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# *Trematodon ambiguus* (HEDW.) HORNSCH. (Musci: Bruchiaceae) reported from Northern Tyrol, Austria: Spore germination and protonemal development

by

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S y n o p s i s : The moss *Trematodon ambiguus* was discovered in 2001 on a wet mountain slope above Sölden, Northern Tyrol. Distribution (local and remote), propagation and ecology are shortly discussed. Experiences with culture of spores that were stored under herbarium conditions for prolonged time and the development of special resting cells in protonemata are presented.

K e y w o r d s : *Trematodon ambiguus,* propagation, sporebank, Iceman, Northern Tyrol

## 1. Introduction:

The discovery of *Trematodon ambiguus* (HEDW.) HORNSCH. near Sölden in Northern Tyrol, Austria, was made in September 2001 during surveys of selected areas of the Ötztal Alps (Austria and Italy) and the Vinschgau region (Italy) in connection with the preserved body of the 5200 year old Tyrolean Iceman. See DICKSON (2000, 2003) and DICKSON et al., (1996, 2005, 2009) for discussions of the bryogeographical, ethnobotanical and palaeoenvironmental significance of the bryophytes associated with the Iceman.

*Trematodon ambiguus* (Bruchiaceae) is a small acrocarp which produces abundant sporophytes with a distinctive apophysis. Spores are of a medium size and measure about 30 $\mu$m (SAUER 2000, HILL et al. 2007). This is in agreement with most other authors (e.g. NYHOLM 1987, STEBEL & OCHYRA 1997, CORTINI-PEDROTTI 2001) but stands in contrast with YU et al. (2000) who reported the spore size to range from 18. 8 - 19.1µm. *T. ambiguus* grows on open and wet loamy or peaty soil or gravel, after the vegetation is removed by natural (e.g. trampling of animals) or anthropogenic causes (e.g. agricultural machines). DIERSSEN (2001) observed that the plant shows a clear association with disturbed anthropogenic habitats, typically occurring on well lit, lime free nutrient poor soils. The plant

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prefers acid soil with a pH below 5 (ELLENBERG et al. 1991, HILL et al., 2007). *T. ambiguus* is classified as a short-lived shuttle (DIERSSEN 2001), typically occurring for a limited time (few years) at any one place. For this reason, it is not considered threatened in Europe (SÖDERSTRÖM 2002). In contrast to other ruderal or pioneer species, the appearances of this plant are very sporadic, both in time and space. Therefore prolonged survival of the spores (i.e. in a diaspore bank) should be considered.

## 2. Propagation, distribution and ecology:

### 2.1. The Sölden locality:

*Trematodon ambiguus* occurred on a wet mountain slope at 1930 m above the timberline, near the mountain guesthouse Silbertal-Alm far above the village of Sölden. The extent of the population covered about 1.5 to 2 m² comprising several thousand plants. The superficial vegetation had been skimmed off by machine for the preparation of ski runs, leaving disturbed, bare ground. The dark peaty soil contained a high proportion of mineral particles, including mica and quartz, derived from the underlying schistose bedrock. The pH of the soil removed from the air dried specimen ranged from 4.7 to 5.0 (pH-electrode pH315i; Wissenschaftlich-Technische Werkstätten). In the field the size of the abundantly fruiting plants varied, but the curved strumose capsules showed the characteristically long apophysis with a shorter, cylindrical fertile part. The size of the broadly oval-shaped and densely papillose spores ranged from 28.1 µm to 31.6 µm at the widest.

### 2.2. Herbarium search:

The cryptogamic herbarium of the Botanical Institute of the Leopold-Franzens University in Innsbruck, where a voucher of the finding is deposited, was searched for comparative material, including that of the closely related *T. longicollis* MICHX. Unexpectedly an unpublished voucher specimen of *T. ambiguus,* collected by H. Gams in 1929 (Auf feuchtem Glimmerschiefergrus über Flaurling [w. Innsbruck]. ca. 900 m. 2. VII. 29) was discovered. An attempt by the first author to refind the plant in 2006 was unsuccessful, hardly surprising in that the locality given by Gams was imprecise.

### 2.3. Germination of spores:

In 2007 and 2009 germination trials were carried out using spores from the Sölden material which had been air dried and stored in the dark at room temperature (20 to 23°C) for more than seven years. Capsules were removed and their spore content spread on 'Medium M' nutrient agar (BASLEROVÁ & DVOŘÁKOVÁ 1962). From eight to ten days after inoculation spores began to germinate, ranging from about 5% (2009 trial) to 20% and 50% per capsule. Spores from single capsules failed to germinate completely which might be due to immaturity, as suggested by microscopic investigation. Possibly some spores remained dormant even under favourable conditions (sometimes obviously intact, but not germinating spores were found, even when germination of others occurred), a strategy of some ruderal plants when not all spores germinate at any one time (McLetchie 1999). Thus it is shown for the first time that spores of *T. ambiguus* retain the ability to germinate after more than seven years of air dry storage. Further germination experiments using herbarium material of various age classes and of the soil diaspore bank from known historical or current populations of *T. ambiguus* should be done to gain additional data on spore longevity under laboratory conditions and in nature.

**2.4. Protonemal development:**

Following successful germination of spores, slide cultures were prepared. The nutrient agar described above was thinly coated onto a microscope slide, inoculated with spores and a coverslip placed on top. In order to provide adequate humidity the prepared slides were set on an agar plate containing the same nutrient agar and sealed with parafilm. The slides were maintained on a moderately well-lit window sill, south-west facing without direct sunlight, at room temperature until germination was detected with a dissecting microscope (Stemi 2000-CS, Carl Zeiss) followed by detailed investigation in use of a transmission microscope (Axioscop 40, Carl Zeiss). Spore germination (Fig. 1) was recorded via a series of digital photomicrographs (Sony cybershot MPEGMOVIE EX DSC-S75, Sony).

Agar plate-cultures with established protonemata were observed microscopically over a period of three months, but gametophores did not develop, perhaps because of a deficien-

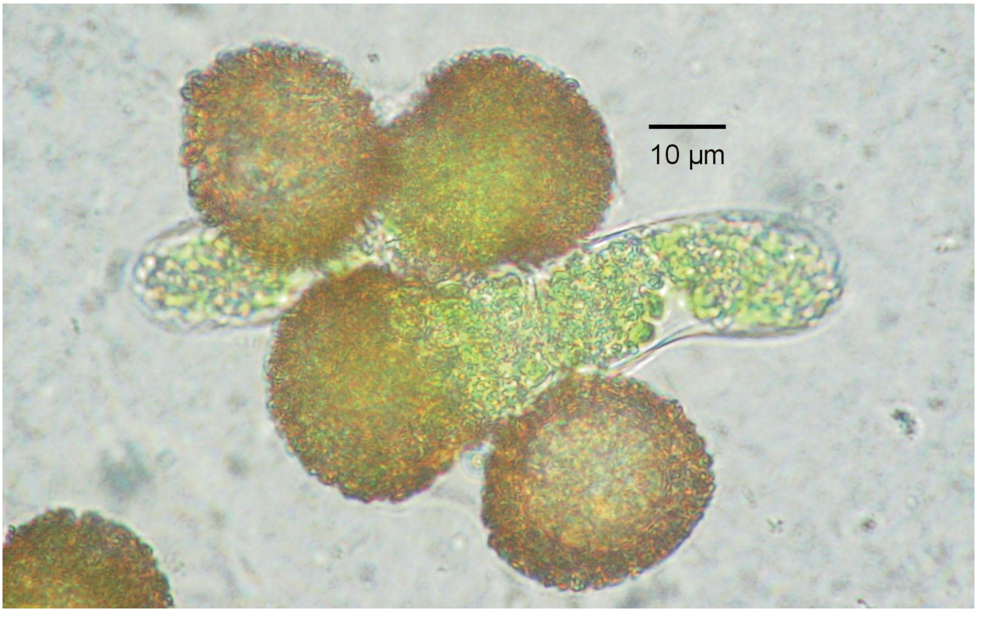


**Figure 1:** Germination of *Trematodon ambiguus* spores on slide cultures. Several spores, two of them are germinating. The other spores are possibly still inactivated. The oblique partition of the growing cells is a typical character of bryophyte protonemata. Scale bar 10 µm. Picture made by W. Hofbauer.

cy in the nutrient medium. The Petri dishes were gently shaken to dislodge condensation that had developed on the lids, with the result that water irrigated the protonemata. After about two months following the establishment of the cultures, secondary protonemata were observed. Use of a transmission microscope revealed that the secondary protonemata had developed from specialised thick-walled 'resting' cells and also from small branches that had broken off from the original protonemata (Fig. 2). The thick walled cells develop inside of a protonemal mother cell and are liberated through mucilaginous lysis of the old cell wall. Two resting cells often develop from a single mother cell, with numerous small oil droplets in the cell lumen (Fig. 2A). Disintegration of the old protonema was extensive. The fragmentation of the protonemal branches obviously did not occur by development of specialised abscission cells termed 'tmema' cells (CORRENS 1899, DUCKETT & LIGRONE 1992), but by the formation of a secondary cell wall and the lysis of the old one (Fig. 2B).

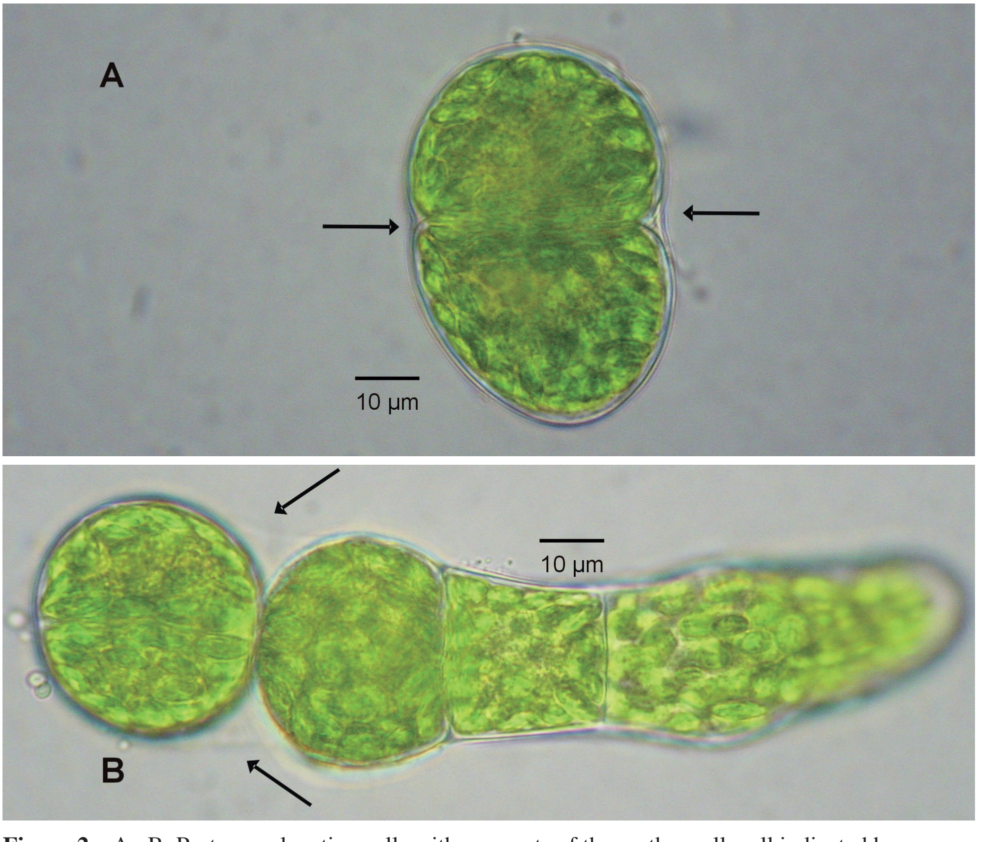


**Figure 2:** A– B: Protonemal resting cells with remnants of the mother cell wall indicated by arrows. Note that there are numerous small oil droplets in the centre of the cells. A: Two resting cells, still connected by the mother cell wall. B: Whereas on the left hand resting spore formation is already finished, on the right hand the branch of the protonema is still growing. Scale bar 10 µm. Pictures made by W. Hofbauer.

## 2.5. Distribution of *Trematodon ambiguus*:

*Trematodon ambiguus* has a wide distribution, occurring in Europe, Asia and North and Central America (e.g. ZANDER & ECKEL 2002). In Europe it is rather scarce, belonging to the European boreal-montane element (HILL & PRESTON 1998), and only in the Scandinavian countries does it occur with any frequency, particularly in Sweden where it is relatively common with stable populations (NYHOLM 1987; HEDENÄS et al. 2002, HALLINGBÄCK et al. 2006).

In the rest of Europe it is a rare plant. It has been found only once in Britain (Mid Perthshire, Scotland) and never refound (PORLEY & HODGETTS 2005). There are very few records for France, although there is one recent record which has been under surveillance for many years now (FRAHM 2003, 2005ab, 2008). In Italy *T. ambiguus* is also rare with older records in Piemonte, Lombardia, Trentino/Alto Adige and Liguria; only in the provinces of Piedmonte and Trentino/Alto Adige have there been post-1950 records (DALLA TORRE & SARNTHEIN 1904, CORTINI-PEDROTTI 2001). DÜLL (1991) gives an additional locality in Schnalstal near Kurzras (Vinschgau, Alto Adige) towards the peak of Bildstockjoch at 2200 m, recorded in 1965; this is the highest altitude ever reported for the plant. In Switzerland the species has been found at a few localities (about six from 2000 onwards) in recent times (SCHNYDER et al. 2004;, NISM 2004). In Germany *T. ambiguus* is very sporadic and is considered to be rare or in some regions extinct (DÜLL & MEINUNGER 1989; MEINUNGER & SCHRÖDER 2007). In Baden-Württemberg there are just two recent locations (SAUER 2000). It is somewhat more frequent in Bavaria (Bayern) where it is nevertheless regarded as threatened (BERTSCH 1966, SAUER, 2000). It has been suggested that the species core range is northern Europe (FRAHM 2003) and is occasionally brought further south by water birds.

In Austria, particularly in the western region, the species is considered to be endangered (GRIMS & KÖCKINGER 1999). DALLA TORRE & SARNTHEIN (1904) cites a record in eastern Tyrol near the village Innervillgratten. DÜLL (1991) reports the species is absent from the Austrian part of Tyrol, and mentions an occurrence in Vorarlberg, near the border of Northern Tyrol. According to GRIMS (1999) *T. ambiguus* has been recorded from several federal countries/provinces in Austria, including Kärnten (about four localities), Niederösterreich (two), Oberösterreich (two), Salzburg (about four), Steiermark (about 12), Vorarlberg (two) and eastern Tyrol (one, the old locality from DALLA TORRE & SARNTHEIN 1904), but notes that only very few recent records exist, and none in the Austrian part of Tyrol. In Eastern Europe it appears to be particularly rare, and only two localities have been reported from Poland (STEBEL & OCHYRA 1997).

There is some indication that in recent years the species is spreading in Europe (FRAHM 2003, DURING et al. 2006, HERAS PEREZ & INFANTE SANCHEZ 2006), possibly partly associated with sod cutting as a conservation management tool (DURING et al. 2006). In Belgium and the Netherlands, where the species was thought to be extinct, it has been reported from several new localities (DURING et al. 2006). In Spain, the species was discovered recently in the Aragonian Pyrenees (HERAS PEREZ & INFANTE SANCHEZ 2006).

**2.5. Ecology of species, establishment, dispersal and persistence:**

The dispersal capacity for spores by air is correlated with spore size (CRUM 1972, MILES & LONGTON 1992). Thus the theoretical range for small spores of 8 - 12 µm could be at least 19,000 km but in the range of 320 km for spores of 25-28 µm (CRUM 1972; MILES & LONGTON 1992, HALLINGBÄCK 2002). DURING (1979) considered that spores less than 20 µm would have the best chance of long-range aerial dispersal, whilst larger spores would be deposited within a few meters of the parent plant. It seems quite unlikely that large *T. ambiguus* spores could be transported by air over several hundred kilometres through air, although long-distance transport facilitated by other means, e.g. animals, is a possibility.

There is substantial evidence that spores can remain viable in the diaspore bank for several years (TOOREN VAN & DURING 1988, JONSSON 1993, SÖDERSTRÖM 1995; HALLINGBÄCK 2002, PORLEY 2008). In the case of dry stored material, such as in *Anoectangium aestivum* (HEDW.) MITT., spores have been germinated after 19 years air dry storage (MALTA 1921); spores of *Oedipodium griffithianum* (SM.) SCHWAEGER. after 20 years (CHALAUD 1932) and spores of *Physcomitrium pyriforme* (L.) BRID. after 55 years (PASCHKE 1965). In forming a bryophyte diaspore bank large diaspores (>20 resp. 25 µm) are favoured since they are deposited locally and may be better at surviving for a long time, which is in contrast to the observations on phanerogams where small seeds are often more durable (JONSSON 1993, DURING 2001). Considering the available information it seems entirely plausible that *T. ambiguus* is able to form a persistent spore bank by virtue of its spore size and life strategy. It is not yet clear if spores of the species can survive for decades, as is suggested by the frequency of the reports of occurrences in nature.

Resting stages in moss protonema have been known since BRISTOL (1916) observed them in soil samples stored for more than 45 years. MUELLER (1972) and HANCOCK & BRASSARD (1974) reported resting stages or perennial protonemal stages in *Buxbaumia aphylla* HEDW. and GOODE et al. (1993) described an experimental study on formation of brood cells in moss protonemata. MALLÓN et al. (2006) described in vitro development of thick walled brood cells that contained oil droplets in protonemata of *Splachnum ampullaceum* HEDW. in which vegetative propagation was hitherto unknown. The formation of specialized propagules that are resistant to desiccation after treatment with abscisic acid was recently reported in cultures of *Ditrichum plumbicola* CRUNDWELL (ROWNTREE et al. 2007). It is thus clear that protonemal stages of mosses from different taxonomic groups are able to produce some kind of resting stages or secondary dispersal organs. The thickened cell walls and oil droplets observed in the resting cells of *T. ambiguus* may enable the moss to survive for long periods. They could facilitate both a short distance dispersal mechanism that does not require the adult plant to produce sporophytes and a further mechanism for survival in the soil. However, it is not known under what conditions the resting cells are formed, and if these resting cells are produced in nature; further studies on protonemata in nature are needed.

Considering the spores of *T. ambiguus* remain viable after storage of more than seven years, together with the formation of persistent vegetative cells on the protonemata, the occurrence of a long lived diaspore bank in this species seems likely. Whether the plant is able to survive in soil for several decades or whether it is brought to new locations by long distance transport still remains unclear. Further study to assess the longevity of the spores and the presence of the spores in the diaspore bank is desirable.

## 3. Summary:

In 2001 *Trematodon ambiguus* was collected from recently disturbed soil near Sölden in Northern Tyrol, Austria. Spores, which had been stored in the herbarium for more than seven years, were germinated under laboratory conditions, indicating that *T. ambiguus* may persist, under favourable conditions, in a soil diaspore bank. Thick walled resting cells containing numerous oil droplets were also observed on laboratory grown protonemata; these may play a role in short distance dispersal and potentially provide a mechanism by which the moss may persist through unfavourable periods. A search of the cryptogamic herbarium of the University of Innsbruck revealed a second specimen of this rare plant collected in 1929 from a locality near Innsbruck. The wider distribution of *T. ambiguus,* especially in central Europe, is discussed with some ecological observations.

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