

Notes on the Genus *Taphrina*.

BY

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DURING the winter of 1886-7 I had an opportunity to study, from dried and alcoholic material, a number of American and European species of the genus *Taphrina*. As the literature of the group, particularly on the American forms, is rather scanty, the notes which I have been able to make may be of assistance to those who wish to continue the study of this interesting group. In the systematic examination of European species much valuable aid has been derived from the papers of Sadebeck¹ and of Johanson². These writers, it will be noticed, differ in the names they retain for the group; and a brief explanation of the synonymy of the genus will not be out of place.

The species, combined by Sadebeck, in 1883, into a single genus, were formerly classed in three closely related genera, *Taphrina*, Fries, *Ascomyces*, Mont. et Desm., and *Exoascus*, Fuckel. Of these genera the first is the oldest, having been described by Fries as early as 1815 under the name of *Taphria*, which, to avoid possible confusion with an insect genus, was in 1825 altered to *Taphrina*. In his paper just mentioned Sadebeck has preferred, although without stating his reasons, to retain for the combined genus the youngest of the three names, that of *Exoascus*, Fuckel. Johanson agrees with Sadebeck in thinking that all the species should be combined into a single genus, but, seemingly with much

¹ Untersuchungen über die Pilzgattung *Exoascus*, in Jahresbuch der wissenschaftlichen Anstalten, Hamburg, 1883, pp. 93-124.

² Om Svampsläktet *Taphrina*, in Öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar, 1885, Stockholm, N: o I, pp. 29-47.

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more regard for the rules of priority in nomenclature, retains the name *Taphrina* of Fries. There appears to be all the more reason for this from the fact that, as early as 1866, Tulasne¹ revised the genus of Fries and expanded its limits so that it might take in all the species then known of *Ascomyces* and *Exoascus*, thus using the name *Taphrina*, so far as the knowledge of the time enabled him, in the same sense as it is at present employed. From these considerations it seems best to follow Johanson in calling the group '*Taphrina*, Fries, char. a Tulasne emend.,' a sort of nomenclature which, if not brief, is yet in accord with priority, and incapable of being misunderstood.

The members of this genus are in structure among the simplest of the Ascomycetes, and in them no trace of sexual function has yet been found. They present also some features of similarity to the Saccharomycetes, to which group there seems a growing tendency to consider them closely related². With one possible exception, all the species known are parasitic in their habit. They seldom attack herbs, but are commonly found on shrubs or trees, especially those of the Rosaceae, whence the chief economic importance of their study. Their mycelia penetrate the tissues of the host to various depths where, in some species at least, they pass the winter. In the spring they begin their development anew, and enter the young shoots and leafy parts of the plant attacked; here they spread their hyphae beneath the cuticle, or in some species just below the epidermis, forming a branching network. From this sort of hymenium the asci arise. They are more or less cylindrical in form, and usually occur in great numbers, densely packed together. They are found between the cuticle and epidermis, being developed in the species which have their hymenia beneath the epidermis, as enlarged ends of vertical threads which,

¹ Super Friesians Taphrinarum Genere, in Ann. des Sciences nat., sér. 5, Tome v, 1866, p. 122.

² See De Bary, Vergl. Morph. und Biol. der Pilze, Mycetozen und Bacterien, Leipzig, 1884, pp. 286-294.

arising from the subepidermal network, make their way between the cells of the epidermis and become developed into asci which, as in the other species, are formed between the cuticle and epidermis. In several species each ascus is borne on a specialized portion of the mycelium known as the stalk-cell. These cells vary considerably in form, being sometimes long and slender, cylindrical or obconical, or, on the other hand, short and broad with flat and truncate bases. Within each ascus generally eight nearly spherical spores are formed, but the octosporic condition is often not permanent, for while yet in the ascus the spores divide by a process closely resembling the budding of the *Saccharomycetes*. In this way the asci frequently become filled with very numerous reproductive bodies, sometimes resembling the eight original spores, except in their smaller size and rather more oblong or oval form, in other cases becoming very minute and bacteria-like. The asci of several species are always polysporic at maturity, and no eight-spored condition is readily discernible in their development. Even in them, however, there seems reason to believe that the many-spored form is secondary, resulting from spore-division. As the asci grow they raise up the cuticle from the epidermis, and at some period, early in some cases, near maturity in others, break through to the surface. The release of the spores when the asci have not been subjected to any violent rupture, to which their delicate structure and superficial position render them liable, seems to be effected through a rather small orifice at the summit of the ascus.

The presence of a *Taphrina* is manifested by the host in one or more of several ways: namely, by the occurrence on the leaves of roundish or irregular blotches, varying in colour from yellow to purple according to the species of the parasite; by a curling or crisping of the leaves, sometimes accompanied by a toughening or cartilaginous modification of the leaf-texture; by the swelling out of the softer parts of the leaves between the nerves, rendering the surface convex on one side and concave on the other; by deformity

of the fruit; and, lastly, by the swelling and distortion of the twigs and young branches.

In showing in some degree the affinities within the group, as well as in furnishing a means of ready determination of the individual species here described, the following synopsis of the American species which I have been able to examine may be found useful. Tulasne, in subdividing his new genus, *Taphrina*, had regard to the lines of division between the older genera of which it was composed, and accordingly grouped his species into those with so-called polysporic asci (*Taphrina*, Fries, and *Ascomyces*, Mont. et Desm.), and those with eight-spored asci (*Exoascus*, Fuckel). But, as just stated, the polysporic condition is probably secondary, and the spores of all the so-called octosporic species are very liable to multiply within the ascus. This distinction therefore does not seem of primary importance, and in arranging the American species it is better to follow Sadebeck and Johanson in grouping the species according to the depth to which their mycelia penetrate the tissues of the host-plant. It will be understood that the following synopsis is not intended to be exhaustive, as there are several forms of *Taphrina* more or less perfectly known in America which I have been unable to examine.

SYNOPSIS OF AMERICAN SPECIES EXAMINED.

I. Mycelium penetrating intercellularly the inner tissues of the host.

- (1) Fertile portion of the mycelium between the epidermis and the cuticle,
 - (a) Asci raised on stalk-cells,
 - T. Pruni* (Fuckel), Tul.
 - T. deformans* (Berk.), Tul.
 - (b) Asci without stalk-cells,
 - T. purpurascens* (Ellis et Evh.).
- (2) Fertile portion of the mycelium beneath the epidermis,
 - T. Potentillae* (Farw.), Johans.
 - T. flava*, Farw.

II. Mycelium spreading itself just below the cuticle, and not entering the tissues of the host.

(a) Asci with stalk-cells,

T. alnitorqua, Tul.

(b) Asci without stalk-cells,

T. aurea (Pers.), Fries.

T. caerulescens (Mont. et Desm.), Tul.

For *Exoascus Wiesneri*, Rathay, and *Ascomyces Quercus*, Cooke, see *Taphrina deformans* and *T. caerulescens* respectively.

T. PRUNI (Fuckel), Tul.

Exoascus Pruni, Fuckel, *Ennumeratio Fungorum Nasoviae*, p. 29.

This species occurs frequently in the United States upon *Prunus domestica*, L., and causes a peculiar hollow deformity of the fruit, the so-called 'plum-pocket' (Narren-Taschen). Late in June the infected plums reach almost their mature size, but consist merely of a thin shell having instead of pulp and stone only a few threads stretched irregularly across the cavity within. A *Taphrina*, probably identical with this, attacks several of our native species of *Prunus*, and has been found on *P. maritima*, Wang., Dartmouth, Mass., on *P. virginiana*, L., near Lake Willoughby, Vt., and on *P. serotina*, Ehr., Cambridge, Mass. On the last-mentioned host the fruit, which is normally nearly spherical, when infected becomes elongated or even somewhat spindle-shaped, and early attains a size several times greater than at normal maturity. The stamens and floral envelopes also suffer hypertrophy and remain attached to the base of the fruit in an involucre-like mass.

The asci are formed in very great numbers; early in their development they break through and almost obliterate the cuticle, and form a dense and continuous layer over the whole surface of the fruit, which later becomes hoary from the escaping spores. In general form the asci are long and slender, cylindrical, truncated or rounded at the summit,

and slightly tapering below. On *P. domestica* nearly all the asci examined have been more slender in proportion to their length than those described by Sadebeck. Furthermore there appears to be a sort of dimorphism among them, such as Johanson describes in the asci of *T. alnitorqua*; for, beside the long and very slender ones, which are usually octosporic at maturity, there are others, more often polysporic, which are considerably shorter and thicker. In length the slender asci vary from 43μ to 60μ and in thickness from $5\frac{1}{2}\mu$ to 7μ , while the asci of the stouter kind are $27-35\mu$ in length and $9-12\mu$ in thickness. The stalk-cells are $12-18\mu$ long and $5-8\mu$ thick; they rest upon the epidermis, but do not intrude between the cells. The nearly spherical spores are normally eight with a diameter of $3-4\frac{1}{2}\mu$, but become much more numerous and smaller by division.

T. DEFORMANS (Berk.), Tul.

Ascomyces deformans, Berk., Outlines of British Fungology, p. 376.

Ascosporium deformans, Berk., *ibid.*, in description of plate I.

Exoascus deformans, Fuckel, Ennumeratio Fungorum Nassoviae.

Exoascus Wiesneri, Rathay, in Oesterreichische Botanische Zeitschrift, Jahrgang xxx, No. 7, p. 225.

The ordinary form of this species occurs upon peach-trees, and causes the crisping and wrinkling of the leaves known as the 'peach-curl.' On infection by the parasite, the leaves not only are distorted but become much thickened and take on a sort of cartilaginous structure. The asci are borne on both sides of the leaf, but in greater numbers upon the lower surface. Although the material which I examined was shown by the perfection of the spores to be mature, the asci were considerably shorter than those described by Sadebeck. The measurements were as follows: length of asci $26-32\mu$, thickness $6-10\mu$; height of stalk-cell $9-12\mu$, mean thickness $3\frac{1}{2}-4\frac{1}{2}\mu$, thickness at base often as low as 2μ . The spores,

when eight in number, are nearly spherical and $3\frac{1}{2}$ – $5\frac{1}{2}$ μ in diameter, but by division their size is reduced to about 2 μ .

Beside this form on the peach, a *Taphrina* has been found at Germantown, Pa. (Mr. Mehan), on the leaves of 'escaped cherry-trees.' As to the species or variety of the host, I regret to say, I can give no exact information. The parasite is probably the *Exoascus Wiesneri* of Rathay, which is now regarded merely as a form of *T. deformans*. As in the peach-curl, the infected cherry-leaves become much wrinkled and distorted; the small branches attacked are also somewhat modified and show a tendency toward forming 'witches' brooms' (Hexenbesen), such as are described by Rathay¹. The asci are developed on both surfaces of the leaf, and closely resemble those of the typical form on the peach, though perhaps a little more slender; in length they are 27–33 μ , in thickness 5–8 μ . The stalk-cells are taller than any I have seen on peach-leaves, and do not taper so much below; they are 17–18 μ high, and 5–7 μ thick.

A *Taphrina*, probably the same as this, has been found several times in Massachusetts deforming the leaves and branchlets of *P. serotina*, Ehr.

T. PURPURASCENS, sp. nov.

Ascomyces deformans, var. *purpurascens*, Ellis et Everhart, North American Fungi.

This form occurs on the leaves of *Rhus copallina*, L., and has been found in Massachusetts at Dartmouth, Salem, Wood's Holl, and other localities; in Connecticut at New London; and also in New Jersey. The infected leaflets may be recognized by their dark purple colour and wrinkled appearance, as well as by their limp and pendent condition. Furthermore, it may be noted that the softer parts of the leaf tissue swell out between the nerves and become convex above and concave beneath. The dark colour is at first

¹ Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Math. und Naturwiss. Kl., Wien, Band lxxxiii (1881), p. 267.

confined to roundish blotches, but these soon become irregularly confluent and cover much or all of the surface of the leaflet. Microscopically, the most noticeable modification in the infected parts of the leaf is the very compact and palisade-like structure which the spongy parenchyma and epidermis assume.

The asci are formed on both sides of the leaf, and reach maturity late in June or early in July. They are 24–32 μ long, and somewhat dumb-bell shaped in outline, being constricted in the middle apparently by the cuticle of the host; the thickness of the exerted portion is 9–14 μ , of the constricted part 6–11 μ , and of the broad base 9–21 μ . In size and shape the asci closely resemble those of the European *Exoascus Carpini*, Rostrup; from that species however this form on *Rhus* is well distinguished by the presence of a mycelium which penetrates the inner tissues of the host-leaf. From *T. deformans*, of which it was once classed as a variety, *T. purpurascens* differs not only in the size and form of its asci but in having no stalk-cells. The spores are eight in number and ellipsoidal in form; their maximum diameter is 3½–5 μ and minimum 2½–4 μ . Like the spores of other species they are very liable to division while still in the ascus.

The first notice of this form is in 'Notes on the Third and Eleventh Centuries of Ellis's North American Fungi'¹ by Dr. Farlow, who gave a partial description of specimens found at Dartmouth, Mass., by Dr. B. D. Halsted. It was there considered as possibly a variety of *Exoascus deformans* or, at least, a related species. Mention was made of a similar form on an African *Rhus* described by Magnus, as the writer believed, although he could not at the time recollect where it was published. I have since been informed by Dr. Farlow that he was in error, and that the description which he had in mind was by Dr. F. Thomas instead of Magnus. In the article, published in 1883², Thomas describes a deformation of

¹ Proceedings of the Amer. Acad., vol. xviii (1883), p. 85.

² Berichte der Deutschen botanische Gesellschaft, Bd. i (1883), Berlin.

some leaves of *Rhus pyroides*, Burch., from South Africa, which he ascribed to the presence of a parasitic fungus. He states, however, that from his dried material he could only make out several minute processes, on the surface of the leaf, resembling the basidia of an *Exobasidium*. It seems not improbable that this form, on further investigation, may prove the same as our American species, especially as in his description of the changes in the infected leaves, Thomas speaks of a dense and palisade-like structure taken on by the spongy parenchyma.

T. POTENTILLAE (Farw.), Johanson.

Exoascus deformans, var. *Potentilla*, Farw., in Proceedings of Amer. Acad. vol. xviii (1883), p. 84.

This distinct and well-marked species has been frequently found in various places in Massachusetts and Connecticut. Early in June it causes, on the leaves of *Potentilla canadensis*, L., little, roundish, yellow spots, which become convex above and concave beneath, and soon deepen in colour from yellow to brown and then to purple. Johanson, in describing the deformities produced by this species on *P. Tormentilla*, Scop., speaks of the swelling of the petioles and curling of the leaves; but although I have looked over a number of dried and a few fresh specimens of *P. canadensis*, attacked by the parasite, I have not succeeded in finding any deformity in the petioles or stems.

The peculiarities of the mycelium in this and the succeeding species have been noted already in the synopsis. The sub-epidermal position of the fertile threads naturally influences the form of the ascus so that the upper part only becomes expanded and contains the spores, while the lower portion is merely a very slender pedicel which, passing between the cells of the epidermis, connects the ascus with the mycelium below. In *T. Potentillae* the asci, which are borne on both sides of the leaf, are club-shaped and very slender. The spore-bearing portion is 25–33 μ long and 8–10 μ thick, while the slender pedicels, which are usually longer on the upper

than on the under surface of the leaf, vary from 20–30 μ in length, and are often less than 2 μ thick. The spores are eight or many, 3–4 μ in diameter.

T. FLAVA, Farw., in Proceedings of Amer. Acad. vol. xviii (1883), p. 84.

Exoascus flavus, Farw., Ellis' N. A. Fungi (1879), No. 300.

This species must be carefully distinguished from the more recent and very different *Exoascus flavus* of Sadebeck, which Johanson, with deference to the priority of Dr. Farlow's name, has called *Taphrina Sadebeckii*. *T. flava*, Farw., is also quite distinct from *Exoascus Betulae*, Fuckel, which also occurs in roundish spots on the leaves of various species of *Betula*, but has not, to my knowledge, been found in America. If it does occur here it may be distinguished from *T. flava* by its shorter and more slender asci, its well-developed stalk-cells, and the absence of any subepidermal mycelium.

T. flava, Farw., has been found most often on *Betula alba*, var. *populifolia*, Spach., in Eastern Massachusetts and New Hampshire, but has also been collected on Mt. Washington, N. H. (E. Faxon), on *B. papyracea*, Ait. It appears on the leaves of either host in June as bright yellow, circular spots, which vary considerably in diameter. In some dried material examined these spots were distinctly concave above and convex beneath. The asci are very numerous and densely packed together on both sides of the leaf. In outline they are rectangular, being truncated at each end; their length is 31–52 μ , and thickness 17–26 μ . Within each ascus there is a great number of very small oblong spores. The asci have no proper stalk-cells, but in a thin section the subepidermal mycelium (hymenium) is seen to be connected with the asci by very slender pedicels which pass vertically upward between the cells of the epidermis and expand abruptly into the asci above. When the upper portion only of such a pedicel is seen, it may appear like a downwardly directed process.

from the ascus, resembling, except in its more slender form, one of the rootlike appendages which are really developed downward from the asci of *T. aurea* and *T. caerulea*; but its different nature becomes clear when its connection can be traced with the mycelium below. From the position of its mycelium and the mode of forming its asci, it is evident that this species is closely related to *T. Potentillae*, just described, however dissimilar it may seem in the size and shape of the asci themselves and the spores they contain.

T. ALNITORQUA, Tul., in Ann. des Sciences Nat., sér. 5,
Tome v. p. 130.

Ascomyces Tosquinetii, Westendorp, in Bull. de l'Académie royale de Belgique des sciences, sér. 2, Tome xi.
p. 655.

Exoascua Alni, De Bary.

Exoascus alnitorquus, Sadebeck, Untersuchungen über die Pilzgattung *Exoascus*, p. 115.

This species is common in Massachusetts on the bracts of the fertile catkins of the alder. It develops a month or two earlier than the other *Taphrinae*, and, although easy to find, it is for some reason seldom in good condition for microscopic study. The bracts which are attacked grow abnormally long and thick, are variously curled and twisted, and become hoary with the escaping spores. The asci are borne on all parts of the infected bracts; they are 29–37 μ long and 6–10 μ thick. Although, as these measurements show, there is considerable variation in the length and thickness of the asci, I fail to find here the dimorphism mentioned by Johanson in the asci of this species in Sweden. Each ascus is furnished with a cylindrical stalk-cell 15–17 μ high and 6–8 μ thick. The spores are usually eight, sometimes many, spheroidal in form, and $3\frac{1}{2}$ –6 μ in diameter.

In Europe *T. alnitorqua* has a form which occurs on the leaves of the alder, and, although not yet found in America, this form may well be looked for, as it is not improbable that it occurs here also.

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T. AUREA (Pers.), Fries.

Erineum aureum, Persoon, Synop. Method. Fungorum,
p. 700.

Taphrina populina, Fries.

Exoascus Populi, Thümen, in Hedwigia, Band xiii.
p. 98.

Exoascus aureus, Sadebeck, Untersuchungen über die
Pilzgattung *Exoascus*.

The only form of this species yet found in America attacks the fertile catkins of poplar trees. It is of frequent occurrence, and has often been collected on *Populus grandidentata*, Michx., in Massachusetts, at Springfield, Newton, and elsewhere. In the infected catkins several of the ovaries grow abnormally large, and, late in April or early in May, when the fungus reaches its fruiting stage, become golden-yellow from the orange-coloured asci of the parasite. The mycelium is only subcuticular, and does not enter the inner tissues of the host; each ascus, however, sends down an irregular rootlike process 20–40 μ long, which, making its way between the cells of the epidermis, even enters a little distance the hypoderm below. The entire length of the ascus, the process included, is 80–114 μ , and the thickness 16–19 μ . These measurements do not differ very much from those of Sadebeck, but Johanson, in describing the Swedish form which occurs on the leaves of *P. nigra*, L., gives the total length of ascus as only 47–49 μ . The spores are very numerous and of minute size.

T. CAERULESCENS (Mont. et Desm.), Tul., in Ann. des
Sciences Nat., sér. 5, Tome v.

Ascomyces caerulescens, Mont. et Desm., Ann. des
Sciences, sér. 3, Tome x. p. 146.

Exoascus caerulescens, Sadebeck, Untersuchungen über
die Pilzgattung *Exoascus*.

Ascomyces Quercus, Cooke, in Ravenel's Fungi Amer.
No. 72.

This is one of the most common and wide-spread species of the genus. It occurs on a number of our American oaks,

having been found on *Quercus alba*, L., and *Q. tinctoria*, Bart., at New London, Conn. (Dr. Farlow); on *Q. coccinea*, Wang., at Stoughton, Wis. (Prof. Trelease); on *Q. rubra*, L., at Bald Cap Mt. (3000 ft.), N. H., also at Ithaca, N. Y. (Prof. Trelease); on *Q. aquatica*, Catesby, and *Q. laurifolia*, Michx., at Green Cove Spring, Fla. (the late Dr. Geo. Martin); and on *Q. cinerea*, Michx., at Aiken, S. C. (Ravenel's Fung. Amer. No. 72). The fungus appears on the leaves of its host during June in roundish spots, which vary in size, and are grey or somewhat bluish in colour. On the leaves of *Q. rubra*, which I have examined, these spots were pretty definite in outline, and only 2–5 mm. in diameter; on *Q. tinctoria*, on the other hand, they were 10–12 mm. in diameter, and irregular in shape. The habit of the asci in regard to the side of the leaf upon which they are developed does not seem to be uniform on the different hosts. In his original description of *Ascomyces caeruleus*, cited above, Desmazière speaks of the asci as 'hypophyllus,' and that undoubtedly is their usual position, but upon the leaves of *Q. tinctoria* I have found them only on the upper surface. In general form the asci somewhat resemble those of *T. aurea*, but their rootlike processes are generally shorter and penetrate the interstices of the epidermis to a less depth than in that species. The asci may furthermore have two or even three of these processes, which, in that case, are apt to be short and blunt. In length the asci are 55–78 μ , and in thickness 18–24 μ . The spores, like those of the preceding species, are very numerous, minute, and bacteria-like.

By the kindness of Dr. Farlow I have had an opportunity to examine some of the original material of *Ascomyces Quercus*, Cooke, which was distributed as No. 72 in Ravenel's Fungi Americani. This parasite, which occurs on the leaves of *Q. cinerea*, corresponds perfectly, so far as I can see, with *T. caeruleus*, not only in the extent and shape of the spots in which it occurs, but in the size and form of the asci, which in both forms are polysporic. The only difference that I could find was in the size and shape of the spores. In *Ascomyces Quercus* they are oval in form, and vary in size from 4 μ

down to 1μ and less, while in *Taphrina caerulescens* they are oblong or cylindrical, and usually less than 2μ in diameter. As the size of the spores in these polysporic asci depends upon the extent of the subdivision of the original eight spores, a process which is very probably influenced by external circumstances, the diameter of such polyspores, so variable in the same species, can hardly be considered a character of sufficient definiteness to warrant the separation of forms which differ in no other particular.

In closing I wish to express my sincere thanks to Dr. W. G. Farlow, who very kindly furnished me with the material for studying this group, and aided my work with many valuable suggestions.

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