), 107; Sacc., Syll. vii. (1888), no. 1761; *Uredo olida*, Riess, in Klotzsch-Rabenh., Herb. Myc., 1695.

HOSTS.—*Brachypodium pinnatum*, Beauv.; *Brachypodium sylvaticum*, Beauv.

HAB.—Austria, Germany.

Exsicc.—Klotzsch-Rabenh., Herb. Myc., 1695; Rabenh., Herb. Myc., ed. 2, 500; Rabenh., Fung. Eur., 2293; Rabenh.-Wint., Fung. Eur., 3703.

The only species with reticulated spores that forms long sori, or streaks, on leaves. The reticulations are smaller and more numerous than in *Tilletia Caries*. Specimens from the exsiccata quoted above, examined.

Fig. 16, spore of *T. endophylla*.

25. **Tilletia Sesleriæ**, *Juel in Öfvers. af Kongl. Vet. Akad. Förhandl. Stockholm*, 1894, 494.—Spore-mass forming very long, thin black streaks on the leaves; spores irregularly globose, dark brown, 25–28 μ diam., epispore furnished with ridges which anastomose to form a network.

HOST.—*Sesleria cœrulea*, Ard.

HAB.—Gothland.

The author compares this species with *Tilletia endophylla*, Wint., from which it differs more especially in the larger spores. Not examined.

26. **Tilletia Berkeleyi**, *Massee*.—Spore-mass forming blackish streaks on the culm, up to 1 cm. long, not foetid when moistened; spores constantly globose, brown, 15–18 μ diam., border 1 μ wide,

epispore furnished with very thin, slightly raised ridges, which anastomose to form a very small-meshed network ; mesh averaging 1·5 μ diameter.

HOST.—*Triticum vulgare*, Vill.

HAB.—England ; King's Cliffe, Northamptonshire, *Berkeley*.

A very distinct species, included by Berkeley under *Tilletia Caries*, in his herbarium. Differs from the last-named, and from all other described species in the small-sized spores, and in the very small mesh formed by the thin, slightly raised ridges on the epispore. Forming blackish lines on the culm ·5–1 cm. long.

Fig. 23, spore of *T. Berkeleyi*.

27. **Tilletia Sphagni**, *Nawaschin in Bot. Centralbl.* 43 (1890), 289.—Spore-mass brown, filling the capsules of *Sphagnum* ; spores globose, 11–12 μ diam. ; epispore clear brown, ornamented with a polygonal network.—Sacc. Syll. ix. (1891), no. 1180.

HOST.—*Sphagnum squarrosum*, Pers.

HAB.—Russia.

This species is probably widely diffused, although only definitely recorded from Russia. The *Tilletia* spores are those bodies which have previously been spoken of as the microspores of *Sphagnum*, and the capsules in which they are produced were known as microsporangia. Not examined.

Doubtful Species.

28. *Tilletia Avenæ*, Ule in Hedwigia, 1886, 113 ; Sacc. Syll. vii. (1888), no. 1784.

There is no published description of this species.

29. *Tilletia Fischeri*, Karsten in Finska Vetenskaps-Societeten, 1879, 10 ; Myc. Fenn. iv. p. 10.—Spore-mass formed in the ovary, black ; spores globose or sub-globose, brown, about 14 μ diam. or 16 × 12 μ.—Sacc., Syll. vii. (1888), no. 1799.

HOST.—*Carex canescens*, Linn.

HAB.—Finland.

The brief and incomplete diagnosis prevents placing this species in any one section employed in the present paper, and it is not wise to trust to the host for the discrimination of a species.

30. *Tilletia Vulpiæ*, P. Magnus in Verhandl. d. Zool.-Bot. Gesell. Wien, xlix. (1899), 89, t. 2, figs. 7–12. Spore-mass produced in the ovary, blackish, 19·2 × 16·9 μ ; epispore with a raised network.

HOST.—*Festuca Myurus*, Linn.

HAB.—Kurdistan.

Not examined. The diagnosis is too vague to admit of indicating its affinities.

Excluded Species.

31. *Tilletia corona*, Scribner in Bot. Gaz. xxiii. (1896), 210.

HOSTS.—Infesting the ovary in *Leersia oryzoides*, Swartz; *L. virginicus*, Willd.; *L. lenticularis*, Michx.; *Panicum virgatum*, Linn.; *P. sanguinale*, Linn.; and *Oryza sativa*, Linn.

HAB.—United States.

Exsicc.—Ellis, N. Amer. Fung., 1896.

This is obviously a species of ***Neovossia***, and will stand as *Neovossia corona*. The specimen in Ellis, N. Amer. Fung. 1896, examined.

32. *Tilletia* (?) *glomerulata*, Cocc. et Mor., Enum. Funghi, Bologna, Cent. ii., 6, tab. 1, figs. 1–3; Sacc., Syll. vii. (1888), no. 1782.

Judging from the description and figures, this is certainly not a species of *Tilletia*.

33. *Tilletia ? irregularis*, Pazschke in Rabenh.-Wint.-Pazschke Fung. Eur. et Extra-Europ., 4004 (with description); Hedwigia, Beibl. (Elench. Fung. nov.), 1896, xxi.

HOST.—On living leaves of *Andropogon* sp.

HAB.—Brazil; Sta. Catharina.

Examination of material from the exsiccata quoted above shows very clearly that the fungus is not a *Tilletia*, but some Hyphomycetous form with dark olive spores arranged in lines, and distinctly springing from a pseudoparenchymatous stroma immersed in the substance of the leaf.

34. *Tilletia **Moliniæ***, Wint. in Rabenh., Krypt. Flora, Pilze, i. (1884), 109; Sacc., Syll. vii. (1888), no. 1778. *Neovossia **Moliniæ***, Körn. in Oester. Bot. Zeitschr. xxix. (1879), 217; Brefeld, Unters. Mykol. xii., 210, t. x., fig. 8–28. *Vossia **Moliniæ***, Thümen in Oester. Bot. Zeitschr. xxix. (1879), 18.

HOST.—In ovary of *Molinia cærulea*, Moench.

HAB.—Carniolia.

EXSICC.—Roum., Fung. Sel., 4922 (comm. Voss); Flor. Ex. Austro-Hung., 353 (comm. Voss); Thümen, Fung. Austr., 1216.

This species differs from *Tilletia* in the mode of spore-germination, and must consequently return to *Neovossia; Vossia*, the name originally given by Thümen, being already used for a genus of grasses. Portion of the type specimen sent by Thümen to Herb. Kew, also the material in the quoted exsiccata, examined.

Figs. 2 and 3, spores of *Neovossia Moliniæ*.

35. *Tilletia Orizæ*, Pat. in Bull. Soc. Myc. France, iii. (1887), 124, t. x., fig. 2.—Spores globose or ovoid, 3–5 μ diam., olive brown, warted, united into a hard blackish green mass, mixed with slender hyaline filaments with an irregular outline.—Sacc., Syll. ix (1891), no. 1179.

HOST.—Attacks the fruit of rice, *Oryza sativa*, Linn., which becomes enlarged, black, and hard like a sclerotium.

HAB.—Japan ; Environs of Yokosha, Island of Nippon.

The description proves that this fungus is not a *Tilletia*, in fact it forms the type of a new genus—*Ustilaginoidea*, established by Brefeld, who cannot indicate its affinities. There are two species, *U. Oryzæ* and *U. Setariæ*. Perhaps it would have been wiser not to have established a new genus until it could have been diagnosed by other features than spore-germination alone. Every mycologist is deeply indebted to Brefeld for his marvellous researches on spore-germination, but as to whether mycologists have accepted the idea that everything systematic rests on this one feature, or whether it is really to be regarded as the fundamental and only feature of value, remains yet to be decided.

36. *Tilletia sterilis*, Ule in Verhandl. bot. Ver. Brandenburg, 1884, 214 ; Hedwigia, 1886, 114 ; Sacc., Syll. vii. (1888), no. 1788, under "Species minus notæ."

HOST.—*Festuca ovina*, Linn. ; *Kœleria cristata*, Pers.

HAB.—Germany.

Exsicc.—Rabenh.-Wint., Fung. Eur., 3605 (comm. Ule).

The different accounts of this hypothetical species, as given by Ule, are very unsatisfactory. The author on finding certain black streaks on leaves appears to have assumed that a *Tilletia* was the cause, but lacking satisfactory evidence called the species *sterilis*, probably as a reproach for its sterility. The specimen furnished by Ule to Rabenhorst's exsiccata conforms with the specific name, and may, so far as the Kew copy is concerned, be described as *sterilis*.

37. *Tilletia Thlaspeos*, Beck in Verhandl. Zool.-Bot. Gesell. Wien, 1885, 361.—Spore-mass ochraceous, produced in the ovules ; spores globose or rarely subglobose, ochraceous, semipellucid, 14·7–17·5 μ diam. ; epispore densely verruculose-aculeate.

HOST.—*Thlaspi alpestre*, Linn.

HAB.—Austria.

Developing in ovules of scarcely deformed fruit of *Thlaspi alpestre*. Not examined. Judging from the description, the present fungus is not a *Tilletia* but a *Sorosporium*.

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Specific names in *italics* are those not retained.

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„ 4. Spore of *Tilletia Rauwenhoffii*, × 750.
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DCLVII.—CENTRAL AMERICAN RUBBER.

(*Castilloa elastica*, Cerv.)

Some account of *Castilloa* rubber, and of the species producing it, was given in the *Kew Bulletin* for 1887, pp. 13–16. Since then its cultivation as a source of rubber-supply has attracted some attention in Mexico and the West Indies. It has not, however, been easy to obtain any trustworthy data as to the practical methods to pursue or as to the cost and return to be expected. The following account is therefore reprinted from the United States Consular Reports (May, 1899, pp. 147–151). It appears to have been drawn up by a man conversant with the subject and with a good deal of care :—

" Consul-General Beaupré sends from Guatemala, under date of January 28, 1899, a translation of an article on rubber prepared by Mr. José Horta, of the city of Guatemala. Mr. Horta, adds the Consul-General, is an experienced agriculturist, and has handled the subject ably. Extracts from his report are given below.

" In Guatemala *Castilloa elastica*, Cerv., is found in the wild state, and covers an immense zone in Central America; the rubber which this tree produces is one of the best and most valuable for the industry.

" The *Castilloa elastica* is a tall, well-shaped tree, with smooth, greenish-white bark. At a height of from 15 to 20 yards from the ground there start from the trunk (of spongy and porous