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Anatomy and cytology of *Taphrina entomospora* during infection of *Nothofagus*

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ABSTRACT

Taphrina entomospora is one of the few species of the genus described on native plants of the Southern Hemisphere and also one of the few leaf pathogens known on *Nothofagus* species. The anatomical changes it produces on *N. pumilio* leaves, and its morphology, cytology, and sporogenesis were studied. The fungus is a perennial species that overwinters as mycelium in the foliar buds and infects the developing leaves, so the whole blade develops the disease symptoms. Interveinal areas of the leaves become chlorotic, thickened and rounded. Palisade parenchyma fails to develop, with spongy parenchyma developing as packed, rounded, isodiametric cells with little intercellular space. The mycelium is subcuticular, dikaryotic, and produces ascogenous hyphae, asci, and ascospores as described for other species in the genus. Before ascus discharge, ascospores bud in a regular, unique way. The life-cycle of *T. entomospora* is compared with other representative taxa in the genus and the distribution of this pathogen is discussed.

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Introduction

Taphrina (*Taphrinales*, *Ascomycota*) comprises biotrophic organisms characterized by a parasitic, dikaryotic, mycelial state that grows on the host and forms naked asci and ascospores, and a saprophytic, yeast phase, which is haploid and uninucleate, and can be isolated and cultured, reproducing itself by budding (Alexopoulos *et al.* 1996; Webster 1980). *Taphrina* taxa are pathogens on a variety of hosts ranging from ferns to angiosperms, and produce infections and diverse symptoms on leaves, stems or fruits. Mix (1949, 1954) reviewed the genus and recorded more than 100 species. Rodrigues & Fonseca (2003) reviewed the taxonomy on the basis of DNA studies and showed the group to be monophyletic. Few regional monographs have been published (Rodrigues & Fonseca 2003). Studies of the genus deal with species from the Northern Hemisphere, particularly those that are pathogens of plants important to agriculture and forestry. Taxa produce a variety of symptoms on different hosts, i.e., leaf spots, leaf curling, witches' brooms, thickening of leaves, deformed organs (twigs, flowers, carpels and/or fruits), plum pockets, leaf blisters and leaf galls. The best known species is by far *T. deformans*, a pathogen on peach and almond trees.

From the known *Taphrina* taxa (Mix 1949) only 15 have been cited from Central and South America [*Fungal Databases*, http://nt.ars-grin.gov/fungaldatabases/ (accessed 22 December 2005) *et al.* 2006; Viégas 1961], six of which are associated with introduced hosts. Of the nine *Taphrina* species known to parasitize native hosts from Central and South America, five have been described on ferns and three on tropical

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angiosperms (Table 1). Few *Taphrina* species have been described on native plants of the Southern Hemisphere, and these are still relatively unknown and poorly studied. An example of this is *Taphrina entomospora*, which was found and described by the American mycologist Ronald Thaxter on living leaves of *Nothofagus antarctica* in the early 20th century (Thaxter 1910) and, almost 60 y later, was recorded on *N. pumilio* by Roivainen (1977); both tree species are caducifolious. The life-cycle of this fungus and the symptoms produced in the leaves of *N. antarctica* has, so far, only been described by Thaxter (1910).

Nothofagus is the only native member from *Fagaceae* in the Southern Hemisphere, in Argentina being represented by six species, and constitutes the dominant tree genus of the Patagonian Andes forests. The latter is one of the most characteristic biogeographic formations of Argentina (Cabrera & Willink 1980; Donoso 1993; Hueck 1978), and belongs to the Antarctic Region, Subantarctic Domain and Subantarctic Province (Cabrera 1971). It is well known that the biota of southern South America is historically and biogeographically linked to Australia, Tasmania, New Guinea, New Caledonia and New Zealand (Crisci *et al.* 1991), as is the case of *Nothofagus*. *N. pumilio* is one of the main tree species in the Patagonian Andes, covering more than 1M ha, being an important forest resource (Bava 1998).

In this work we aimed to study the anatomical changes that *T. entomospora* produces in *N. pumilio*, the host–parasite relationship and the morphology, cytology and sporogenesis of the pathogen.

Materials and methods

Twigs with diseased and healthy leaves of *Nothofagus pumilio* were gathered monthly from mid-November 2000 through March 2001. All materials were collected in Cañadón Huemules, Futaleufú, Chubut Province, Argentina, leg. M. Rajchenberg nº 12070 (16 November 2000), 12071 (21 December 2001), 12072 (16 January 2001), 12073 (14 February 2001), and 12074 (22 March 2001). Materials were preserved in FAA and stored at the Forest Pathology Herbarium, Centro Forestal CIEFAP and at BBB.

For histological preparations fixed/preserved specimens were dehydrated in an ethyl alcohol/butyl alcohol series and preserved in Paramat (Merck). Transverse and paradermal sections 5–10 μm thick were obtained with a rotary microtome.

For host–parasite relationship and foliar anatomy studies, sections of healthy and diseased leaves were stained with safranin-fast green (Johansen 1940). For vegetative mycelium detection, sections were stained with toluidine blue and orange G. Measurements of the pathogen were made from free hand sections mounted in 5 % potassium hydroxide and stained with Trypan blue (Deckert *et al.* 2001). Fungal mycelium and developing asci were stained with Heidenhain's haematoxylin, following the 4-4 scheme (or short scheme) protocol (Langeron 1949; Sass 1958). All observations were done using a Leitz SM-LUX brightfield compound light microscope and a Nikon Eclipse 600 microscope, and documented with Wild Semiphotomat MPS 25 microphotography equipment and Nikon Coolpix 950 digital camera.

Results

Healthy leaves of *Nothofagus pumilio* were dark green, simple, alternate, elliptic, with obtuse bases and crenate edges, approximately 4 cm in length and 3 cm wide; with a prominent central rib at the back; parallel or sub-parallel secondary ribbings, between which were two lobes (Fig 1A). They showed the typical dorsiventral layered structure of dicotyledonous plants (Fig 1B–C). The superior epidermis was a layer of

Table 1 – *Taphrina* taxa recorded from Central and South America [according to *Index Fungorum*, http://www.indexfungorum.org (accessed: 12 February 2005), *Fungal Databases*, http://nt.ars-grin.gov/fungaldatabases/ (accessed 22 December 2005) and Viégas (1961)]

Species	Host	Location	Distribution
Taphrina amplians	*Pteris orizabe*[a]	Guatemala	?
T. andina	*Prunus serotina* var. *salicifolia*	Mexico	Mexico, Colombia, Equator
T. blechni	*Blechnum* sp.[a]	Brazil	?
T. bullata	*Pyrus* sp.	Eurasia	Cosmopolitan?
T. deformans	*Prunus* spp.	Europe	Cosmopolitan[b]
T. ecuadorensis	*Dryopteris cheilanthoides*[a]	Equator	?
T. entomospora	*Nothofagus antarctica*[a]	Chile	Argentina and Chile
T. populina	*Populus nigra*	Europe and Canada	Cosmopolitan[b]
T. pruni	*Prunus domestica*	North America?	Cosmopolitan[b]
T. pteridis	*Pteris* spp.[a]	Brazil	?
T. randiae	*Randia* sp.	Tropical	Cosmopolitan?
T. sebastianae	*Sebastiania ypanemensis*[a]	Brazil	?
T. thaxteri	*Dryopteris poiteana*[a]	Trinidad Tobago	?
T. ulmi	*Ulmus rubra*	USA	Cosmopolitan[b]
T. wiesneri	*Prunus* spp.	Europe and USA	Cosmopolitan[b]

?, Data unknown.
a Native host.
b Follows the host.

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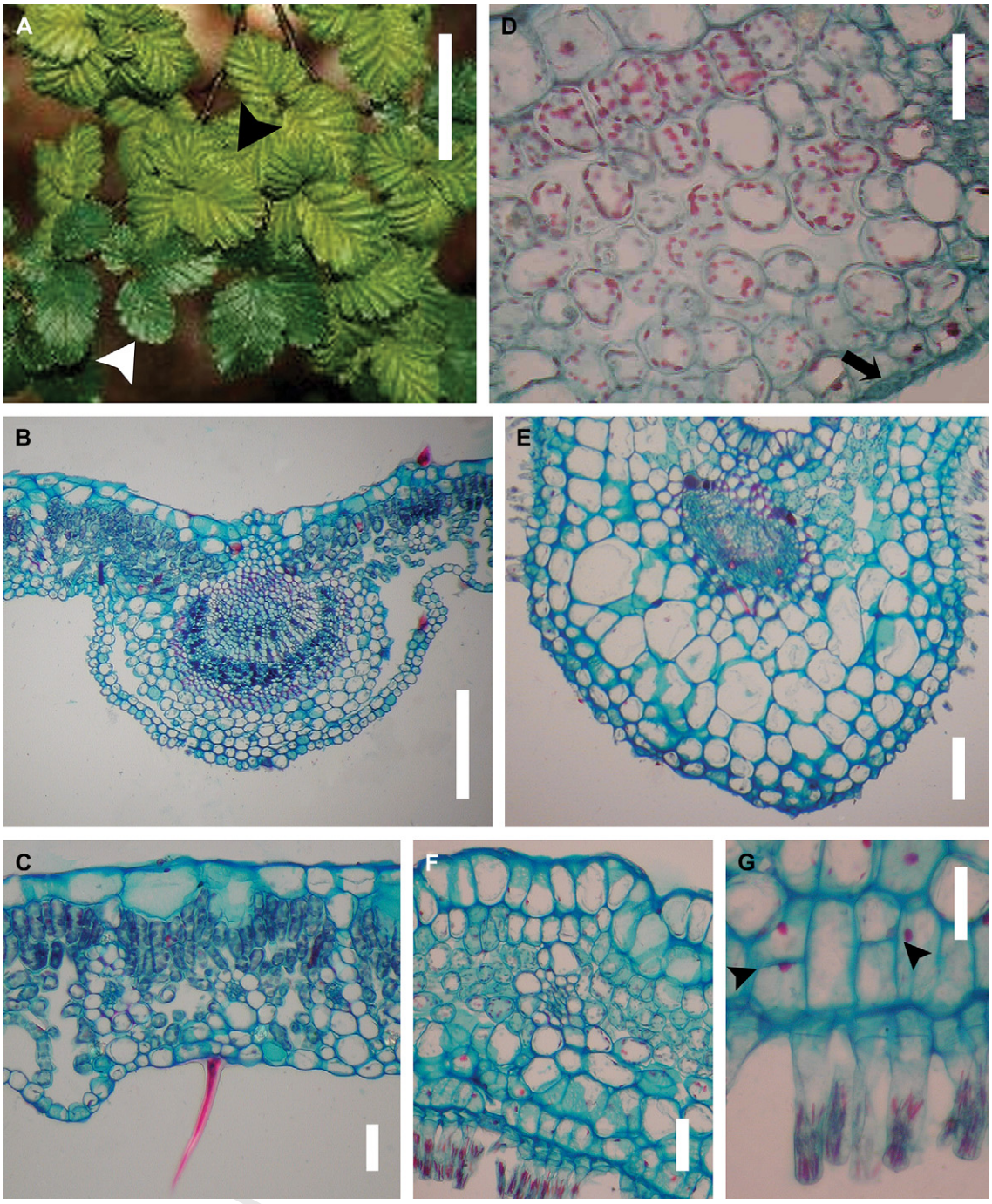

Fig 1 – Macroscopic and microscopic features of healthy and infected leaves of *Nothofagus pumilio*. (A) Healthy (white arrowhead) and infected (black arrowhead) leaves. Bar = 5 cm. (B–C) Transverse sections through healthy leaves with the typical dorsiventral layered structure. Bars: (B) = 250 μm, (C) = 50 μm. (D) An infected bud in first stages of infection by *Taphrina entomospora*. Arrow points to the subcuticular mycelium. Bar = 50 μm. (E–F) Transverse sections of leaves in advanced stages of infection. Notice the lack of intercellular spaces in the mesophyll. Bars: (E) = 100 μm, (F) = 50 μm. (G) Abaxial epidermis of an infected leaf showing periclinal divisions (arrows). Bar = 50 μm. (B–G) Safranin-fast green.

thin-walled, non-specialized, large cells. The mesophyll had two to three palisade parenchyma layers formed by polyhedral cells, rectangular in transverse section, with numerous chloroplasts, and a variable number of strata of spongy parenchyma formed by spherical cells separated by large intercellular spaces. The inferior epidermis was composed of smaller polyhedral cells. Stomata were found only in the abaxial epidermis. They were apiculate, anomocytic, with elliptic guard cells surrounded by five to eight cells. Non-glandular, thick-walled, unicellular hairs appeared on the inferior epidermis (Fig 1C).

The diseased leaves were chlorotic throughout, light green, since their formation in spring and through summer,

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becoming brownish to light yellowish at the end of summer (Fig 1A), much earlier than the normal senescence of healthy leaves that occurs in autumn (mid-March through April). In summer the lower side became homogeneously whitish, correlated with the development of asci. All leaves attached to a twig and originating from the same bud, were diseased (Fig 1A). Thickness of the leaves became greater due to an increase in cellular size and in the number of cells present between the abaxial and adaxial epidermis (Table 2). This, coupled with the unaffected veins gave the blade a cabbage-like appearance.

Cells from the adaxial epidermis became isodiametric, rectangular to square-shape in transverse section, occasionally also showing periclinal divisions (Fig 1E–F). From the very beginning of leaf development, the palisade parenchyma did not form (Fig 1D). Instead, a parenchyma with few intercellular spaces was formed, with rounded cells on the abaxial side. Also the spongy mesophyll in the adaxial side changed into a less aerated tissue composed of larger and rounded cells, but smaller in size than those from the abaxial side and still interconnected in a chain-like way (Fig 1E–F). No change was found in the vascular bundles; the xylem and phloem cells were similar to those found in the healthy leaves. The single change observed was a slight enlargement of the size of the parenchymatous cells of the bundle sheath (Fig 1F).

Cells of the abaxial epidermis were larger, longer and rectangular in transverse section (Table 2) and had conspicuous nuclei. Periclinal and oblique divisions could be observed (Fig 1G). Guard cells did not suffer any apparent change. No change was found at the petioles.

The mycelium of *Taphrina entomospora* was found to be exclusively subcuticular in growth, being present in the buds (Fig 1D) and in the foliar blades (on both abaxial and adaxial sides) but not in the petioles. Mycelial cells varied from cylindrical to short ovoid (Fig 2A). Those from the abaxial side were wider and more numerous than those from the adaxial side. All mycelial cells were binucleate (Fig 2B–C). Before asci formation, they enlarged and fragmented, forming a homogeneous layer of ovoid ascogenous cells (the hymenium), with thicker walls and dense cytoplasm (Fig 2D). Within each ascogenous cell, karyogamy occurred resulting in a large nucleus with a conspicuous nucleolus (Fig 2E). Meanwhile, the ascogenous cell elongated resulting in a mature ascus that emerged through the broken cuticle (Fig 2F). Each nucleus divided by mitosis, resulting in two nuclei, one located distally and one in the basal portion of the ascus. These nuclei became separated by a septum that divided the ascogenous cell in two: a basal cell and an upper young ascus cell. The protoplast of the basal cell disintegrated leaving it empty (Fig 2G). The nucleus in the young ascus cell underwent meiosis and mitosis resulting in the formation of eight nuclei. Primary ascospores (Fig 2H) were eight, ovoid to ellipsoidal, hyaline, smooth and regular in size (8–11(–20) × 4–5 μm). They began to bud in a regular way while still in the asci. First, one terminal bud at each apex appeared (Fig 3E). These were cylindric, hyaline, smooth, and regular both in shape and size (9–12 × 2–3 μm). Then, near the base of each bud, two to four sub terminal, cylindric buds appeared (Fig 3F arrow, 3G–H). They were always thinner (*ca* 1 μm) and, equal in length or longer than the primary buds (15–24–30 μm). Each mature ascospore showed a central body, two primary buds and two to four secondary ones (Figs 2I, 3A, 3D). Ascospores were liberated through the simple rupture of the ascus wall (Figs 2J, 3B–C arrowheads). In liberated ascospores the central body (corresponding to the primary ascospore) appeared empty and buds showed a dense cytoplasmic content (Fig 3I). Terminal buds that remained attached to subterminal buds, but were separated from the central body of the spore, were frequently observed (Fig 3J).

Table 2 – Comparison between healthy and infected with *Taphrina entomospora* leaves of *Nothofagus pumilio*

	Healthy	Infected
Size of cells from abaxial epidermis	27–43 × 15.5–24 μm	54.5–90 × 47–66 μm
Number of mesophyll cells	5–7	8–11
Thickness through blade	260–300 μm	270–360 μm

Discussion

Taphrina species infecting leaves can grow within the host tissue in three ways: hyphae may be subcuticular, intercellular or sometimes they can grow within the walls of the epidermal cells of the host (Kramer 1960). *T. entomospora* is an example of the subcuticular type as are *T. betulina* and *T. carveri* (Kramer 1960), but changes induced on the mesophyll are comparable with those produced by *T. deformans*, a species with an intercellular habit which can grow both below the cuticle and the epidermis and deeply in the mesophyll. Although the resulting mesophyll is similar in both infections, there are differences in the epidermal response. *T. entomospora* induces pronounced changes in both epidermal layers: upper epidermal cells become isodiametric and lower epidermal cells show periclinal and oblique divisions resulting in enlargement, while anticlinal divisions are observed only occasionally. The hymenium of *T. deformans* develops mainly on the adaxial side of leaves, while the size of the upper epidermal cells is reduced due to cell division (Syrop 1975a, 1975b).

In many plant–microbe interactions the distortion of the host tissue has been associated with the imbalance of plant hormones due to the phytopathogen infection. Comparison of healthy and infected tissue showed that leaves infected with *T. deformans* contain increased cytokinin activity, increased indole-3-acetic acid (IAA) and tryptophane content (Sziràki *et al.* 1975) and *Taphrina* spp. forming witches' broom have been known to produce auxins (Tanaka *et al.* 2003).

An increase in the size and number of host cells are suggestive of a high IAA content within tissues and hypertrophy implies cytokinin involvement (Chung & Tzeng 2004; Tsavkelova *et al.* 2006). High IAA can result from direct production by pathogens, stimulated synthesis of the host plant, or suppression of degradation by pathogens. However, direct evidence for the involvement of IAA in plant diseases is available only for plant pathogenic bacteria, and fungal production of IAA in plants has never been shown (Maor *et al.* 2004). Conversely, Sommer (1961) demonstrated that ethanolic extracts of *T. deformans* contain a cytokinin-like substance that promotes cell division in the presence of exogenous IAA. Johnston &

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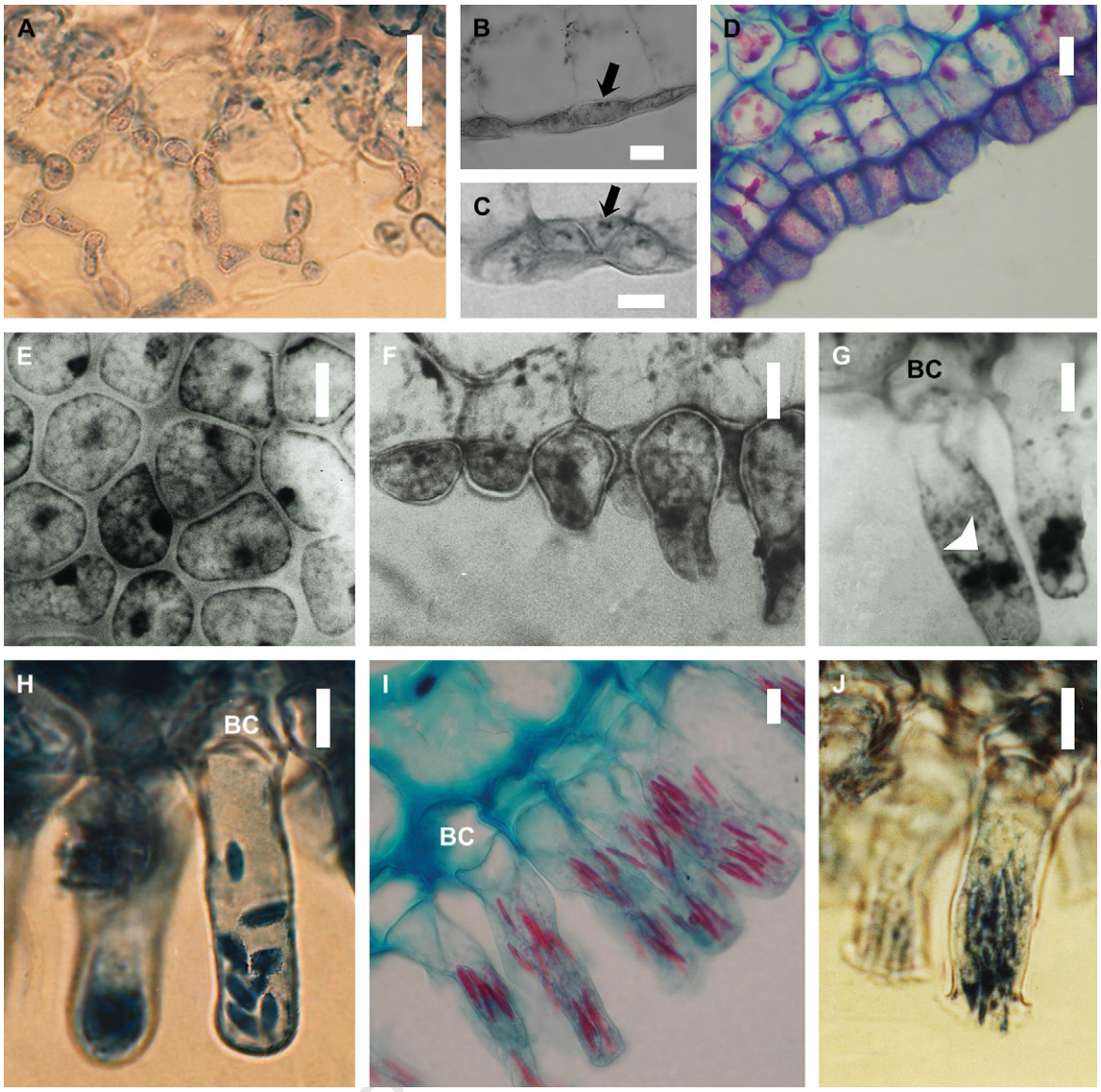

Fig 2 – Microscopic details of *Taphrina entomospora*. (A) Paradermal section of an infected leaf of *Nothofagus pumilio* showing the vegetative mycelium of *T. entomospora*. Bar = 25 μm. (B–C) Transverse sections of infected leaves. Notice the dikaryotic condition of the individual cells from the vegetative mycelium (arrows). Bars = 15 μm. (D) Continuous layer of young ascogenous cells (abaxial side of leaf). Bar = 25 μm. (E) Paradermal section of ascogenous cells, each with one large nucleus. (F) Elongating ascogenous cells. (G) First division of the nucleus (arrowhead) in a fully developed ascus. (H) Primary ascospores. (I) Mature ascospores inside asci. (J) Liberation of ascospores through simple rupture of asci tips. Bar = (E–J) 10 μm. (J) Trypan blue, (B–C, E–G) Heidenhain's haematoxylin, (D,I): safranin-fast green.)

Trione (1974) also showed cytokinin production in *T. cerasi* and *T. deformans*. They proposed that both types of hormones (cytokinins and auxins) may play a role in producing the abnormal growth responses of the host plants.

Camp & Whittingam (1974) observed that in *T. caerulescens*, a parasite of oak leaves, cytological changes occurred almost exclusively in those tissues (epidermis) most closely associated with the mycelium; accordingly they suggested that there must exist an intimate contact between the host cells and the mycelium to elicit these responses.

The drastic changes induced by *T. entomospora* beyond the interface between the fungus and the host suggest that a mechanism of exchange of chemical signals must be involved and this requires further study.

Thaxter (1910) regarded the *T. entomospora* infection as perennial considering the fact that all adjacent leaves on twigs were completely infected. In *T. whetzelii*, the mycelium invades the buds of the host (*Alnus*) and becomes systemic, deforming the whole shoot of the current season (Kramer 1960). Our observations confirm Thaxter's results; i.e. we found mycelium in the unfolded leaves in young buds.

Martin (1940), Syrop (1975a), and Syrop & Beckett (1975) showed multinucleate hyphal compartments with nuclei arranged in pairs in *T. deformans*. Vegetative mycelium of

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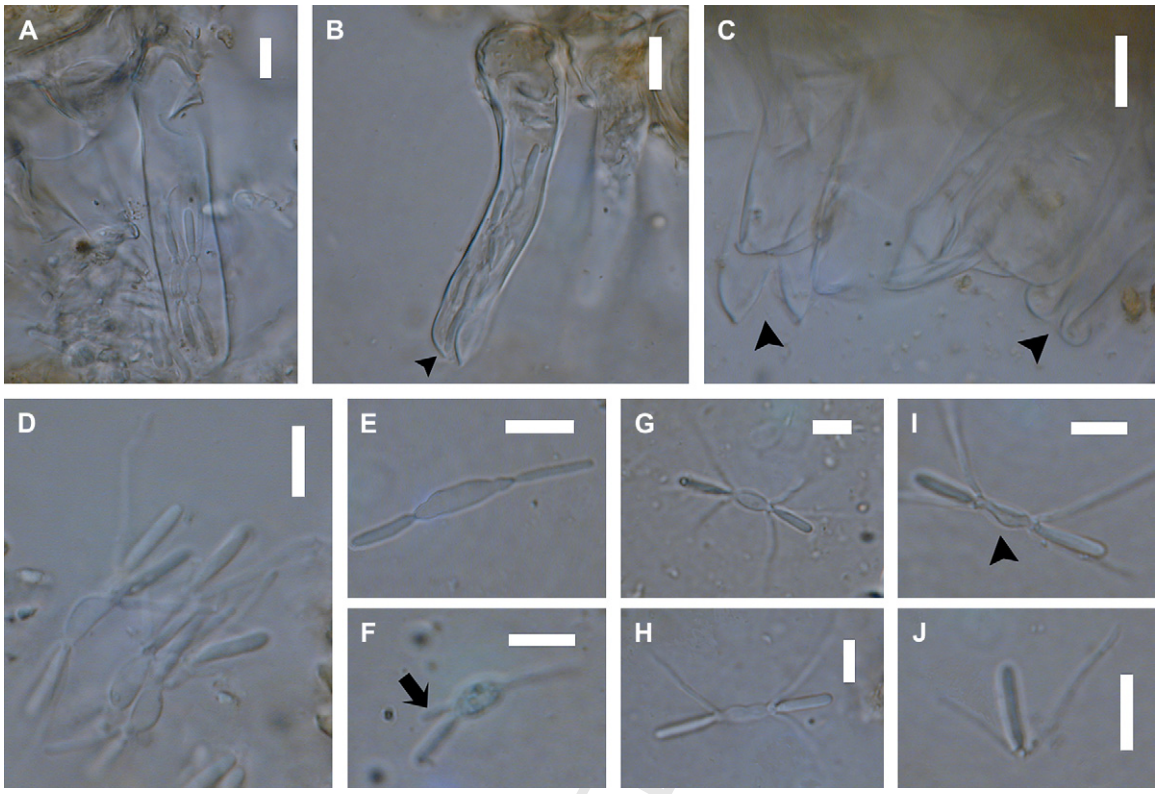

Fig 3 – Cytological details of *Taphrina entomospora*. (A) Ascus with ascospores. (B) Mature ascus beginning the liberation of ascospores (arrowhead). (C) Empty asci. Arrowheads point to the ruptured wall. (D) Mature, liberated ascospores. (E–H) Different stages of ascospores' budding. (F) Arrow points to a sub-terminal bud. (I) Ascospore with the central body (corresponding to the primary ascospore) almost empty (arrowhead). (J) Liberated terminal buds. Bars = 10 μm. (A–J) Water mount.

T. entomospora was found to be regularly dikaryotic, with a nuclear behaviour that follows the pattern described by Kramer (1960) for species with a basal cell. Ascospores are passively discharged through bursting of the apex. This is in agreement with the situation described in *T. deformans*; in *T. tosquinetii* there is active discharge of octosporous asci while multisporous asci (a result of ascospore budding) discharge passively (Bond 1956; Syrop & Beckett 1975). Syrop & Beckett (1975) considered that the budding of ascospores in the asci would indicate unfavourable environmental conditions. In *T. entomospora*, unlike other species in the genus, the process of budding follows a regular pattern that ends with separation of buds from the collapsed primary spore. Thus, each primary bud along with the secondary ones would act as propagules, the longer sub-terminal buds are probably aids that collaborate in dissemination favouring air dispersal, a fact also observed by Thaxter (1910). *Taphrina entomospora* along with *Uncinula magellanica*, *U. nothofagi* (*Erysiphales*, *Ascomycota*), *Mikronegeria alba* and *M. fagi* (*Urediniales*, *Basidiomycota*) are biotrophs exclusive of American *Nothofagus* species, unknown in Australasian taxa. Ridley *et al.* (2000) point out that the evolutionary pressure of the large coevolution between pathogens and their hosts results in the limitation of the taxonomic range of hosts (i.e. susceptible partners) to a single or small group of species, shifts being possible only through short taxonomic distances, often confined to a single host genus or family. Thus, several questions arise regarding the origin of these pathogens and their host in southern South America. Are they ancient pathogens that were lost during the migration of the genus from South America to Australia? This supposition favours the hypothesis of a South American centre of origin for *Nothofagus* (Swenson *et al.* 2000).

Rodrigues & Fonseca (2003) used two molecular methods to study cultures (yeast states) of about one third of the currently recognized species of *Taphrina* (all strains derived from culture collections from North Hemisphere). They corroborated, for most species studied, the separation of taxa as defined on the basis of conventional criteria such as host range, geographical distribution, type and site of infection, and morphology of the sexual stage.

T. entomospora is the only member in the genus that, other than presenting an austral distribution, is restricted to southern South America and is pathogenic on *Nothofagus*. In addition, its sexual spores have a peculiar morphology, and a strongly specialized way of dispersion. We conclude that *T. entomospora* is an odd species that is geographically and taxonomically isolated from other species in the genus. Future work must include this species along with others described from South America native trees in order to clarify the phylogenetic relationship and biogeographic distribution of *T. entomospora vis à vis* other taxa in the genus.

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REFERENCES

Alexopoulos CJ, Mims CWM, Blackwell MB, 1996. *Introductory Mycology*, fourth ed. Wiley, New York.

Bava J, 1998. Los bosques de lenga en Argentina. In: Donoso C, Lara A (eds), *Silvicultura de los Bosques Nativos de Chile*. Editorial Universitaria, Santiago, Chile, pp. 273–293.

Bond TET, 1956. Notes on *Taphrina*. *Transactions of the British Mycological Society* **39**: 60–66.

Cabrera AL, 1971. Fitogeografía de la República Argentina. *Boletín de la Sociedad Argentina de Botánica* **14**: 1–42.

Cabrera AL, Willink A, 1980. *Biogeografía de América Latina*. In: *Monografía no 13, Serie de Biología*. Secretaría de la Organización de los Estados Americanos, Washington D.C.

Camp RR, Whittingam WF, 1974. Ultrastructural alterations in oak leaves parasitized by *Taphrina caerulescens*. *American Journal of Botany* **61**: 964–972.

Chung KR, Tzeng DD, 2004. Biosynthesis of indole-3-acetic acid by the gall-inducing fungus *Ustilago esculenta*. *Journal of Biological Sciences* **4**: 744–750.

Crisci JV, Cigliano MM, Morrone JJ, Roig-Juñent S, 1991. Historical biogeography of southern South America. *Systematic Zoology* **40**: 152–171.

Deckert RJ, Melville LH, Peterson RL, 2001. Structural features of a *Lophodermium* endophyte during the cryptic life-cycle phase in the foliage of *Pinus strobus*. *Mycological Research* **105**: 991–997.

Donoso ZC, 1993. *Bosques Templados de Chile y Argentina*. Editorial Universitaria, Santiago, Chile.

Hueck K, 1978. *Los Bosques de Sudamérica*. Sociedad Alemania de Cooperación Técnica (GTZ), Eschborn.

Johansen DA, 1940. *Plant Microtechnique*. McGraw-Hill, New York.

Johnston JC, Trione EJ, 1974. Cytokinin production by the fungi *Taphrina cerasi* and *T. deformans*. *Canadian Journal of Botany* **52**: 1583–1589.

Kramer CL, 1960. Morphological development and nuclear behavior in the genus *Taphrina*. *Mycologia* **52**: 295–320.

Langeron M, 1949. *Precisè de Microscopie*, seventh ed. Masson & Cie, Paris.

Maor R, Haskin S, Levi-Kedmi H, Sharon A, 2004. *In planta* production of indole-3-acetic acid by *Colletotrichum gloeosporioides* f. sp. *aeschynomene*. *Applied and Environmental Microbiology* **70**: 1852–1854.

Martin EM, 1940. The morphology and cytology of *Taphrina deformans*. *American Journal of Botany* **27**: 743–751.

Mix AJ, 1949. A monograph of the genus *Taphrina*. *University of Kansas Science Bulletin* **33**: 3–167.

Mix AJ, 1954. Additions and emendations to a monograph of the genus *Taphrina*. *Transactions of the Kansas Academy of Sciences* **57**: 55–65.

Ridley GS, Bain J, Bulman LS, Dick MA, Kay MK, 2000. *Threats to New Zealand's indigenous forests from exotic pathogens and pests*. In: *Science for Conservation*, **142**. Department of Conservation, Wellington, New Zealand.

Rodrigues MG, Fonseca A, 2003. Molecular systematics of the dimorphic ascomycete genus *Taphrina*. *International Journal of Systematic and Evolutionary Microbiology* **53**: 607–616.

Roivainen H, 1977. Resultados micológicos de la expedición a Argentina y Chile en 1969–1970. *Karstenia* **17**: 1–18.

Sass JE, 1958. *Botanical Microtechnique*, third ed. Iowa State University Press, Ames.

Sommer NF, 1961. Production by *Taphrina deformans* of substances stimulating cell elongation and division. *Physiologia Plantarum* **14**: 460–469.

Swenson U, Hill RS, McLoughlin S, 2000. Ancestral area analysis of *Nothofagus (Nothofagaceae)* and its congruence with the fossil record. *Australian Systematic Botany* **13**: 469–478.

Syrop M, 1975a. Leaf-curl disease of almond caused by *Taphrina deformans* (Berk) Tul. I. A light microscope study of the host–parasite relationship. *Protoplasma* **85**: 39–56.

Syrop M, 1975b. Leaf-curl disease of almond caused by *Taphrina deformans* (Berk) Tul. II. An electron microscope study of the host–parasite relationship. *Protoplasma* **85**: 57–69.

Syrop M, Beckett A, 1975. Leaf-curl disease of almond caused by *Taphrina deformans*. III. Ultrastructural cytology of the pathogen. *Canadian Journal of Botany* **54**: 293–305.

Sziràki I, Balaàzs E, Kiràly Z, 1975. Increased levels of cytokinins and indole acetic acid in peach leaves infected with *Taphrina deformans*. *Physiological Plant Pathology* **5**: 45–50.

Tanaka E, Tanaka C, Ishihara A, Kuwahara Y, Tsuda M, 2003. Indole 3-acetic acid biosynthesis in *Aciculosporium* take, a causal agent of witches' broom of bamboo. *Journal of Genetic Plant Pathology* **69**: 1–6.

Thaxter R, 1910. Notes on chilean fungi. I. Contributions from the cryptogamic laboratory of Harvard University, LXVI. *Botanical Gazette* **50**: 430–442.

Tsavkelova EA, Klimova Syu, Cherdyntseva TA, Netrusov AI, 2006. Microbial producers of plant growth stimulators and their practical use: a review. *Applied Biochemistry and Microbiology* **42**: 117–126.

Viégas AP, 1961. *Índice de Fungos da América do Sul*. Instituto Agronômico, Campinas.

Webster J, 1980. *Introduction to Fungi*, second ed. Cambridge University Press, Cambridge.

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