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**TWO DOWNY MILDEWS OF THE NETTLE:
PSEUDOPERONOSPORA URTICAE (LIB.) SALM.
ET WARE AND PERONOSPORA DEBARYI
NOMEN NOVUM.**

*By Prof. E. S. Salmon and W. M. Ware, M.Sc.,
South-Eastern Agricultural College, Wye, Kent.*

(With six Text-figures.)

I. SYSTEMATIC.

In 1925 we pointed out that *Peronospora Urticae*, germinating by zoospores, should be transferred to the genus *Pseudoperonospora*. In 1926, in the course of further work, we found that a second downy mildew on the Nettle, germinating by a germ-tube, existed. It became necessary, therefore, to review criti-

cally the information on *Peronospora Urticae* given in mycological literature, and to examine the material available in herbaria.

In 1846 Berkeley, in his observations on the "Potato Murrain," wrote in describing *Botrytis infestans* Mont.—now *Phytophthora infestans*—"The peculiar characters of the species consist in the few erecto-patent not forcipated or uncinated branches, the scattered spores and above all the torulose swellings which give it somewhat the appearance of *Gonatotryps*. The spores however are not disposed round the knots as in that genus and *Arthrobotryps*, or even confined to them. The only species which exhibits anything of the kind is the one which has been named *Botrytis Urticae* by Mlle Libert, and which indeed M. Desmazières considered as identical. It appears to me however that it is quite distinct, the flocci being far more divided, the apices bifid, and the colour, instead of white, a greyish lilac. I have had the opportunity, fortunately, of comparing specimens, which occurred in the autumn, at Tansor, in Northamptonshire, with authentic individuals from M. Desmazières."

In 1851 Berkeley and Broome gave a fuller description of the fungus on the Nettle, as follows: "*Botrytis Urticae* Libert MSS. On leaves of the common nettle, Tansor, Norths. Patches small, orbicular, greyish lilac, flocci loosely divided above, branches forming an acute angle, extreme ramuli simple or forked, sometimes curved, very rarely inflated. Spores large, ovate, apex papillaeform. Allied to the last [*Botrytis infestans* Mont.*] but distinct. When the flocci are ruptured, the inner membrane sometimes protrudes, as in the asci of *Sphaeriae*."

In 1855 Caspary transferred the species to the genus *Peronospora*, without giving any description.

In 1860 Berkeley, in *Outlines of British Fungology*, placed the species in *Peronospora* under the name *P. Urticae* Casp.

In 1863 de Bary, in his monographic study of the group, published the following account of a downy mildew on *Urtica*: "*Peronospora Urticae* (Lib.); *Botrytis Urticae* Libert MSS. apud Berkeley, Journ. Hort. Soc. Lond. 1, p. 31. Berkeley et Broome, Notices on Brit. Fungi, in Ann. Mag. Nat. Hist., ser. 2, vol. VII, p. 100.—*Stipites conidiferi humiles, laxae 4-6-ies dichotomi; rami flexuosi, ultimi subulati arcuati saepe deflexi. Conidia magna, late ovoidea vel subglobosa, distincte pedicellata, apice obtusissima, membrana dilute violascente. Oosporae mediocres, episorio sordide fusco.*—In *Urticae urentis* L. foliis legi, in agro francofurtano. In Gallia et Anglia a cell. Desmazières et Berkeley ("On leaves of the common nettle") lecta est. Rara esse videtur in Germania australiore, saltem frustra saepe quaesita est. *Caespites conidiferi maculiformes, densi, humiles,*

* Now *Phytophthora infestans*.

pallide violascentes, in foliorum pagina inferiore proveniunt. Stipites conidiferi illis *Peronosporae effusae* valde similes sunt. Descriptio a cell. Berkeley et Broome l.c. data ad nostram non quadrat. Specimina gallica et anglica non vidi; icone autem visa, quam ad specimina Desmazieriana cel. Berkeley delineavit et cum Casparyo in litteris communicavit, non dubito fungum meum, speciem Libertianam et Berkeleyanam revera sistere."

The species was included by de Bary in his section *Pleuroblastae*, defined as follows: Conidia non papillata, membrana circumcirca aequali hyalina aut violascente praedita, germinando tubum simplicem et aliquo superficiei puncto, plerumque ex latere, protrudentia.

As we shall show later, the species described by de Bary differs *in toto* from the fungus described earlier by Berkeley. Let us first confine our attention to Berkeley's species as determined by the herbarium material available. Berkeley stated (1) that this species had "been named" *Botrytis Urticae* by Libert. No indication is given by Berkeley that Libert ever published a description, and his use of the name "*Botrytis Urticae* Libert MSS." in 1851 would seem to show that he believed that it existed in manuscript only. We have not been able to trace any publication of the name or description of the fungus by Libert, nor have we been able to learn of the existence of any type specimen of *Botrytis Urticae* in Libert's herbarium deposited at the Jardin Botanique de l'État at Brussels. In response to our enquiry, Professor E. Wildeman kindly made a search but has been unable to find a specimen labelled *Botrytis Urticae**

Berkeley's herbarium at Kew contains a specimen labelled, in Berkeley's handwriting: "*Botrytis Urticae* Libert. M. Desmazières. Lille." On this sheet is a drawing, made by Berkeley, showing clearly the rigid branching of the conidiophore and the oval, minutely papillate, conidium. We have examined this fungus, which agreed perfectly with the drawing, and obtained the following measurements: Conidium: $27 \times 18 \mu$, $28 \times 18 \mu$,

* Professor E. Wildeman was good enough to send us two specimens from Libert's herbarium, labelled respectively, in Libert's handwriting: "*Oidium ? species nova*" and "*Oidium Urticae* N. hypophyllum caespitibus rotundis demum confluenso sat expansis floccis erectis ramosis albis articulis dilatibus ovali-oblongis didymis ? an hujus generis. In foliis vivis Urticae dioicae. Autumnno." The second specimen is mounted on a sheet labelled "*Peronospora urticae* (Lib.) de Bary," to which has been added, in pencil, "f. Delogne." The fungus in both these specimens is *Ramularia* and obviously has nothing to do with the fungus called *Botrytis Urticae* by Libert.

In the hope of learning of the existence in Desmazières' herbarium of a specimen of *B. Urticae*, labelled or collected by Libert, we wrote both to Paris and Lille. Professor E. Foëx has informed us that after a search made by him and M. Biers at the Museum (Paris), no specimen of *B. Urticae* could be found there in Desmazières' herbarium, in that of Montagne, in Libert's Reliquiae mycologicae, or in the general herbarium. The Curator of Cryptogams, of the Faculty of Sciences of Lille, has informed us that they possess only the Exsiccati published by Desmazières, in which no example of *B. Urticae* occurs.

$32 \times 20 \mu$, $25 \times 18 \mu$, $33 \times 22 \mu$. Oospore (globose) diameter 30μ , 28μ , 34μ . The host plant is *Urtica dioica*.

The above material doubtless represents the "authentic individuals from M. Desmazières" to which reference is made by Berkeley in his original description in 1846. There is no evidence that this fungus was collected by Libert, but in the absence apparently of any type specimen in Libert's herbarium, we have to rely on this identification by Desmazières. In Berkeley's herbarium also, is a specimen labelled (in Berkeley's handwriting) "*Botrytis Urticae* Libert. Tansor 1845." This fungus, on *Urtica dioica*, has conidia minutely apiculate and borne on conidiophores with rigid, non-flexuose branches. It is clearly identical with Desmazières's specimen. Another example of the fungus exists in Broome's herbarium at the British Museum (Natural History), and is labelled "*Botrytis Urticae* Lib. Tansor, Northampt^e. 1845 ex herb. M.J.B." Two conidia, minutely apiculate, measured $29 \times 18 \mu$ and $28 \times 18 \mu$.

Turning now to the diagnosis given by de Bary of his *Peronospora Urticae*, we find that in place of the "ovate" conidium, with "apex papillaeform" of Berkeley's *P. Urticae*, we have the "broadly ovoid or subglobose" conidium, with apex "very obtuse." It is not surprising then that de Bary remarked that Berkeley and Broome's description of their species did not agree with his. De Bary himself explains that in spite of this obvious discrepancy he used Berkeley's name because he saw a drawing, made by Berkeley, on specimens collected by Desmazières, which had been sent by Berkeley in a letter to Caspary, and this drawing convinced him that his species was in very truth ("revera") the same as that of Libert and of Berkeley*.

De Bary, then, considered the evidence furnished by this drawing of greater importance than the characters given in Berkeley and Broome's diagnosis. After de Bary's pronouncement that his *Peronospora* with very obtuse conidia was really identical with Berkeley's *Peronospora* with apiculate conidia, all systematists for the next sixty-five years followed him in misapplying Berkeley's name. As a result, Exsiccati sent out contain two perfectly distinct species under the name *Peronospora Urticae*.

Out of this misunderstanding, a new entity soon appeared—a fictitious compound arising from the confusion. Cooke, in 1865, under *Peronospora Urticae* Casp., described the conidia as "large, broadly ovoid or subglobose...apices very obtuse"—the diagnosis being obviously copied from de Bary. Cooke then adds: "On leaves of the Common Nettle," whereas de Bary's

* One is led to speculate whether possibly Berkeley sent to Caspary a drawing in which the shape of the conidium was not so clearly indicated as on the specimen in his herbarium at Kew.

species was described from examples on *Urtica urens*, on which species alone it occurs. In 1871, Cooke, in his *Handbook of British Fungi*, describing *P. Urticae* Casp., quoted references both to de Bary and to Berkeley and Broome and gave a diagnosis consisting, first, of that given by de Bary ("acrospheres large, broadly ovoid or subglobose...apices very obtuse") and then of that of Berkeley and Broome ("acrospheres large, ovate, apex papillaeform"). No doubt Cooke was puzzled—as we are to-day—by de Bary's pronouncement on the subject, and perhaps he did the best that was possible at that time by giving without comment, under the one species, the two diagnoses.

Massee, in his *Phycomycetes and Ustilagineae* (1891), described *P. Urticae* de Bary as having "broadly elliptical or subglobose" conidia with the apex "very obtuse," and adds: "Cooke says that the gonidia [conidia] have the apex papillaeform, but very obtuse." In this last sentence we reach the depth of the confusion*.

In 1888 Berlese and de Toni, in Saccardo's *Sylloge Fungorum* (6), in describing *P. Urticae* (Lib.) de Bary†, give de Bary's diagnosis ("conidiis...apice obtusissimis") and the size of the conidia as $22-26 \times 17-20 \mu$. References are given to de Bary, Berkeley and Broome, and Cooke. This fictitious species is stated to occur on *U. urens* and *U. dioica* in France, Belgium, England, Germany and North America‡.

In 1898 Berlese, in his *Icones Fungorum*, described *P. Urticae* (Lib.) de Bary as having "conidia broadly ovoid or subglobose," and the measurement of the conidium is given as $20-27 \times 18-22 \mu$, and that of the oospore as $30-32 \mu$. In Tab. LXIII the conidium is represented as broadly ovoid, very obtuse at the apex and with no apiculus. It is stated that this plate was drawn from the specimens sent out in Linhart's *Fungi hungarici*, No. 487, and compared with many others. We have examined the fungus in Linhart's *Exsiccati* and found it to be de Bary's species; Berlese's Tab. LXIII well illustrates the spore with its very obtuse apex. References are however made to Berkeley and Broome, and probably on this account *Urtica dioica* is inaccurately given as a host-plant.

In 1904 Berlese, in his "Saggio di una Monografia delle Peronosporacee," gave the same diagnosis with very similar drawings, quoting the following *Exsiccati*: Fuckel, *Fungi Rhen.*

* The same confusion is shown in Massee's *Diseases of Cultivated Plants and Trees* (1910), p. 110, where it is remarked that the "broadly elliptical" conidia "have generally a suggestion of a papilla at the apex."

† As we have previously pointed out (17), Caspary and not de Bary was the first to place the present species in *Peronospora*.

‡ We are not attempting to deal in the present paper with the records of *P. Urticae* from America.

1510; Thuem, Myc. univ. 345; Linhart, Fungi Hungar. 487; Rabenh., Fungi Eur. 1665; Schneider, Herb. Schles. Pilze, n. 36, 270. With the exception of the last named, we have examined examples of all the above Exsiccati in the British Museum (Natural History) London and can state that the fungus is in each case de Bary's species with non-apiculate conidia, and in every instance the host plant is *U. urens*. From the above it is clear that the species known to Berlese as *P. Urticae* was de Bary's and not Berkeley's species.

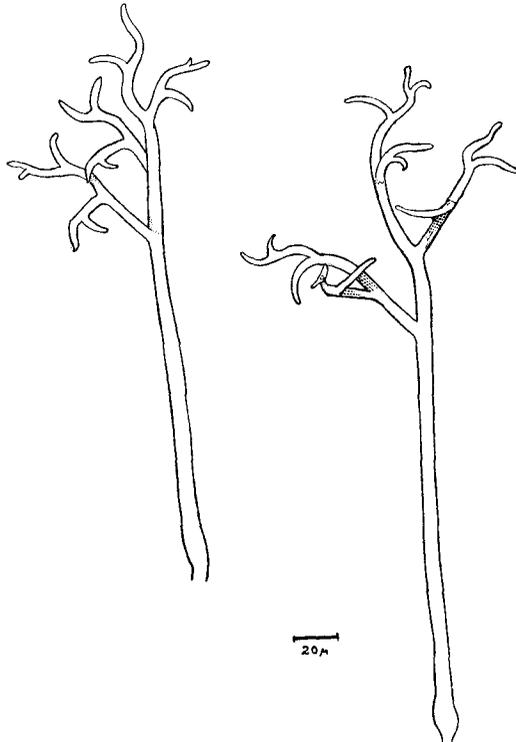


Fig. 1. *Peronospora de Baryi*. Conidiophores. ($\times 250$.)

Fischer, in 1892, described *P. Urticae* (Lib.) de Bary as having conidia "breit eiförmig, stumpf, durchschnittlich 20μ breit, 26μ lang," and as occurring on *U. dioica* and *U. urens*, but more frequently on the latter. Since, so far as we know, de Bary's species with non-apiculate spores occurs only on *U. urens*, it would appear either that Fischer did not notice the different conidial characters of the fungus occurring on *U. dioica*, or that he added this host species because he found it given in Berkeley's account, to which he refers.

Migula, in 1910, under the name *P. Urticae*, described the

conidia as "kurz eiförmig, stumpf, etwa 20μ dick, 26μ lang"; this description fits de Bary's species, but again the host plants are given as *U. dioica* and *U. urens*.

In 1923 Gäumann's important work "Beiträge zu einer Monographie der Gattung *Peronospora*" appeared. In his treatment of *P. Urticae* Gäumann relies on de Bary for the specific diagnosis and gives a figure showing a conidiophore with flexuose branches and subglobose conidia with very obtuse non-apiculate apex. He gives *Urtica urens* as one of the host plants and under

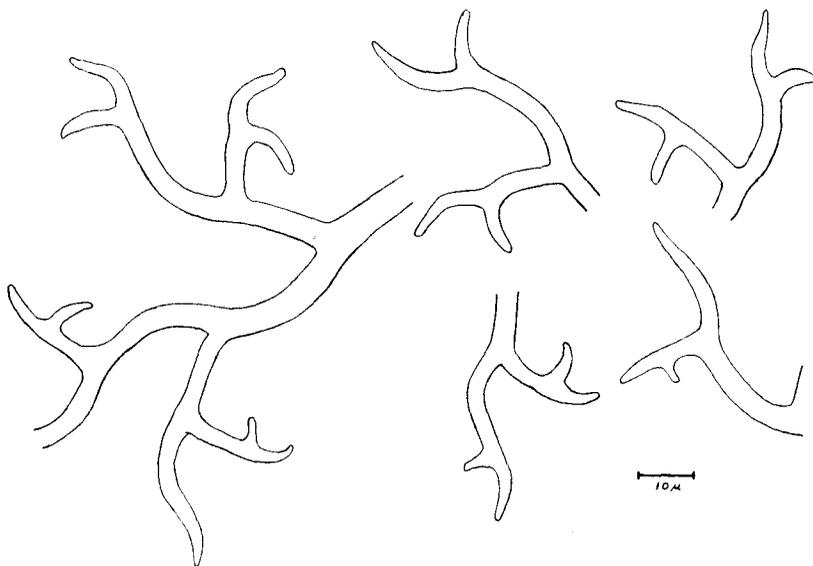


Fig. 2. Ultimate branches of the conidiophore. ($\times 750$.)

this host plant quotes eight Exsiccati all of which (except one, viz. Roumeguère F. sel. exs. 4256) we have seen and found the contained fungus to be de Bary's species. Gäumann also gives *Urtica dioica* as a host plant and quotes Vestergren, Microm. rar. sel. 1672, as the material on which he bases the statement. We have examined the example in this published set in the Herbarium of the British Museum (Natural History) and can state that the fungus here is certainly the true *P. Urticae* and not de Bary's species. The conidiophores have non-flexuose branches and the conidia are ovate or oval, with a distinct apiculus*. As we have noted above, we have not met with de Bary's species on any host but *U. urens*, although *P. Urticae* occurs on both *U. dioica* and *U. urens*.

* Dr Gäumann has kindly sent us an example, labelled *P. Urticae* (Lib.) de Bary, collected by him "on *Urtica (urens?)*, Siders (Wallis) 7 Sept. 1924." Here again the fungus is de Bary's, and not Berkeley's, species.

In 1925 we pointed out the close morphological resemblance of the conidial stage of a Downy Mildew which we found at Wye on *Urtica dioica* and on *U. urens* with that of *Pseudoperonospora Humuli* (Miy. and Takah.) Wils., and made a comparative study of the two. From the diagnostic characters given (3), we referred the Nettle Downy Mildew to Berkeley's species but had no suspicion at the time that the name *P. Urticae* was being used by many writers for another totally distinct species. As the result of the measurement of 105 conidia, the average size was found

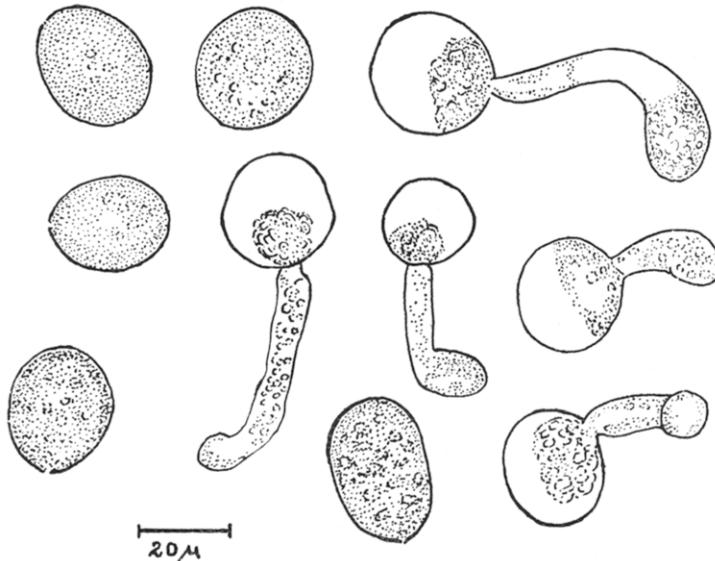


Fig. 3. Conidia, showing mode of germination. ($\times 600$.)

to be $27 \times 18 \mu$, with the limits for length $22-40 \mu$, and for breadth $14-22 \mu^*$. The size of the five conidia found on the "authentic individuals from M. Desmazières" in Berkeley's herbarium (see above, p. 40) falls well within the limits. The conidium in all our specimens showed the oval shape and the small apiculus, as depicted in Berkeley's drawing referred to above (p. 40). As regards the size of the oospore, we found this to average, from 80 measurements, $30 \times 29 \mu$, the limits of both length and breadth (for oval and globose spores) being $16-38 \mu^\dagger$. Here again the size of the three oospores observed in Desmazières's specimens is in accordance.

In our investigations in 1924 (17) we discovered that the coni-

* Blattny gives (7, pp. 153, 157) the size of the conidia of *P. Urticae* as $29.25 \times 21.25 \mu$ on *U. dioica* and $28 \times 20.5 \mu$ on *U. urens*.

† Blattny (p. 156) gives the size of the oospore as averaging in one case $27 \times 26 \mu$, and in another $29 \times 28.5 \mu$, the limits of size being $19-37 \mu$.

dium germinates by means of zoospores and on this account we removed the species from the genus *Peronospora* to *Pseudoperonospora*. It was not until 1926 that we first met with and had the opportunity of studying living examples of the second species of Downy Mildew which occurs, as far as we know, on *U. urens* only. We first found this on September 24th, 1926, in a hop garden near Wye on plants of *U. urens* growing thickly between the rows of hops. The branches of the conidiophore were flexuose and not so straight as in *P. Urticae* (Fig. 1); the conidia were broadly ovoid or subglobose, with no apiculus (Fig. 3) and measured $24\text{--}31 \times 21\text{--}24\mu$, the average of twenty conidia being $29 \times 23\mu$. When placed in water, the conidia germinated readily within twelve hours by the production of a germ tube. The haustoria, as observed in the stem and petioles, were vermiform and either simple or, more commonly, bifurcate (Fig. 5).

On October 2nd, 1926, the same fungus was found, on plants of *U. urens*, growing in great profusion in an apple plantation near Marden, Kent*. The shape of the conidiophore, conidium

and haustorium agreed with that of the fungus previously found at Wye. One hundred measurements of conidia were made; the limits of length were $23\text{--}32\mu$ and of breadth $19\text{--}24\mu$. The average size was $28 \times 22\mu$ and the mode was the same.

On November 8th, 1927, the plantation near Marden was revisited and the species was found again plentifully on *U. urens*. In some of the plants examined oogonia and oospores were present in the curled and brown tips of conidiophore-infested leaves of the lateral shoots. The size of the oogonium† in six examples was $44\text{--}55 \times 43\text{--}50\mu$, and thirty oospores‡, globose in shape, with thick, smooth, colourless walls, measured $30\text{--}36\mu$. One hundred conidia were measured and the average size was

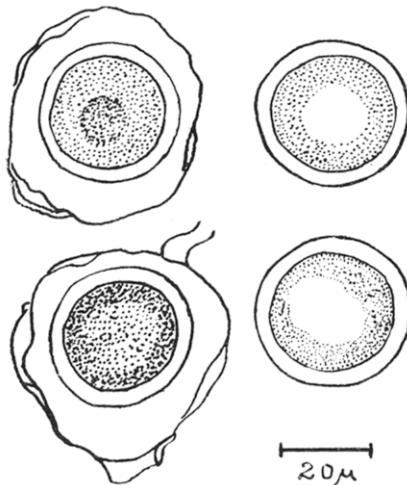


Fig. 4. Oospores. Two are still enclosed in the remains of the oogonium. ($\times 600$.)

* At the edge of the plantation, *U. dioica* occurred, attacked by *Pseudoperonospora Urticae*.

† One oogonium was seen which measured 60μ , and contained an oospore of 34μ diam.

‡ One oospore measured 39μ ; it was still enclosed by the oogonium which measured 50μ .

found to be $27 \times 23 \mu$. The variation was $23-30 \times 20-25 \mu$, and the mode $28 \times 22 \mu$.

On reference to systematic literature, and by the examination of authentic specimens, we found, from Berkeley and Broome's diagnosis, that we had been correct in using the name *Peronospora Urticae* for the apiculate-spored species, which we had transferred in 1925 to *Pseudoperonospora*. It became clear to us also that the second species we were now studying was that described as *Peronospora Urticae* in 1863 by de Bary under the mistaken assumption that it was Berkeley's species. We propose to give this latter species the name of *Peronospora*

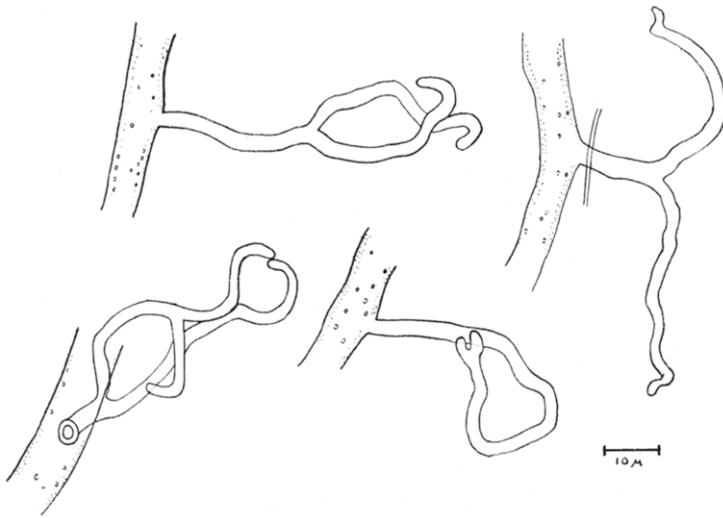


Fig. 5. Vermiform haustoria. ($\times 700$)

deBaryi, in view of the fact that this author was the first to describe its characters. The chief diagnostic characters of the two species are as follows:

Pseudoperonospora Urticae. Caespites conidiferi griseo-violacei; conidiophori ramis non flexuosis rigidis; conidia elliptica $22-40 \times 14-22 \mu$, plerumque $27 \times 18 \mu$, apice minute apiculata; oosporae globulosae $16-38 \mu$ diam., plerumque $30 \times 29 \mu$.

Peronospora deBaryi. Caespites conidiferi albidi vel pallide griseo-violascentes; conidiophori ramis flexuosis; conidia late ovoidea vel subglobosa, apice obtusissima, non apiculata, $23-32 \times 19-25 \mu$, plerumque $28 \times 22 \mu$; oosporae globulosae $30-39 \mu$ diam.

The synonymy is as follows:

Pseudoperonospora Urticae (Lib.) Salm. et Ware. *Ann. App. Biol.* XII, 141 (1925).

Botrytis Urticae Lib. MS. Berk., *Journ. Hort. Soc. Lond.*

1, 31 (1846); Berk. and Broome, *Ann. and Mag. Nat. Hist.* ser. 2, VII, 100 (1851).

Peronospora Urticae (Lib.). Caspary in *Ber. Verhandl. Königl. Akad. d. Wissensch. Berlin* 330 (1855); Berk., *Outlines of Brit. Fungology* 349 (1860); Cooke, *Rust, Smut, etc.* 216 (*pro parte*) (1865); *Handbook Brit. Fungi* 595 (*pro parte*) (1871); Masee, *Phycomyc. and Ustilag.* 124 (*pro parte*) (1891); *Mildews, Rusts and Smuts* 34 (*pro parte*) (1913).

Peronospora deBaryi nomen novum.

Peronospora Urticae de Bary (*synon. exclusis*). *Ann. sci. nat.* 4 sér., XX, 116 (1863); Berlese et De Toni in *Sacc. Syll. Fung.* VII, 257 (1888); Fischer in *Rabenh. Krypt.-Fl. Deutschl.* IV, 473 (1892); Berlese, *Ic. Fung.* 39 (1898); Berlese, *Riv. Pat. veg.* X, 269 (1904); Migula, *Krypt.-Fl. Deutschl.* III, 175 (1910); Gäumann, *Beitr. Krypt. Schweiz*, V, 302 (1923).

P. Urticae Caspary. Cooke, *Rust, Smut, etc.* 216 (*pro parte*) (1865); *Handb. Brit. Fungi* 595 (*pro parte*) (1871); Masee, *Phycomyc. and Ustilag.* 124 (*pro parte*) (1891); *Mildews, Rusts and Smuts* 34 (*pro parte*) (1913).

The distribution* of the two species, based on examination of Exsiccati and other specimens in our national Herbaria, is as follows:

Pseudoperonospora Urticae (Lib.) Salm. et Ware on *Urtica dioica*.

Exsicc. Vestergr., *Micromyc. rar. sel.* 1672; Krieger, *Fungi sax.* 1045; Cooke, *Fungi Brit. ann. exsicc.* 292. Sub *Peronospora Urticae*.

England; Tansor, Northamptonsh., 1845; Berkeley (Herb. Berkeley in Herb. Kew and Herb. Brit. Museum). Shere, Surrey, October 1866 M. C. Cooke. Scotland; West Kilbride, Ayrsh. July, 1897 leg. D. A. Boyd (in Herb. Brit. Mus.).

France; Lille (Desmazières), in Herb. Berkeley in Herb. Kew. Sweden; Stockholm. Germany: Königstein.

In addition to the above records we can add the following:

On *U. dioica*:

England; Kent, common near Wye 1925-1927 (Salmon and Ware); Middlesex, Twickenham, October 1924 (Salmon); Kent; Harbledown, near Canterbury, September 1926 (Ware). Scotland; Balgownie near Aberdeen, August 25th, 1886 (Herb. J. W. H. Trail)†.

* It appears probable that in Belgium both species occur. Lambotte (*Fl. Myc. Belge*, 97 (1880)) mentions a species on *U. urens* which from the description must be *Peronospora deBaryi*, and Bommer and Rousseau (in *Bull. Soc. Roy. bot. Belg.*, XXIII, (1884) 235) record a species on *U. dioica* which is doubtless *Pseudoperonospora Urticae*.

† In Trail's "Revision of the Scotch Peronosporae" (*Scottish Naturalist*, III (1887-1888), 77), the following note occurs: *P. Urticae* (Lib.), "on *Urtica urens*, common. *U. dioica*, rare, once near Aberdeen, differing to some extent from the form on *U. urens*." Trail appears therefore to have been the first

France; Grignon (coll. MM. Schad and Fourmont, July 1927).
(Communicated by Professor Ducomet.)*

On *U. urens*:

England; Kent, near Marden, October 8th, 1924 (Salmon and Ware); Lincs., Haxey, September 5th, 1927 (H. H. Stirrup).



Fig. 6. *Urtica urens*. Upper portion of the main stem of a plant attacked by *Peronospora deBaryi*; the upper leaves and terminal bud have assumed a silvery yellow colour, the result of systemic infection. Collected Marden, Kent, November 8th, 1927. $\frac{2}{3}$ nat. size.

We have not seen, either in Exsiccati or in herbaria, any examples of *P. Urticae* on *Urtica urens*. So far, two cases only to suspect that more than one species occurs on *Urtica*. Dr Gäumann has called attention (13) to Trail's opinion, and expressed disagreement. Dr Gäumann however, as we have noted above (p. 44), is unaware of the existence of one of the two species.

* Recent communication:—Czechoslovakia; Destnice, Saazer Gebiet, May, June, 1928 (Dr C. Blattny).

of the occurrence of this species on *U. urens* are known to us, the first, collected by us in 1924 near Marden, Kent, and the second, by Mr H. H. Stirrup, at Haxey, N. Lincs., in 1927. In an article now in the press, we record the results of certain inoculation experiments carried out by us in 1927 which show that *Pseudoperonospora Humuli* is able to infect, and form spores on *U. urens*. As we have already pointed out (17), the conidial stage of *P. Humuli* and of *P. Urticae* agree in their morphological characters. Since, however, we have found that the conidia of *P. Urticae* on *U. dioica* are able to infect fully *U. urens*, it may be assumed that the species found in nature on this latter host plant is *P. Urticae* rather than *P. Humuli*. It would, however, be of considerable interest to know of the existence of herbarium examples of *P. Urticae* on *U. urens* collected before 1920, so as to preclude the possibility of the fungus in question being *P. Humuli*, which was not recorded in Europe until that year*.

Peronospora deBaryi nomen novum.

Exsicc. Vestergr., Microm. rar. sel. 198; Linhart, Fungi hungar. 487; de Thuem, Myc. univ. 345; Fuckel, Fungi Rhen., 1510; Rabenh., Fungi Eur., 1665; Syd., Myc. March. 1347; Schneider, Herb. Schles. Pilze, n. 36; Sacc., Myc. Ital. 888; Krieger, Fungi Sax. 2128. Sub *Peronospora Urticae*.

Germany; Russia; Hungary; Italy.

In addition to the above records of *P. deBaryi* on *U. urens*, we can add the following:

England; Shropshire; Wellington, 1874. Herb. Wm. Phillips (Herb. Brit. Mus.). Kent; Wye, September 1926, 1927 (Salmon and Ware), Marden, October 1926, November 1927 (Salmon and Ware). Scotland; Old Aberdeen, August 23rd, 1886, Portsoy, August 17th, 1886 (Herb. J. W. H. Trail) †.

Switzerland; Siders (Wallis), September 7th, 1924 (leg. E. Gäumann). France; Grignon (coll. MM. Schad and Fourmont, July 1927). (Communicated by Professor V. Ducomet ‡.)

Czechoslovakia; Carpathorussia, 1920 Dollia. (Communicated by Dr C. Blattny.) §

* It seems clear, from the specific characters mentioned by Blattny (7) that a *Pseudoperonospora* occurs in Czechoslovakia on *U. urens*. It is probable that this is *P. Urticae* rather than *P. Humuli*.

† We are indebted to Professor Craib, of the University, Aberdeen, for having kindly lent us these specimens.

‡ V. Ducomet (in *Rev. Path. vég.* XII (1925), 251), in combating our view of the morphological identity of the conidial stage of *Pseudoperonospora Urticae* and *P. Humuli*, has stated that *P. Urticae* clearly differs from *P. Humuli* in the shape and dimensions of the conidium. The explanation here is that he was probably dealing with *P. deBaryi* and not *P. Urticae*.

§ Recent communications:—England; Haxey, Doncaster (J. W. Ewan, Sept. 11th, 1928). Scotland; Edinburgh (Dr M. Wilson, July 1928). Moravia; Krumlov (Dr E. Baudys, June 7th, 1928).

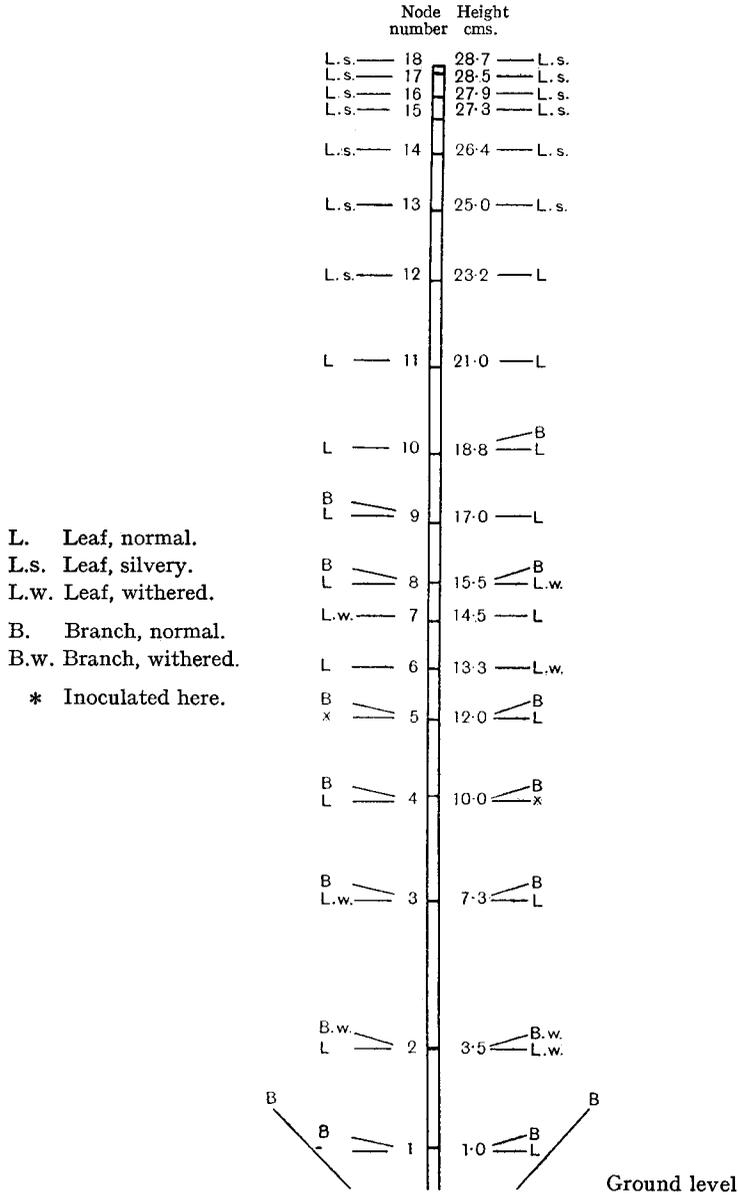
2. BIOLOGICAL.

The following observations concern the species *P. deBaryi* on *U. urens* which was first found in the open in a hop garden near Wye (Kent) on September 24th, 1926. The foliage of some of the annual nettles which were growing thickly between the rows of hops was of a bright silvery yellow at the tips of the main stems. With a lens, branched conidiophores were distinguished on the lower surface of many of these coloured leaves. The yellowing of the upper surface of the leaf was somewhat similar to that induced on other plants in the early stages of an attack of "red spider." The same colour on the lower surface of the leaf was often masked by a growth of conidiophores and conidia which was very pale grey with a scarcely perceptible violet tinge. In this respect the present fungus differed from *Pseudoperonospora Urticae*, which forms dark, greyish lilac masses of conidiophores and conidia. The discoloration at the tip of the main stem, or of its branches, involved about eight pairs of leaves covering a length of stem of approximately $2\frac{1}{4}$ inches. This and the general distribution of the fungus over the leaf surface, suggested systemic infection. Inflorescences in the axils of the yellow leaves were healthy and seeds were maturing.

It was further noted that the fungus occurred on isolated leaves and it was not by any means invariable that those symptoms which indicated systemic invasion of the whole apical portion of a shoot were present. When the fungus occurred on a leaf which on account of its colour could not be included amongst those described as systemically infected, it was present on the lower surface in small, usually angular patches of about 4 mm. diameter. Nearly as frequently it was found covering much larger areas which might extend from one end of the lamina to the other. The sides of these long areas were commonly bounded by the mid-rib or by the large veins on either side of the mid-rib. For example, on a leaf the lamina of which measured 46×40 mm., the fungus occurred on an area 46×13 mm.*, the long sides of the area being limited by the mid-rib and by one of the larger veins. The fungus itself was pale grey.

On the upper surface of the leaf the place of attack was very clearly defined by bright yellow-green which formed a sharp contrast to the dark green of the rest of the lamina and made it possible to distinguish from a distance most of the infected leaves. No brown or black discoloration of small areas of the lamina was seen, such as is typically caused by *Pseudoperonospora Urticae* on this host species.

* This was the widest space between the mid-rib and the other limiting vein.



Diagrammatic representation of a plant of *Urtica urens* two months after inoculation at the fourth and fifth nodes with *Peronospora deBaryi* nom. nov. Mycelium is present in the main stem from the apical bud to below ground level. For description see pp. 55-58.

Specimens with yellow leaves at the apex of the stem were taken to the laboratory and systemic invasion by the fungus was confirmed. In one plant seventeen inches high, with thick hypocotyl and the root extending a further three inches, the hyphae were traced by means of radial longitudinal sections, from the apical bud of the main stem to a position in the hypocotyl three-quarters of an inch below ground level, close to the beginning of the large white tap-root and at a place where lateral roots arose. The hyphae were plentiful in the pith and followed a longitudinal course on the periphery, very close to the primary xylem. Some mycelium was also found in the parenchyma of the secondary xylem. The haustoria were vermiform and were either simple or more commonly bifurcate.

Some of the fallen "seeds" were examined and one was found with conidiophores covering the perianth segments which appeared grey in comparison with the bright green perianths of other "seeds." The fruit (nut) was carefully removed from the perianth and was examined after maceration in Azo Blue. Quantities of mycelium, conidiophores and spores were found, and though a few conidiophores had been seen on the inside surface of the perianth segments, the fungus found on the fruit after it had been removed from the perianth, had actually been invading it and was probably producing conidiophores on the fruit itself.

The morphological characters of the conidia and conidiophores of *P. deBaryi* have been described above.

The disease was found persisting in the same hop-garden on October 17th and a further investigation of infected plants was made. In one typical plant, twelve inches high with tap-root three inches long, sections cut across the tip of the stem in the unthickened region showed hyphae situated between the collenchyma, which is grouped at the angles of the stem, and the vascular bundles. In the pith, hyphae were also present near the protoxylems. Mycelium was found in parenchyma tissue in the stem at ground level and in the hypocotyl region below ground. It was further traced into the tap-root and was present at a spot below the origin of lateral roots. In the root, the pitted vessels were invaded, as many as nine hyphae being found in one vessel. The parenchymatous tissues of the root were also generally invaded. The fungus was not present externally except on the leaves of the leading shoot for a distance of three and a half inches from the terminal bud.

One of the plants collected on October 17th was kept in water in the laboratory and was examined after five days. Oogonia were found in the wood-parenchyma and pith of the main stem. One oospore with colourless, smooth, thick wall (diameter 26μ)

was still enclosed in the oogonium. Hyphae were also found in the lumen of pitted vessels in the main stem. In a few instances an antheridium was seen at the side of the oogonium but it was not possible to determine whether these arose from the same or different hyphae. The antheridia measured $14-16\mu$ in diameter and the oogonia (somewhat pressed out between the cell walls) measured $40-58 \times 33-42\mu$.

The following year (1927), on September 26th and 30th, further visits were paid to the hop-garden near Wye in which the fungus had first been found in 1926. Annual nettles were again plentiful and many of the plants showed the small yellowish leaves at the tips of main or lateral shoots. The length of stem bearing coloured leaves was from one to two inches and was considerably shorter than had been seen in the previous year. On this occasion, also, the leaves with isolated yellow spots or streaks caused by the fungus were extremely rare. Conidiophores and conidia occurred in dense grey tufts on the yellow leaves and were particularly grouped at the extreme tips of the marginal serrations. Some leaves were affected to such an extent that the margin was brown, dead and inrolled.

On November 8th, 1927, an apple plantation near Marden, in which the fungus had been found the previous year, was again visited. The disease occurred plentifully amongst the annual nettles which showed, however, only here and there the spotted or streaked leaves which had been so abundant in 1926. The yellow-coloured leaves at the tips of the stems (both main and lateral stems) were everywhere conspicuous. Some of the plants were brought to the laboratory and sections showed that there was a general systemic invasion, the mycelium extending from the apical bud through the whole length of the main stem (fifteen inches) but not into the hypocotyl or roots. Some of the laterals on a plant were systemically invaded whereas others were quite healthy. Of the two laterals at a node, it was common to find one diseased and one healthy.

On October 1st, 1927, inoculation experiments were made with conidia obtained from *Urtica urens*, collected on the previous day near Wye, in the hop-garden to which reference has already been made. The spores were taken up by means of a wet brush (previously cleaned by immersion in alcohol) and were placed in a watch-glass of distilled water. A drop of the suspension was placed on the leaf to be inoculated. Two leaves on each of five plants of *Urtica dioica* and two leaves on each of five plants of *U. urens* were inoculated, and, in addition, one leaf on each of five plants of both *Humulus lupulus* and *H. japonicus*. Spores were also placed in a drop of water on two slides which were kept in a damp dish. It was observed that ger-

mination on the glass slides was very slow and after two days only about one per cent. of the spores had produced germ-tubes. The inoculum must therefore be regarded as having been very weak.

All of the plants, except the Japanese hops (which were too large), were kept under bell-jars with a moist atmosphere and were given occasional ventilation daily. They were examined on October 8th and only on four plants of *U. urens* were any effects visible; the fifth plant and all the others (*U. dioica* and *Humulus* spp.) were thrown away.

The four annual nettles showed, on all of the eight leaves inoculated, large brown water-soaked areas confined by the larger veins. No conidiophores were present. Owing to there being such conspicuous effects on the inoculated leaves all of the plants were retained (uncovered) in a well-lighted position in the laboratory.

In order to discover whether there had been any penetration by the fungus, sections were cut on October 25th in the petioles of both the inoculated leaves on one plant. This plant, being not otherwise damaged, was kept for future examination. Both the laminae were then starting to wither. Hyphae, bifurcate haustoria, oogonia and oospores were found in the petioles. The size of three oogonia which were measured was $50 \times 40 \mu$, and two oospores, still enclosed in oogonia, measured 30μ . One exceptionally large haustorium was seen which extended 20μ into the host cell, and then branched into two vermiform parts each of which measured 50μ in length. The thickness of the main axis of the haustorium was approximately 3μ .

Some of the older primary leaves of the main stem on all of the four plants became more or less withered in the course of the next month (November), but no symptoms of disease were noticed such as had been easily seen in plants growing naturally in the open. It was not until the end of the second month after inoculation (on November 30th), when the plants were being watered, that it was noticed with some surprise that the stems of all four had developed those silvery-yellow tips which were so well known as characterising systemic infection of *U. urens* in the open.

A close examination was made of one of the four plants which was the same as that from which the two inoculated leaves were removed for sectioning on October 25th. Notes were made of the symptoms and of the internal position of the fungus in relation to the symptoms. (Diagram, p. 52.) This plant was 28.7 cm. high and had eighteen nodes on the above-ground portion of the stem. One leaf of each pair at the fourth and fifth nodes had been inoculated, but they had already been removed (October 25th).

The bright silvery-yellow colour was visible on both the leaves at every node from the eighteenth down to the thirteenth; at the twelfth, only one of the pair showed this coloration. The length of stem bearing obviously discoloured foliage (nodes 12-18) was 5.5 cm. and this part of the plant was first examined. There were no conidiophores on any of the yellow leaves. Mycelium was plentiful in the petiole of the one silvery-yellow leaf at the twelfth node and oospores were crowded in the lamina, especially near the apex and in the apical serrations. They measured 30-39 μ and some were still enclosed in the oogonium. The other leaf at the twelfth node was healthy. One leaf at the thirteenth node was silvery-yellow from the base to the apex of the lamina, but on one side of the mid-rib the lamina was green and healthy. Numerous oospores occurred in the discoloured part. The other leaf at this node was completely silvery-yellow and contained young oospores in large numbers.

Both the leaves at the five nodes 14-18 were thickly infested with hyphae, oogonia, and oospores and particularly round the edges of the lamina where the silverying was more pronounced. A small inflorescence at the fourteenth node was found to contain in the main axis, hyphae with typical haustoria and oospores. The latter were also found in the perianth lobes round the ovary.

The plentiful occurrence of hyphae in the main stem having been established, this was next cut off immediately below the fourth node which was 10 cm. from ground level. Sections were cut through this node and hyphae were found. It could be seen easily with the naked eye that the pith of the main stem was brown. A median longitudinal section was cut through the node to include both the petioles* and no hyphae were found passing into the petiole of the one healthy leaf, nor into the lateral shoot in its axil. On the other side hyphae were found starting from the shrivelled and pinched-off stump of the petiole and extending into the main stem where they joined the general mass in the pith. The hyphae were not densely granular but appeared to be empty with only small scattered oil globules here and there. Haustoria were numerous. The upward course of the mycelium was next followed and it was found that the brown colour of the pith was visible from the fourth node as far as, and including, the seventh. Hyphae were found in the internodes and were present also in all the other internodes above, though here the pith was not discoloured.

As regards the leaves situated above the node already investigated, at the fifth node there was a leaf, opposite the one

* The base of the petiole of the inoculated leaf which had been removed on October 25th still remained.

inoculated, having a brown tinge on the exterior of the petiole. The lamina was beginning to shrivel at the extreme base near to the petiole and it appeared that the fungus was just about to enter it. Hyphae and oospores (the latter in great numbers) were found in the affected parts. At the sixth node, one leaf was withered and numerous oospores were present in the lamina and in the brown and withered petiole. The other leaf, judging by the presence of a light-coloured area on the lamina, was being invaded by the fungus. The petiole showed faint brown marks externally and hyphae and oospores were found in this and in the lamina. At both the seventh and eighth nodes, one of each pair of leaves was healthy and green and the other showed a light-coloured area close to the base of the lamina. The petioles of the invaded leaves were streaked with brown on the outside. The pairs of leaves at the ninth, tenth and eleventh nodes were all healthy and of good colour. Mention has already been made of the one leaf at the twelfth node which was green and healthy in contrast to its counterpart on the other side of the node which was silvery yellow.

All parts of the plant above the lowest place of inoculation (node 4) having been found infected, the base was next examined. Sections cut through the fourth node, already described, had revealed hyphae in the pith of the main stem. In addition to those traced upwards, there were some which extended to the extreme base of the sections (*i.e.* the lowest part of the node) and their presence there suggested that a downward penetration must also have taken place. The internode (3-4) was split longitudinally and it was found that the pith was brown and contained mycelium. At the third node one leaf was withered and its petiole was shrivelled as far as 5 mm. from the base (*i.e.* from the lamina downwards) but it contained no fungus to account for the injury. The other leaf and two lateral shoots at this node were healthy. Longitudinal sections of the node itself showed that the pith was crowded with hyphae and haustoria, and it was remarkable that neither the lateral shoots nor the two petioles were invaded.

The pith of the next internode (2-3) was brown and contained hyphae. At the second node, one leaf was withered and the other healthy; both the axillary shoots were withered. Oospores and hyphae were found in the lamina and petiole of the one leaf and in its axillary shoot. As regards the other leaf, which was normal, sections of the node showed that there was no invasion of this petiole but that the lateral shoot in its axil was thickly infested. The mycelium was present in the pith of the next internode (1-2) and this again was indicated by the brown colour. At the first node there was one normal leaf; the other

was missing, but the petiole remained. There were two long lateral shoots (9 cm.) which were healthy. Sections of the node showed that the pith contained mycelium but the axillary shoots and the petioles subtending them contained none. At this node the hyphae were of somewhat different appearance from that of hyphae seen in the higher parts of the host plant. They were even less granular and more transparent—a feature which was thought to indicate reduced vigour. All the sections had been treated with alkaline Azo Blue and the hyphae present in the first node showed a further difference in that they took up the stain less readily. The haustoria, however, were rapidly stained. In the internode 0-1, the hyphae were found extending nearly to node 0 which was below the level of the soil. Two lateral shoots from this node were healthy. No mycelium was found in the hypocotyl, nor in the roots.

From this examination it would appear that the conidia had germinated and had infected the plant within eight days without production of conidiophores. The fungus was able to form oospores in the petioles of the infected leaves and to pass on into the pith of the main stem. Here, presumably, it had grown both upwards and downwards (though faster and further in the former direction) until, near the apex of the plant, it had invaded and caused the discoloration of the leaves. It is remarkable that (as we have observed also in the Downy Mildew of the Hop), one leaf or lateral at a node may escape attack while the other becomes invaded, and while this may be explained on the assumption that the hyphae are sometimes by chance present on only one side of the main stem, it is more difficult to explain why, as at node 2, a lateral shoot should be invaded and the subtending leaf petiole remain free when the points of attachment of both to the main stem are in the same vertical line and extremely close together.

The silvery-yellow coloration of the uppermost leaves appears to be the most constant macroscopic feature of the disease. The large light-coloured areas or streaks which are to be seen on the leaves (not necessarily those near the apex of the stem) are less constant symptoms, and are apparently dependent on seasonal conditions. It seems probable that the main primary infection is brought about by the conidia produced on the yellow-coloured foliage at the top of the stems; these conidia presumably are carried to healthy leaves and under suitable weather conditions are able to infect and to form small angular spots bearing fresh conidiophores. Under some conditions, probably connected with the age of the host plant or with lack of humidity in the atmosphere, the fungus, often without fruiting on the surface of the lamina, spreads rapidly internally and

finding its lateral expansion limited by the veins, grows in a direction approximately parallel to them and thus finds its way into the petiole. A great many of the brightly-coloured areas seen on leaves under natural conditions extend to the base of the lamina at the place of junction with the petiole. It is probable that these large yellow-coloured streaks are indicative of an attempt at systemic infection rather than a result thereof*.

SUMMARY.

1. *Peronospora Urticae*, founded by Berkeley in 1846 on *Botrytis Urticae* Libert MSS., has an oval conidium, minutely apiculate at the apex—as described by Berkeley and Broome. The present writers have previously pointed out that the conidium germinates by means of zoospores and that the species is therefore to be referred to the genus *Pseudoperonospora*.

2. In 1863 de Bary described a species having a broadly ovoid or subglobose conidium, very obtuse at the apex and with no apiculus and, misled through seeing a drawing sent by Berkeley to Caspary, identified it as *Peronospora Urticae* (Lib.). Subsequent authors (*e.g.* Berlese, Fischer, Migula, Gäumann) have followed de Bary in this identification.

3. The examples sent out under the name *Peronospora Urticae* in various Exsiccati are sometimes Berkeley's and sometimes de Bary's species.

4. The name *Peronospora deBaryi* nomen novum is proposed for de Bary's species.

5. *Pseudoperonospora Urticae* occurs on *Urtica dioica* and *U. urens*, and *Peronospora deBaryi* on *U. urens* only. The distribution of each species is given.

6. Living examples of *P. deBaryi* were first met with by the writers at Wye, Kent, in 1926; the study of these and the evidence obtained in an inoculation experiment have shown that *P. deBaryi* causes a systemic infection of the host-plant.

We wish to thank Mr J. Ramsbottom, of the British Museum (Natural History), London, and Miss E. M. Wakefield, of the Herbarium, Royal Botanic Gardens, Kew, for their helpful advice on numerous occasions.

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* A similar discoloration of the lamina has sometimes been observed in *Humulus Lupulus* after inoculation with *P. Humuli*.

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THE STRUCTURE AND MODE OF REPRODUCTION OF *SIPHULA TABULARIS* NYL.

By *S. Garside, M.Sc., Bedford College, London.*

(With Plate I and 4 Text-figures.)

THERE are some genera and species of lichens of which little or nothing is known about the spore-producing organs. In such, the systematic position cannot, as a rule, be determined with certainty, as the evidence indicating affinity must be derived entirely from the structure of the vegetative organs.

The genera *Thamnolia*, *Endocena* and *Siphula* have been included in the Usneaceae because of the structure of the vegetative thallus.

In *Thamnolia vermicularis* (Sw.) Ach., a widely distributed arctic and alpine lichen, pycnoconidia have been discovered, but apothecia are extremely rare, and the two descriptions of them which have been published differ in important respects.

In *Endocena* (one species, *E. informis* Cromb. in Patagonia) and *Siphula* (about fourteen species, widely distributed) the spore-producing organs are still unknown.

In all three genera, vegetative reproduction is probably the efficient means of dispersal, portions of the thallus becoming detached and distributed by the wind, on the feet of birds, or in other ways.

I have had an opportunity of studying in the field the three South African species of *Siphula* which occur frequently on the