

The Genus *Taphrina* in Scotland

BY

D. M. HENDERSON

Taphrina was first described by Fries in 1815 as *Taphria*, but he later dropped this name as it was pre-empted to a genus of insects. In 1825 he re-described the genus as *Taphrina*, which since then has been variously interpreted. A series of genera, *Ascomyces* Desm., 1849, *Exoascus* Fuckel, 1860, *Endoascus* Magnus, 1875, *Magnusiella* Sadebeck, 1893, have been proposed, and in discussion by nineteenth-century mycologists their limits were changed repeatedly. Several criteria, such as presence or absence of basal cells, of perennial mycelium and of budding of spores in the ascus, were variously used for segregation of these genera, but none appeared satisfactory. In the most recent monograph of the group by Mix (1949) only one genus is recognised.

The limits of the species of *Taphrina* have often been determined purely by the taxonomy of their hosts. The few cross-inoculation experiments which have been conducted (Sadebeck, 1888) suggest that they are closely specialised to their hosts. However, the tendency towards splitting of species purely on host relationships has gone too far. There seems little justification for the view that two morphologically similar fungi on different but closely related hosts should be considered distinct species—they should be specialised forms at most.

The present treatment is limited to the Scottish representatives. This has made it possible to examine and describe fresh material of every species recorded, except for *T. caeruleascens*, of which I have seen no Scottish specimens. Of the British species only *Taphrina ulmi*, recorded from Surrey by Mix (1949), and *T. rhizophora* have not been found in Scotland.

Previous Scottish authors have given some account of the species. Stevenson in his "Mycologia Scotica" listed three species, *Ascomyces pruni*, *A. tosquinetii* and *A. trientalis*. The last is not one of the *Taphrinas* but a stage of *Tuburcinia trientalis*. J. W. H. Trail's account of Scottish fungi increased the number recorded to ten. Except for the lists of fungi causing economic diseases (Alcock & Foister, 1931, and Dennis & Foister, 1942) and Wilson's account of the Uredineae (1934) there has been no comprehensive account of Scottish fungi in recent years.

The distribution of species has been arranged according to the system suggested by Buchanan White (1871), based on the main river drainage basins. The records are compiled from the accounts of Trail and Dennis & Foister (1942), supplemented by my own collections and herbarium material in Scotland. My collections are deposited in the herbarium of the Royal Botanic Garden, Edinburgh.

For the loan of specimens and for information thanks are due to Dr. R. W. G. Dennis, Kew; J. England, Edinburgh; Dr. C. E. Foister, Edinburgh; Dr. J. Grainger, Auchincruive; Dr. E. G. Gray, Aberdeen; Dr. M. Noble, Edinburgh; and Dr. Malcolm Wilson, Edinburgh.

KEY TO SPECIES

1. Basal cell present	2
1. Basal cell absent	12
2. Asci with yellow epiplasm	3
2. No coloured epiplasm	4
3. Ascus apex rounded. On <i>Populus</i> leaves	1. <i>populina</i>
3. Ascus apex truncate. On <i>Alnus</i> leaves	3. <i>sadebeckii</i>
4. Spores uniseriate, budding sparingly; asci less than 10μ in diameter	5
4. Spores irregularly arranged, budding freely; asci usually more than 10μ	6
5. Asci sub-truncate. On <i>Prunus</i> leaves	15. <i>cerasi</i>
5. Asci rounded at apex. On <i>Alnus</i> leaves	4. <i>tosquinetii</i>
6. Basal cells not inserted	7
6. Basal cells inserted	8
7. Asci sub-truncate at apex. On <i>Crataegus</i> leaves	11. <i>crataegi</i>
7. Asci rounded at apex. On <i>Betula</i> leaves	7. <i>betulae</i>
8. Asci less than 30μ long. On <i>Prunus</i> and <i>Amygdalus</i> leaves	14. <i>deformans</i>
8. Asci more than 30μ long	9
9. Ascus apex truncate. On <i>Pyrus</i> leaves	10. <i>bullata</i>
9. Ascus apex rounded	10
10. Basal cells more than 15μ broad. On <i>Betula</i> leaves	8. <i>betulina</i>
10. Basal cells less than 15μ broad	11
11. Asci more than 15μ broad. On <i>Prunus padus</i> fruits	16. <i>padi</i>
11. Asci less than 15μ broad. On fruits of other <i>Prunus</i> spp.	13. <i>pruni</i>
12. Asci narrow, less than 15μ broad	13
12. Asci more than 15μ broad	15
13. Asci inserted between epidermal cells. On <i>Potentilla</i>	12. <i>potentillae</i>
13. Asci subcuticular only	14
14. Asci rounded at apex. On <i>Carpinus</i> leaves	6. <i>carpini</i>
14. Asci truncate at apex. On <i>Alnus</i> carpel scales	5. <i>amentorum</i>
15. Asci with yellow epiplasm	16
15. Asci without yellow epiplasm. On <i>Quercus</i> leaves	9. <i>caerulescens</i>
16. Asci subcuticular only. On <i>Populus</i> leaves	1. <i>populina</i>
16. Asci inserted between epidermal cells. On <i>Populus</i> fruits	2. <i>johansonii</i>

1. TAPHRINA POPULINA Fries, Syst. Mycol. iii, 520 (1832).

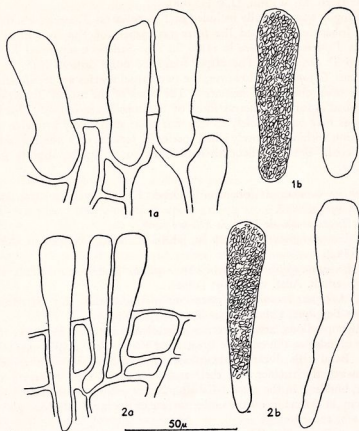
Syn.: *Taphrina aurea* auct.*Exoascus populi* Thumen in Hedwigia, xiii, 97-98 (1874).*Exoascus aureus* Sadebeck in Jahrb. Hamburg. Wissensch. Anst. i, 93-124 (1884).*Exoascus flavo-aureus* Cocconi in Mem. R. Acad. Sci. Inst. Bologna, iv, 187-198 (1894).

Asci hypophyllous, rounded at apex, developing from subcuticular mycelium, not inserted between epidermal cells, $70-88\mu \times 18-22\mu$, epiplasm bright yellow. Basal cell present or absent. Spores budding immediately to produce numerous minute blastospores, $1-2\mu \times 1\mu$. Causing bullate yellow spots on *Populus nigra* var. *betulifolia*, *nigra* var. *italica*, *certinensis* (= *laurifolia* \times *nigra* var. *italica*), *eugenei*, *generosa* (= *trichocarpa* \times *angulata*). [See Mix, 1949,

p. 39] and *P. balsamifera* [Farquharson in Ann. Scot. Nat. Hist., 1911, p. 241]. Occasionally a whole leaf may be affected. [Fig. 1, a and b.]

Distribution. Forth (Royal Botanic Garden, Edinburgh, on *P. eugenei*, D.M.H. 153; on *P. nigra* var. *betulifolia*, D.M.H. 152; on *P. nigra* var. *italica*, D.M.H. 151; on *P. certinensis*, D.M.H. 150), Tay (Auchtermuchty on *P. nigra*, D.M.H. 230), Dee, Moray, Clyde.

This species is of frequent occurrence especially on the *nigra* group of poplars. Most authors have reported that basal cells are present in some collections. Sadebeck (1893) distinguished two types of asci, the one, slender with a basal cell deeply inserted between the epidermal cells, commonly on *P. nigra* var. *italica*, the other, with subcuticular not inserted asci often lacking basal cells, on *P. nigra*. According to Mix both types of asci may be found on any one host. Basal cells are rarely present in my material, but they occur on several hosts. Similarly, the ascus dimensions vary slightly on different hosts but not sufficiently to merit even varietal recognition. Field observation suggest that cross-infection takes place between host species.



Figs. 1 & 2

1. *Taphrina populina* a. Habit b. Asci. 2. *T. johansonii* a. Habit b. Asci.

This species has been generally known as *T. aurea*, a name used by Fries in his *Systema orbis vegetabilis*. However, as the names in his *Systema mycologicum* take precedence over all others used during the period of its publication, 1821-32, the name used by Fries in it in 1832, *Taphrina populina*, is the correct one.

2. *TAPHRINA JOHANSONII* Sadebeck in Jahrb. Hamburg. Wissensch. Anst. viii, 61-95 (1890).

Syn.: *Taphrina rhizophora* Johanson in Bih. Svenska Vetenskakad. Handl. xiii, 3-28 (1887), *pro parte*.

Exoascus johansonii Sadebeck in Jahrb. Hamburg. Wissensch. Anst. x, 5-110 (1893).

Exoascus aureus auct.

Asci apex truncate, deeply inserted between the epidermal cells of the fruit, arising from the intercellular mycelium, $83-113\mu \times 18-21\mu$. Epiplasm bright yellow. Basal cell lacking. Ascospores not seen, budding immediately to produce numerous blastospores. On carpels of *Populus tremula*. [Fig. 2, a and b.]

Distribution. Tweed (Dawyck, Peeblesshire, Herb. East Craigs), Forth (Gifford: Herb. M. Wilson, D.M.H. 198).

This fungus was originally included in *T. populina* (as *T. aureus*) by Magnus (1884). Johanson described the form on carpels of *Populus alba* and *P. tremula* as *Taphrina rhizophora* in 1887. In 1890 Sadebeck separated *T. johansonii* from *T. rhizophora*. The carpel fungi are quite distinct from the leaf spot species *T. populina*. However, the two carpel species are separated only by rather small character differences. The bases of the asci of *T. rhizophora* are described as forked, whereas those of *T. johansonii* are simple. That these distinctions may be due solely to different hosts seems very probable when the variation within the closely allied species *T. populina* on a number of hosts is considered. Both the Scottish collections show simple, slightly lobed, ascus bases.

3. *TAPHRINA SADEBECKII* Johanson in Öfvers Kongl. Svenska Vetenskakad. Forhandl. 29-47, 1886.

Syn.: *Exoascus alni* de Bary, in litt. *pro parte*.

Exoascus flavus Sadebeck in Jahrb. Hamburg. Wissensch. Anst. i, 93-124 (1884).

Exoascus epiphyllus Sadeb. var. *maculans* Sadebeck in Jahrb. Hamburg. Wissensch. Anst. viii, 61-95 (1890).

Ascomyces tosquinetii Westendorp in Bull. Acad. Roy. Sci. Lett. et Beaux-arts Belgique, 2 ser. xi, 644-660 (1861), *pro parte*.

Asci hypophyllous, arising from a subcuticular mycelial network, rather abruptly broader at sub-truncate apex, filled with yellow epiplasm, $32-47 \times 15-16\mu$. Basal cells distant, subcuticular, not inserted between epidermal cells, consistently broader than their asci, $13-21 \times 18-21\mu$. Spores $4-5\mu$ in diameter, budding in the ascus. Causing bright yellow, unthickened spots, up to 1 cm. in diameter, on the under surface of the leaves of *Alnus glutinosa*. [Fig. 3, a, b, and c.]

Distribution. Forth, Tay (Loch of Lowes, Dunkeld, D.M.H. 215; Loch Tay, D.M.H. 214; Kindallachan, D.M.H. 213; Collesie, Fife, D.M.H. 212), Dec, Clyde, Argyll.

This species has been found frequently in the same locality as *T. tosquinetii*, occasionally even on the same twig. It usually matures somewhat later (July–August) than *T. tosquinetii* (May–July). Mix (1949) states that *T. klebahnii*, forming yellow leaf spots on *Alnus incana*, is but a secondary infection of *T. epiphylla*. From field observations it appears that the same relationship may exist between *T. sadebeckii* and *T. tosquinetii*. But the morphology of these two species is very different. The mycelium of *T. tosquinetii* [Fig. 4, a] is composed of globular, budding, yeast-type cells, whilst *T. sadebeckii* [Fig. 3, a] produces well-developed hyphal elements which periodically bear irregular swollen cells—the young basal cells. The connecting hyphae of *T. sadebeckii* do not take part in the formation of asci. In *T. tosquinetii* all the subcuticular cells form asci. Unless infection experiments show otherwise, *T. sadebeckii* and *T. tosquinetii* should be considered distinct.

However, there seems to be little to differentiate *T. sadebeckii* from the leaf-spot phase of *T. epiphylla* described by Wieben (1927) as *T. klebahnii*. The curious ascus shape—abruptly widening to a truncate apex—the yellow epiplasm, the basal cell broader than the ascus, occur in both. The account of the subcuticular mycelium and development of asci in *T. epiphylla* given by Sadebeck (1893) would serve *T. sadebeckii* equally well. Nor could they be readily distinguished by dimensions of asci, basal cells or spores as given by Mix. The only difference is in host relations. *T. epiphylla* causes brooms and yellow leaf spots on *Alnus incana* and is confined to Europe.

4. *TAPHRINA TOSQUINETII* (Westend.) Tulasne in Ann. Sci. Nat. 5 Ser. Bot. v, 122–136 (1866).

Syn.: *Ascomyces tosquinetii* Westendorp in Bull. Acad. Roy. Sci. et Beaux-arts Belgique, 2 Ser. xi, 644–660 (1861).

Taphrina alnitorqua Tulasne in Ann. Sci. Nat. 5 Ser. Bot. v, 122–136 (1866), *pro parte*.

Exoascus alnitorquus (Tul.) Sadebeck in Jahrb. Hamburg. Wissensch. Anst. i, 93–124 (1884), *pro parte*.

Exoascus alni de Bary, in litt. *pro parte*.

Taphrina media Palm in Arkiv. Bot. xv, 1–41 (1917).

Asci amphigenous, rounded at apex, arising from budding subcuticular mycelium, $16\text{--}26\mu \times 8\text{--}10\mu$. Basal cells, forming a subcuticular layer, shallowly inserted between the epidermal cells, $8\text{--}21\mu \times 8\text{--}13\mu$. Spores 4μ in diameter usually irregularly uniseriate at first, budding in the ascus. Causing twig distortion and bullate leaf spots on *Alnus glutinosa*. [Fig. 4, a, b and c.]

Distribution. Forth (Aberdour, D.M.H. 226), Tay (Glen Lyon, D.M.H. 229; Loch Tay, D.M.H. 220; Loch Butterstone, Dunkeld, D.M.H. 219), Dee, Moray (Contin, D.M.H. 222), Clyde, Argyll (Onich, D.M.H. 225; Loch Oich, D.M.H. 224; Loch Garry, D.M.H. 228), West Ross (Dundonnell, D.M.H. 227; Loch Hourm, D.M.H. 223; Loch Duich, D.M.H. 221).

This species attacks leaves and shoots of *Alnus glutinosa*. Infected leaves are thick, and the ascus layer confers a whitish bloom to both surfaces of the leaf. Occasionally, only a part of the leaf is affected and a large bullate deformation results. Shoots, especially the sucker shoots arising about the base of trees, are frequently attacked. Only in damp situations, for example, where young plants are crowded, are twigs on the upper parts of trees infected. Large witches' brooms, as are produced by *T. cerasi*, do not develop.

Infected shoots growing from the base of trees are very vigorous, but die in their first or second year. They are very soft, pliable, abnormally thick, and are negatively geotropic. All the leaves on infected shoots are usually completely encompassed by the fungus. Such completely infected leaves are up to twice as large as normal, thickened, rather brittle, and markedly incurved.

Ramsbottom & Balfour-Browne (1951) unite this species with *T. sadebeckii*. The morphology of the two is so distinct that there is no justification for this treatment. Also their *Exoascus alnitorquus* is a mixture of *T. tosquinetii* and the very distinct species *T. amentorum*, which deforms female catkins.

5. *TAPHRINA AMENTORUM* (Sadeb.) Rostrup in Vidensk. Meddel. Naturh. Foren. Kjøbenhavn, 1890, 246-264.

Syn.: *Exoascus amentorum* Sadebeck in Sitzungsber. Ges. Bot. Hamburg, iv, 90 (1888).

Ascomyces alni Berkeley & Broome in Ann. & Mag. Nat. Hist. xvii, 129-145 (1876)—*nom. nud.*

Exoascus alnitorquus (Tul.) Sadebeck var. *alni-incanae* J. Kühn. (Fungi Europaei, 1616.)

Taphrina alni-incanae (Kühn) Sadebeck in Jahrb. Hamburg. Wissenschaft. Anst. viii, 16-95 (1890).

Exoascus alnitorquus (Tul.) Sadebeck var. *alni-incanae* J. Kühn (Fungi Europaeum 1616.)

Exoascus alni de Bary, in litt. *pro parte*.

Exoascus alni de Bary var. *strobilinus* Thumen in Flora, lxiii, 312-322, 323-332 (1880)—*nom. nud.*

Ascomyces tosquinetii Westend. var. *strobilina* Rostrup in Tidsskr. Skogbruk, iv, 113-206 (1880).

Asci amphigenous on the catkin scales, truncate at apex, subcuticular, not inserted between the epidermal cells, $35-44\mu \times 9-16\mu$. Basal cells absent. Spores $3-4.5\mu$ in diameter, budding sparingly on the ascus. On female catkins of *Alnus incana* and *A. glutinosa* [Fig. 5, a and b].

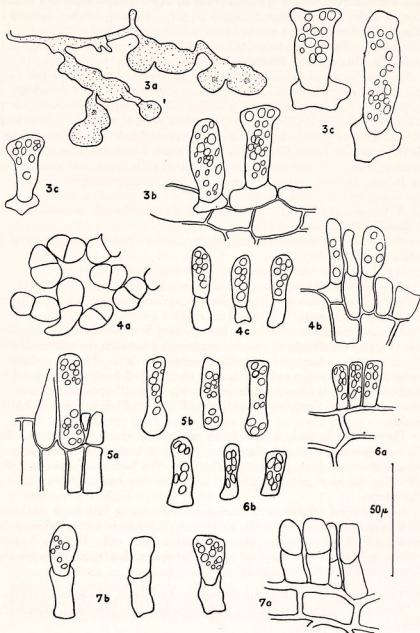
Distribution. On *Alnus glutinosa*: Dee (Midmar, Stonehaven as *Exoascus alni* B. & Br., Trail, 1889), Orkney (Binscarth, Trail, 1889), Argyll (Loch Awe, Herb. M. Wilson). On *Alnus incana*: Tay (Glen Clova, D.M.H. 157), W. Ross (Eigg, Dennis, 1952).

This fungus infects the scales of the female catkins of *Alnus*. As a result of stimulation by the fungus, red, tongue-shaped outgrowths about 1-2 cm. long and 0.5 cm. broad are produced. Infected catkins are quite conspicuous, so that from the few records this fungus appears to be rare in Britain. Mix (1949) records it on *A. glutinosa*, *A. hirsuta*, *A. hybrida*, *A. incana* and *A. rubra*.

This species differs from all others on *Alnus* in lacking a basal cell. This character distinguishes it from *Taphrina robinsoniana*, an exclusively North American species which attacks *Alnus incana* and *A. rugosa*.

The correct name for this species has long been a matter of controversy. Ray (1939) has given a complete account of the case. In 1873 Kühn described *Exoascus alnitorquus* forma *Alni-incanae* on female catkins of *Alnus*. In 1888 Sadebeck described *Exoascus amentorum*. In 1890 Magnus examined Kühn's material and raised Kühn's *forma* to specific rank as *T. alni-incanae* (Kühn) Magnus. This name has been widely used but is antedated by Sadebeck's name. Rostrup (1890) accepted Sadebeck's name and transferred the species to *Taphrina*.

The name *Ascomyces alni* B. & Br. applied in 1876 is inadmissible as it lacks description. The epithet *alni* had been used previously by de Bary to include several species on *Alnus*.



Figs. 3-7

3. *Taphrina sadebeckii* a. Subcuticular mycelium. b. Habit. c. Asci. 4. *T. tosquinetii* a. Subcuticular mycelium. b. Habit. c. Asci. 5. *T. amentorum* a. Habit b. Asci. 6. *T. carpini* a. Habit b. Asci. 7. *T. betulae* a. Habit b. Asci.

6. *TAPHRINA CARPINI* (Rostr.) Johanson in Öfvers. Kongl. Svenska Vetensk. Akad. Forhandl. 29-47 (1886).

Syn.: *Exoascus carpini* Rostrup in Bot. Centbl. v, 153-154 (1886).

Asci hypophyllous, rounded at apex, arising from subcuticular mycelium, not inserted between the epidermal cells $24-29\mu \times 9-10\mu$. Basal cell lacking. Spores eight, ovate to elliptic, usually $3.5 \times 5\mu$. Causing witches' brooms on *Carpinus betulus* [Fig. 6, a and b].

Distribution. Forth (Kirkliston, W. Lothian, D.M.H. 217; Aberdour, D.M.H. 216), Tay (Blairgowrie, Perthshire, D.M.H.).

In most cases of brooming induced by species of *Taphrina* the twigs produced in profusion are strongly negatively geotropic. Attack by *T. carpini* produces a profusion of branches but affects their orientation little. Sadebeck (1895) states that the fungus overwinters as mycelium in the buds. It is present on leaves when the buds are opening, but I am unable to find it in fully dormant buds. The species has no doubt been introduced to Scotland with its host. It is recorded twice in England (Mix, 1949, and Ramsbottom & Balfour-Browne, 1951). These are the first Scottish records.

7. *TAPHRINA BETULAE* (Fkl.) Johanson in Öfvers. Kongl. Svenska Vetensk. Akad. Forhandl. 29-47 (1886).

Syn.: *Exoascus betulae* Fuckel, Jahrb. Nassau. Verein. Naturk. xxvii & xxix, 1-99 (1873-1874).

Ascomyces betulae Magnus, Rab. Fungi Europaei 2734.

Taphrina auctumnalis (Sadeb.) Palm, Arkiv. Bot. xv, 1-41 (1917).

Taphrina betulae (Fkl.) Johanson var. *auctumnalis* Sadebeck, Jahrb. Hamburg. Wissensch. Anst. x, 5-110 (1893).

Asci hypophyllous, rounded at apex, arising from subcuticular mycelium $20-24 \times 11-13\mu$. Basal cell present, not inserted between the epidermal cells $20-25 \times 9-15\mu$. Ascospores, budding in ascus, 5μ in diameter. Causing reddish-brown spots, 1 cm. in diameter, on leaves of *Betula* [Fig. 7, a and b]. *Distribution.* Clyde (Troon as *Exoascus betulae* Fuck. [Cryptogamic Society of Scotland Annual Conference, 1928], Argyll (Eilann Shona, Arisaig, D.M.H. 236).

There is no herbarium material to substantiate the Troon record. The Arisaig specimens were collected in July and bear reddish-brown spots which show on both surfaces of the leaf. The asci are fully ripe. Mix describes the spots as yellowish, but adds that they become brown later in the season.

A number of species have been described causing leaf spots on birch. *T. flava* Farlow and *T. boycei* Mix differ from *T. betulae* in having intercellular mycelium. *Taphrina carnea* Johanson lacks a basal cell. *Taphrina bacteriosperma* Johanson according to Mix's description has much broader asci ($23-30\mu$ at base) than *T. betulae* ($11-13\mu$).

8. *TAPHRINA BETULINA* Rostrup in Tidsskr. Skogbruk, vi, 199-300 (1883).

Syn.: *Exoascus betulinus* (Rostr.) Sadebeck in Jahrb. Hamburg. Wissensch. Anst. x, 5-10 (1893).

Taphrina lagerheimii Palm in Arkiv Bot. xv, 1-41 (1917).

Taphrina lapponica Juel in Svensk Bot. Tidsskr. vi, 353-372 (1912).

Exoascus lapponicus (Juel) Jacewski, Pocket Key for determination of fungi; Part I, Exoascales. Leningrad, 1926.

Taphrina turgida (Sadeb.) Giesenhagen in Flora, lxxxi, 267-361 (1895).

Exoascus turgidus Sadebeck in Jahrb. Hamburg. Wissensch. Anst. i, 93-124 (1884).

Taphrina willeana Svendsen in Nyt Mag. Vidensk. xl, 363-368 (1902).

Asci hypophyllous, rounded at apex, arising from subcuticular basal cell, $41-75 \times 15-21 \mu$. Basal cell $23-26 \times 16-30 \mu$. Ascospores budding immediately to produce numerous small ($2 \times 3 \mu$) blastospores. [Fig. 8, a and b, 9 and 10.]

Causing witches' brooms on *Betula verrucosa* Ehrh., *B. pubescens* Ehrh. ssp. *pubescens* and *B. pubescens* ssp. *odorata* (Bechst.) E. F. Warburg.

Distribution. Recorded on "*Betula alba*" by Dennis & Foister (1942) from Tweed, Forth, Dee, Moray, Solway, Clyde, Argyll.

Material examined: on *B. verrucosa*: Argyll (Loch Garry, D.M.H. 206). On *B. pubescens* ssp. *odorata*: Tay (Bridge of Cally, D.M.H. 204), Ross (D.M.H. 201, 202, 203, 205). On *B. pubescens* ssp. *pubescens*: Tay (Bridge of Cally, D.M.H. 200).

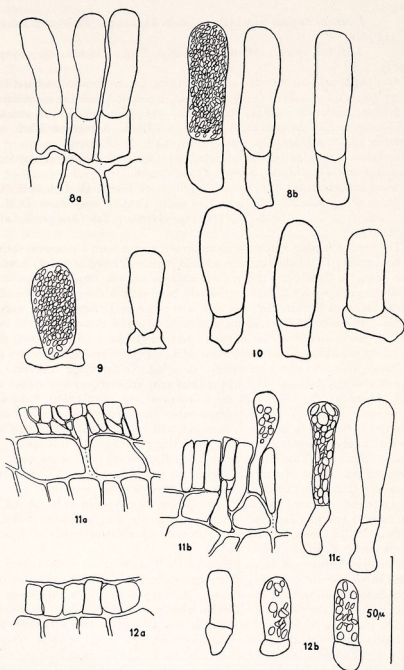
The species causing witches' broom on birch have been a recurrent source of confusion. Two have been recorded in Britain: *T. turgida* and *T. betulina*. According to Sadebeck (1893) *T. betulina* occurs on *Betula pubescens* and *T. turgida* on *B. verrucosa*. He describes the basal cells of *T. betulina* as rounded at the base and broader than the asci, and those of *T. turgida* with wedge-shaped bases inserted between the epidermal cells and as narrow as the asci. Rostrup made several studies of these species and finally decided (1896) that they were distinct and host specialised. Mix (1949) on the contrary lumps the two and gives convincing reasons for so doing. In my single collection on *B. pubescens* ssp. *pubescens* [Fig. 9] the basal cells are certainly wider than the asci. However, the collections on *B. pubescens* ssp. *odorata* [Fig. 8, b] and *B. verrucosa* [Fig. 10] are indistinguishable from one another. The ssp. *pubescens* is reputed to be rare in Scotland, and only one collection on it has been examined. More material may show that the fungus on this subspecies indeed differs from that on *B. verrucosa* and *B. pubescens* ssp. *odorata*, and that doubt of the validity of a second species on *B. pubescens* is due to the examination of mixtures of collections on ssp. *odorata* and ssp. *pubescens*.

Symptoms described by Juel (1909), which were reputed to be caused by yet another species, *Taphrina lapponica*, producing only yellowing and distortion of the leaves, seem to be but early or abortive stages of broom formation by *T. betulina* (Mix, 1949).

The deformations on birch produced by *T. betulina* are quite typical of other broom formations. Negatively geotropic, precocious shoots grow out from infected areas in dense masses; maturation of the woody tissue is incomplete and the twigs are killed back by frosts. A second type of broom occurs on birch in Scotland apparently not associated with a fungus, but generally attributed to a mite—*Eriophyes rudis*. The twigs of these brooms are not thickened as are those affected by the fungus; there is little negative geotropic effect and the leaves develop normally without marked thickening.

9. *TAPHRINA CAERULESCENS* (Mont. & Desm.) Tulasne in Ann. Sci. Nat. 5 Ser. Bot. v, 122-136 (1886).

Syn.: *Ascomyces caerulescens* Mont. & Desm. in Ann. Sci. Nat. 3 Ser. Bot. x, 342-361 (1848).



Figs. 8-12

8, 9 and 10. *Taphrina betulina*. 8. On *B. pubescens* ssp. *odorata*. a. Habit b. Asci.
 9. On *B. pubescens* ssp. *pubescens*. 10. On *B. verrucosa*. 11. *T. bullata* a. Cuticular
 mycelium b. Habit c. Asci, 12. *T. crataegi* a. Mycelium b. Asci,

Ascomyces alutaceus Thumen in Verhandl. K.K. Zool. Bot. Ges. Wien, xxix, 523-524 (1880).

Ascomyces extensus Peck in New York State Mus. Nat. Hist. Ann. Rept. xxxix, 30-70 (1886).

Ascomyces rubrobrunneus Peck in New York State Mus. Nat. Hist. Ann. Rept. xl, 39-77 (1887).

According to Mix's description the asci of this species are very variable. On *Quercus rubra* $50-54\mu \times 19-25\mu$, on *Q. sessiliflora* $46-72\mu \times 15-27\mu$. They are cylindric or clavate, rounded at the apex, with a blunt or truncate base, or on some *Quercus* species the base is branched bearing rhizoidal appendages. A basal cell is lacking. Ascospores bud immediately on formation.

Distribution. Tay (Murthly, Perthshire).

This species is recorded by Trail (Trans. Perthsh. Soc. Nat. Sci. ii, pp. 127-131) on oaks at Murthly, Perthshire. He notes: "causing spots, discoloured and prominent above, concave and at first pale below, where the asci are formed after a time. This obscure parasite, though not previously recorded from Scotland, is not rare in various districts from Perth to Aberdeen." There are no specimens either in the Natural History Museum, Perth, nor in Trail's herbarium in the Department of Botany of Aberdeen University.

10. *TAPHRINA BULLATA* (Berk.) Tulasne in Ann. Sci. Nat. 5 Ser. Bot. v, 122-136 (1886).

Syn.: *Ascomyces bullatus* Berk. in Jour. Roy. Hort. Soc. London, ix, 48 (1854).

Exoascus bullatus (Berk.) Sadebeck, Jahrb. Hamburg. Wissensch. Anst. x, 5-110 (1893).

Asci hypophyllous, arising from the subcuticular mycelium, sub-truncate at apex, $9-12\mu \times 32-36\mu$. Basal cells, $6-10\mu \times 8-18\mu$, forming a thick subcuticular layer, some cells deeply inserted between the epidermal cells. Spores 4μ in diameter, budding in the ascus [Fig. 11, a, b and c].

Causing bullate spots on the leaves of pear.

Distribution. Tweed (Kelso, Herb. M. Wilson), Moray, Clyde, Argyll.

This species was described by Berkeley (1854) on pear leaves. The fungi on *Pyrus* and *Crataegus* have both been referred to *T. bullata*, but were later separated by Sadebeck on somewhat doubtful grounds. The two species are discussed under *T. crataegi*.

11. *TAPHRINA CRATAEGI* Sadebeck in Jahrb. Hamburg. Wissensch. Anst. viii, 61-95 (1890).

Syn.: *Exoascus bullatus* (Berk.) Fkl. in Jahrb. Hamburg. Wissensch. Anst. i, 93-124 (1884), *pro parte*.

Exoascus crataegi Sadebeck in Jahrb. Hamburg. Wissensch. Anst. x, 5-110 (1893).

Asci amphigenous, arising from the subcuticular mycelium, subtruncate at apex, $15-18\mu \times 17-26\mu$. Basal cells strictly cuticular not penetrating the epidermis, $7-9\mu \times 5-9\mu$. Spores, ovoid, $3 \times 5\mu$, usually budding in the ascus. Causing leaf spot on *Crataegus* [Fig. 12, a and b].

Distribution. Dee (Aberdeen, Trail in Scot. Nat. N.S. iii, 1887, p. 172), Argyll (Tomdown, D.M.H. 218).

The fungus produces reddish-yellow bullate spots up to 1 cm. in diameter frequently along the margin of the leaf, which is then rather inrolled. The

leaf distortion is very similar to that caused by the aphides, *Myzus oxyacanthae* and *Aphis piri* var. *oxyacanthae*, but may be distinguished macroscopically by the bloom imparted to the leaf surface by the layer of ripe asci. The distortions are also similar but larger and more bullate than the very narrow marginal leaf rolling attributed to *Eriophyes goniothorax*. The species is considered to be very close to *T. bullata* from which it was separated by Sadebeck in 1890, primarily on the basis of host specialisation. It seems doubtful from the description that the two species should be retained, but the Scottish material on pear and hawthorn which I have examined are strikingly dissimilar. They seem to represent the extremes of variation on the two hosts.

T. marginata Lam. & Faut. listed by Ramsbottom & Balfour-Browne (1951) from a record by O'Connor from Ireland is not a fungus according to Mix (1936) but mite injury. The fungus was presumably *T. crataegi*.

12. *TAPHRINA POTENTILLAE* (Farl.) Johanson in Öfvers. Kongl. Svenska Vetenskakad. Forhandl. xlii, 29-47 (1885).

Syn.: *Exoascus deformans* (Berk.) Fkl. var. *potentillae* Farlow in Proc. Amer. Acad. Arts and Sci. xviii, 65-85 (1883).

Tapbrina tormentillae Rostrup in Bot. Tidsskr. xiv, 230-243 (1885).

Magnusiella potentillae (Farl.) Sadebeck in Jahrb. Hamburg. Wissensch. Anst. x, 5-110 (1893).

Asci amphigenous on the leaves and on the stems of *Potentilla erecta* (L.) Rausch, arising from sub-epidermal ascogenous cells, rounded at apex, tapering to a long base inserted between the epidermal cells, 28-45 \times 8-10 μ . Mycelium intercellular in host cortex. Spores 2-3 μ in diameter, budding in the ascus [Fig. 13, a and b].

Causing yellow thickened spots on the leaves and yellow thickening of the stems of *Potentilla erecta*.

Distribution. Forth (Mid Calder, West Lothian, D.M.H. 232), Tay (Ben Lawers, D.M.H. 233), Dee, Solway, Clyde (Arran, Herb. M. Wilson), Argyll (Ben Lui, Herb. M. Wilson), Ross (Loch Maree, D.M.H. 234).

The fungus is frequent on the west coast, and can be collected from most wet ditches where the host occurs. The pale yellow infected stems and leaves are quite conspicuous. This species was separated from *Exoascus* and *Tapbrina*, and made the type of the new genus *Magnusiella* by Sadebeck, because of the sub-epidermal ascogenous cells arising from intercellular mycelium.

13. *TAPHRINA PRUNI* Tulasne, Ann. Sci. Nat. 5 Ser. Bot. v, 122-136 (1866).

Syn.: *Exoascus pruni* Fkl. in Jahrb. Nassau Ver. Naturk. xxiii & xxiv, 1-459, 1869 and 1870.

Tapbrina rostrupiana (Sadeb.) Giesenhagen in Flora, lxxxi, 267-361 (1895).

Exoascus rostrupianus Sadebeck in Jahrb. Hamburg. Wissensch. Anst. x, 5-110 (1893).

Tapbrina insititiae (Sadeb.) Johanson in Öfvers Kongl. Svenska Vetenskakad. Forhandl. 29-47 (1886).

Exoascus insititiae Sadebeck in Jahrb. Hamburg. Wissensch. Anst. i, 93-124 (1884).

Tapbrina pruni Tul. var. *divaricata* Jaczewski, Pocket Key for the determination of fungi; Part I, Exoascales. Leningrad, 1926.

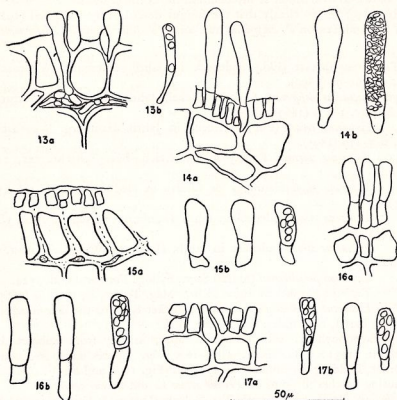
Asci arising from subcuticular mycelium, rounded at apex, narrowing

basally, $46-63 \times 10-14\mu$. Basal cells not inserted, often very crowded $7-11 \times 7-12\mu$. Spores ovoid $4-5\mu$ budding almost immediately on formation producing numerous ovate blastospores. Causing "pocket plums" on *Prunus domestica* and "pocket plums" and shoot distortion on *Prunus spinosa* [Fig. 14, a and b].

Distribution. On *Prunus domestica*: Forth, Dee, Moray, Solway. On *Prunus spinosa*: Tweed (Hardy, Hist. Berwicksh. Nat. Cl. x, 214-215; 1882-84), Tay (Blairgowrie, D.M.H. 123 and 102).

This species is not common in Scotland. It is of rare occurrence on plums (Dennis & Foister, 1942, and unpublished records Plant Pathology Laboratory, Corstorphine). It is only three times recorded on sloe.

The effect on the fruit is similar on both hosts. They are more elongate, often depressed on one side, and lighter in colour than healthy fruits. The asci on sloe fruits are ripe in June. While examining a bush of sloe in July after the infected fruits had fallen, distorted shoots were noticed. Young shoots are probably infected from the fruits. Infected shoots are swollen, stunted, light yellow in colour often tinged with red, and bear reduced strap-like leaves. Intercellular hyphae are present in the stem cortex, and asci arise subcuticularly as on the fruit.



Figs. 13-17

13. *Taphrina potentillae* a. Habit b. Ascus. 14. *T. pruni* on *Prunus spinosa* a. Habit b. Ascus. 15. *T. deformans* on Peach. a. subcuticular mycelium and inter-cellular hyphae. b. Ascus. 16. *T. cerasi* on *Prunus avium* a. Habit b. Ascus. 17. *T. padi* a. Subcuticular mycelium b. Ascus.

14. *TAPHRINA DEFORMANS* (Berk.) Tulasne in Ann. Sci. Nat. 5 Ser. Bot. v, 122-136 (1886).

Syn.: *Exoascus deformans* (Berk.) Fkl. in Jahrb. Nassau Ver. Naturk. xxiii & xxiv, 1-459 (1869-70).

Ascomyces deformans Berkeley, Outl. Brit. Fungi, 376 (1860).

Taphrina amygdali (Jacz.) Mix, Univ. Kansas Sci. Bull. xxiv, 151-176 (1936).

Exoascus amygdali Jaczewski, Pocket Key for the determination of fungi; Part I, Exoascales. Leningrad, 1926.

Asci hypophyllous, arising from subcuticular basal cells, apex rather truncate $19-26 \times 6-12\mu$. Basal cells not inserted $6-9 \times 6-11\mu$. Mycelium intercellular in the leaf. Spores $3-5\mu$ in diameter, budding within the ascus. Causing leaf curl of *Prunus persica*, *P. amygdalus* and *P. amygdalus* var. *amara*. [Fig. 15, a and b.]

Distribution. On *Prunus persica*: Tweed, Forth (Edinburgh, D.M.H. 199), Tay, Dee, Moray, Solway. On *Prunus amygdalus*: Forth, Clyde, Tay. On *Prunus amygdalus* var. *amara*: Tay (St. Andrews, Mix, 1949).

The intercellular mycelium permeates infected leaves and causes hypertrophy and hyperplasia; the infected parts are bright red. This species has been shown to overwinter as mycelium in the dormant buds.

Mix (1949) shows clearly that the fungus described by Campbell (1925) from St. Andrews on *P. amygdalus* var. *amara* is quite typical *T. deformans*.

15. *TAPHRINA CERASI* (Fkl.) Sadebeck in Jahrb. Hamburg. Wissensch. Anst. viii, 61-93 (1890).

Syn.: *Exoascus deformans* f. *cerasi* Fuckel, Jahrb. Nassau Ver. Naturk. xxiii & xxiv, 1-459 (1869-70).

Exoascus cerasi (Fkl.) Sadebeck in Jahrb. Hamburg. Wissensch. Anst. x, 5-110 (1893).

Exoascus wiesneti Rathay in Osterreich. Bot. Zeitschr. xxx, 225 (1880).

Taphrina gilgii Hennings & Lindau in Hedwigia, xxxii, 156-157 (1893).

Taphrina minor Sadebeck in Jahrb. Hamburg. Wissensch. Anst. viii, 61-95 (1890).

Exoascus minor Sadebeck in Jahrb. Hamburg. Wissensch. Anst. x, 5-110 (1893).

Taphrina pseudocerasi (Shirai) Sacc., Sylloge Fungorum, xiv, 524.

Taphrina pseudocerasi Shirai in Bot. Mag. Tokyo, ix, 161-164 (1895).

Exoascus pruni-acidae Jaczewski, Pocket Key for the determination of fungi; Part I, Exoascales. Leningrad, 1926.

Asci hypophyllous, sub-truncate at apex, arising from subcuticular mycelium, $21-31 \times 6-8\mu$. Basal cell $8-16 \times 5-6\mu$. Spores large, irregularly uniseriate, budding occasionally, $4-6 \times 3-4\mu$ [Fig. 16, a and b].

Causing witches' brooms on *Prunus avium* L. and *Prunus cerasus*.

Distribution. On *P. avium*: Forth, Tay, Solway (Dennis & Foister, 1942), W. Ross (Arisaig, D.M.H. 235). On "Cherry": Clyde (Lanark, Alcock & Foister, 1931).

This common species has been thoroughly investigated by several workers. The mycelium is described as perennial in the twigs of the broom. The host

reaction—stimulated precocious twig growth, poor lignification of the sclerenchyma cells, marked negative geotropy of the twigs—are all typical of broom formation. The infected leaves are red and smell of newly mown hay.

The spores of this species are large for the genus and ascus morphology easily separates this species from others on *Prunus*.

16. *TAPHRINA PADI* (Jacz.) Mix in Trans. Kansas Acad. Sci. 1, 77-83 (1947).

Syn.: *Taphrina pruni* Tulasne in Ann. Sci. Nat. 5 Ser. Bot. v, 122-136 (1886) *pro parte*.

Taphrina pruni Tul. var. *padi* Jaczewski, Pocket Key for the determination of fungi; Part I, Exoascas. Leningrad, 1926.

Asci arising from subcuticular basal cells, rounded at apex $23-32\mu \times 50-68\mu$. Basal cells $10-22\mu \times 8-12\mu$ not inserted. Spores $4-5\mu$ in diameter, budding in the ascus. Causing deformation of the flowers and fruits of *Prunus padus* [Fig. 17, a and b].

Distribution. Tay (Glen Lyon, D.M.H. 231; Glen Shee, D.M.H. 124), Moray, Clyde.

The fungus induces hypertrophy of the host tissues which results in the elongation of the infected fruits. The styles are persistent and merge gradually with the fruit apex. Infection of the floral disc has been observed. No infection of shoots comparable to that described for *T. pruni* on *Prunus spinosa* has been found.

This species was distinguished from *T. pruni* by Mix in 1947. In his notes on the species he emphasises the taxonomic remoteness within the genus *Prunus* of the host *P. padus* from the hosts of *T. pruni*, *P. spinosa* and *P. domestica*. He gives the following measurements: "*T. pruni*, asci $17-53 \times 5-17\mu$, stalks cells $5-27 \times 4-13\mu$." For *T. padi* he gives: "asci $26-46 \times 8-13\mu$, basal cells $8-26 \times 7-10\mu$." The dimensions for *T. pruni*, therefore, completely overlap those of *T. padi*, so it would appear impossible to distinguish them apart from their hosts. However, in the limited Scottish material available, differences are well marked. The asci of *T. pruni* on *Prunus spinosa* are narrower, $10-14\mu$, than those on *P. padus*, $23-32\mu$. Basal cells: on *P. spinosa* $7-11 \times 7-12\mu$, on *P. padus* $10-22 \times 8-12\mu$. Examination of more collections would probably show these distinctions to be less clear cut.

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