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DISCOVERY OF THE GAMETOPHYTES OF *TRICHOMANES SPECIOSUM* (HYMENOPHYLLACEAE: PTERIDOPHYTA) IN POLAND AND ITS BIOGEOGRAPHICAL IMPORTANCE

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ABSTRACT

Gametophytes of *Trichomanes speciosum* Willd. (Hymenophyllaceae: Pteridophyta) have been reported for the first time in two localities in the Westsudetian Highland, Lower Silesia, SW Poland. They form the easternmost outposts of this taxon in Europe, suffering the most severe climatic conditions in the extent of its occurrence. At both sites gametophytes occur in horizontal rock fissures in Upper Cretaceous sandstone, surrounded by degraded eastern oak-hornbeam forests. The gametophytes are very small (up to 2cm diameter) and sparse.

INTRODUCTION

The Killarney Fern *Trichomanes speciosum* Willd. (syn. *Vandenboschia speciosa* (Willd.) G.Kunkel) is the only European representative of a predominantly tropical genus. It is a Macaronesian-European endemic (Rumsey *et al*. 1998b), classified as an extremely oceanic *Hymenophyllum wilsonii*-element of pteridophyte flora (Birks 1976). The restriction of *Trichomanes speciosum* sporophyte to areas of hyperoceanic climate, coupled with its historical excessive collection, resulted in legal protection throughout the species range under the Bern Convention (Anon. 1979) and Habitat Directive (Anon. 1992). Sporophytes and gametophytes of *Trichomanes speciosum* are perennial and both phases of its life cycle are capable of vegetative propagation, with extensive clonal development of either generation. They have often existed as spatially separated populations (Farrar 1985), where sporophytes are restricted to the European Atlantic fringe (Jalas & Suominen 1988) and gametophyte distribution extends over the more continental part of Central Europe (e.g. Vogel *et al*. 1993, Rumsey *et al*. 1998b).

The bright green epilithic mats of *Trichomanes speciosum* gametophytes at first glance resemble the protonema of bryophytes or filamentous algae. The gametophyte prothalli consist entirely of highly branched filaments with numerous peripheral chloroplasts (Krippel 2001, Makgomol & Sheffield 2001). Recognition of the distinctive ecology and habitat of *Trichomanes speciosum* gametophytes resulted in independent discoveries in: Britain, France (northern Vosges), Luxembourg (Suisse Luxebourgeoise), Germany (Eifel, Spessart, Rhön, Oberpfälzer Wald, Elbsandsteingebirge) and the Czech Republic (České Švýcarsko, Labské pískovce, Kokořínsko, Český ráj, Parchovské skály) (e.g. Rumsey *et al.* 1990, Vogel *et al.* 1993, Rumsey *et al.* 1998a, Rumsey *et al.* 1998b, Krippel 2001, Turoňová 2002) (Fig. 1).

Gametophytes of *Trichomanes speciosum* Willd. have not been observed so far in Poland but the nearest localities are situated in the close vicinity – in the area of Elbsandsteingebirge and České Švýcarsko, known also as Saxonian-Bohemian Switzerland. These localities are connected with the Lower Turonian sandstone massif dissected by the river Elbe with many deep gorges, whose geomorphology is a crucial ecological factor. These conditions are reflected by a relatively cooler and more humid microclimate in the ravines and determine the frequent presence of rare arctic-alpine, Atlantic bryophytes and vascular plants as well as *Trichomanes speciosum* gametophytes. The presence of scattered Cretaceous sandstones areas in the Sudetes foothills in Poland suggested the possible occurrence of *Trichomanes speciosum* there. The climatic conditions of this area differ from neighbouring Saxonian-Bohemian Switzerland massif in their greater continentality marked by lower mean air temperature – ca. +7 °C to +8 °C, and rainfall – ca. 650 mm to 720 mm respectively (Wiszniewski 1973, Vogel *et al.* 1993).

In early autumn of 2002 we made a reconnaissance of the potential localities of *Trichomanes speciosum* in the central and western part of the Sudetes foothills with the most pronounced oceanic climate features in comparison to the rest of the Sudetes sandstones. During September and October of 2002 we visited the potential localities in this area – both are isolated sandstone rocky formations and old quarries. In two localities we found *Trichomanes speciosum* gametophytes. The classification of plant communities follows Matuszkiewicz (2001). Plant distributions in 10-km grid squares for Poland (ATPOL) are presented accordingly to Zając (1978).

TRICHOMANES SPECIOSUM IN POLAND

In October 2002 we found two sites with only a few colonies of *Trichomanes speciosum* gametophytes in the West Sudetes foothills, Lower Silesia, SW Poland (Fig 1). The first of them, called ‘Niedźwiedzia Jama’ (Bear Pit), is located near Złotoryja (N51º06'20" E15º54'20"; ATPOL BE41). The gametophytes grew on the bare rock surface, free from competition under the overhang of a small cave at ca. 250m altitude on medium-grained sandstone of the lower Turonian. Walls of this cave were colonised by *Pseudotaxiphyllum elegans* (Brid.) Iwats. The cave was located in the upper part of a small valley that had a south-western aspect. The whole valley was covered by managed eastern oak-hornbeam forest (degraded form of *Galio sylvatici-Carpinetum betuli* Oberd. 1957) with very sparse undergrowth. The humus layer was thick and of moder type. The second location, called ‘Panieńskie Skały’ (Maiden Rocks), is 2 km south of Lwówek Śląski (N51º06'15" E15º35'30"; ATPOL BE41) at ca. 260m altitude. Three small patches up to 3 cm2 of *Trichomanes speciosum* gametophytes were found low down, in ca. 50 cm deep south-facing crevices, in coarse-grained sandstone rocks of middle Cenomanian. In these crevices, gametophytes grew together with sparse mosses e.g. *Schistostega osmundacea* and *Distichum inclinatum* (Hedw.) B., S. & G. The sandstone ridge of up to 10 m high was surrounded by mixed forest with dense undergrowth. The herb layer was also sparse and impoverished as in the first locality. The thickness of humus layer and its type were similar too. Both Polish localities were ca. 20km away from each other and had similar climatic conditions with mean yearly temperature of +7.8ºC, mean temperature January of –2.0ºC and mean yearly rainfall of 660 mm (Wiszniewski 1973). The climate in this region is one of the mildest in Poland with pronounced oceanic features. The geomorphology of both localities does not foster temperature inversions.

REMARKS ON ECOLOGY

The narrow ecological amplitude of *Trichomanes speciosum* strongly limits the number of its potential sites. The main factor determining plant distribution is a suitable microclimate with temperature and water supply the most important. The usual habitats of epilithic gametophytes of *Trichomanes speciosum* were deep cracks and small caves with limited light access. Consequently these habitats provide a moderately constant humidity and thermal regime, which prevent drying out or freezing of the delicate plant mats, resulting in desiccation of *Trichomanes speciosum* gametophytes (Farrar 1985).

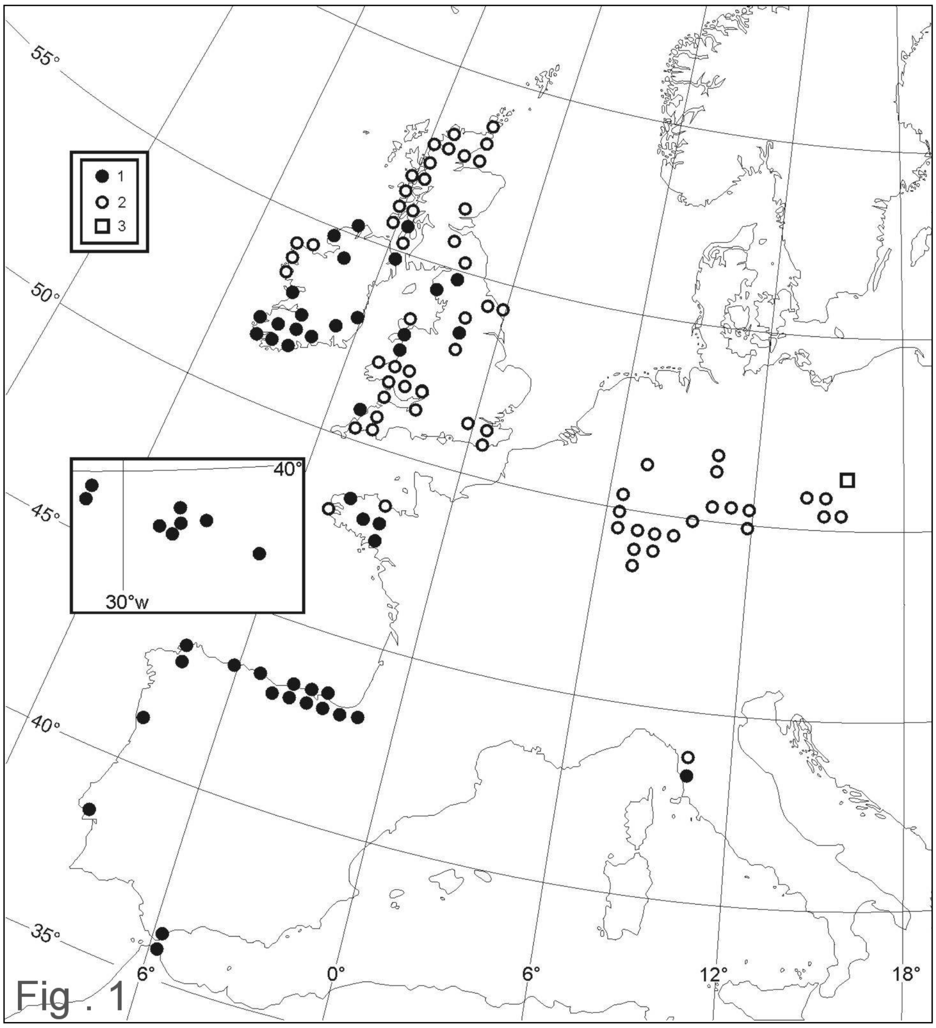

Fig . 1

Figure 1. Distribution of *Trichomanes speciosum* mapped on the 50km UTM grid system. Both generations recorded (1- ●), gametophyte generation only (2- ○), new locality of gametophyte (3 - □). Macaronesian Islands in boxes. After Rumsey *et al.* (1998b) with some additions.

Growth rates noted by Raine & Sheffield (1997) corroborate thermal constraints of *Trichomanes speciosum* gametophytes' geographical distribution. Our observations suggest a wider ecological tolerance of *Trichomanes speciosum* gametophyte, which is adapted to an even more sub-continental climate. The new localities discovered in Poland are presently the easternmost outposts of *Trichomanes speciosum* gametophytes in Europe. Cretaceous sandstone massifs are also located further to the east, in Central Poland, but it seems that mezo- and microclimate conditions are too unfavourable there. The subsequent ultimate factor is the adaptation of gametophytes to growing in extreme low light (PAR < 1 ìmol m-2 s-1) with low respiration rates and therefore a low compensation point, which enables it to survive free from competition from other species, especially shade tolerant bryophytes (Vogel *et al.* 1993, Makgomol & Sheffield 2001). It seems that in the peripheral outposts of *Trichomanes speciosum* gametophytes, very specific but stable microclimatic conditions on a small spatial scale are of high importance, especially high air humidity, which can be supported by a thick humus layer of moder type. Light limitation is not so stringent in lower temperatures (Raine & Sheffield 1997).

We should emphasise that a gradually narrowing substratum 'niche' of *Trichomanes speciosum* gametophyte is observed, from nearly calcareous man-made habitats in Macaronesia (Rumsey *et al.* 2000) or various substrates with some base enrichment in the British Isles (Ratcliffe *et al.* 1993) and Luxembourg (Vogel *et al.* 1993), to Cretaceous quartz sandstones in the north-eastern limit of its distribution area (Vogel *et al.* 1993, Turoňová 2002). The widespread distribution of Killarney Fern gametophytes might act as a kind of 'seed-bank' (Rumsey *et al.* 1999, Rumsey *et al.* 2000) producing very rarely observed sporophytes in favourable conditions (Rasbach *et al.* 1993, Ratcliffe *et al.* 1993). However the most important factor in the dispersal pattern of north-easternmost outposts of the *Trichomanes speciosum* gametophyte is its ability to disperse clonally by gemmae (Vogel *et al.* 1993), which was theoretically elucidated for asexual populations by Peck *et al.* (1998).

BIOGEOGRAPHICAL IMPORTANCE

The present distribution of *Trichomanes speciosum* gametophytes is the result of the ability to establish new colonies by the long distance dispersal of gemmae. They are produced quite frequently on gametophytes and are the only means of dispersal in the absence of sporophytes. Such situations suggest very low or even no genetic variability between populations or within sites. The distribution of multilocus phenotypes of *Trichomanes speciosum* gametophytes in Central Europe (Rumsey *et al.* 1998b) and at its northern limit in Scotland (Rumsey *et al.* 1999) was partitioned primarily between, not within sites, and argued against a purely 'stepping stone' or 'leading edge' type of colonisation. These data support the hypothesis of initial random colonisation of very few potential sites via long-distance spreading with secondary dispersal as gemmae, or limited opportunity for generation of new genotypes through sexual reproduction (Rumsey *et al.* 1998b). The last situation is possible due to sporophyte production that was reported amongst gametophyte mats in Vosges, France or Britain (Rasbach *et al.* 1993, Ratcliffe *et al.* 1993).

The historical and present distribution of *Hymenophyllum tunbrigense* (L.) J.E.Smith closely resembles the pattern of *Trichomanes speciosum*. Sporophytes of both species have very similar ecological requirements and occupy mainly shady, wet, non-calcareous rocks. They are known from a few 'relict' sites in continental Europe

(Dostál 1984, Vogel *et al.* 1993). Former speculations regarding *Hymenophyllum tunbrigense* as a Tertiary relict in Luxembourg and Elbsandsteigebirge presented by Vogel *et al.* (1993) were partly supported by radiocarbon dates of tree charcoal in Belgium Ardennes and Western Slovakia (Stewart & Lister 2001). Both these localities are hypothetical temperate cryptic refugia during the Last Cold Stage at the end of the Pleistocene and could have provided a favourable microclimate for diverse vegetation in the sheltered habitats of deep gorges surrounded by peri-glacial tundra. Late Pleistocene and Holocene colonisation of *Trichomanes speciosum* from the main refugia in southern peninsulas (most probably Iberia) and Macaronesia, should also take into account the facilitation of dispersal by prevailing south-western winds. Cryptic refugia in northern Europe such as in the Ardennes area could probably form hypothetical enclaves only for gametophytes of *Trichomanes speciosum*. Existence of such a refugium in Saxonian-Bohemian Switzerland appears less likely with regard to the proximity of the front of the Last Cold Stage glaciation, so colonisation of Elbsandsteigebirge by long-distance dispersal probably occurred no earlier than in the Atlantic hypsithermal (5000 - 3000 B.P.; Vogel *et al.* 1993). The Holocene migration has formed the present distribution range of *Trichomanes speciosum*, modified by adverse climatic fluctuations. The outposts of the *Trichomanes speciosum* in Central Europe could also reflect cold oscillations in the last Millennium, especially the Little Ice Age (540 - 100 B.P.) with a cooler and wetter climate in this area (Kociánová 2002), and form neo-refugia *sensu* Nekola (1999). Such conditions in Saxonian-Bohemian Switzerland massif were favourable for *Hymenophyllum tunbrigense* and perhaps for production of *Trichomanes speciosum* sporophytes too.

The effects of global warming, with slight signs of shifting to a warmer and wetter climate for the *Trichomanes speciosum* in Central Europe suggest more favourable conditions for completing its life cycle with the sporophyte phase. It reveals that implications for the conservation of an ‘emblem’ species of endangered European pteridophyte disagree with superficial public opinion focused only on celebrated sporophytes of *Trichomanes speciosum*. The Killarney Fern may be less threatened than it was feared (Moore 1998).

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