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The second record of a natural apogamous moss sporophyte worldwide

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Abstract – An apogamous sporophyte is reported on a gametophore of the moss *Fissidens crassipes* subsp. *warnstorfii* (M.Fleisch.) Brugg.-Nann. The apogamous sporophyte is developed in lateral position near the base of the stem of the gametophore. The seta is relatively short and delicate and the capsule without spores. The moss was found growing in a greenhouse in Cairo, Egypt. This is the second record of a natural apogamous moss sporophyte worldwide. A relevant discussion on the phenomenon of apogamy is given.

Apogamy / Egypt / Fissidens / Mosses

INTRODUCTION

Relatively recently the authors began the study of life history aspects of Egyptian mosses. We began with seven mosses growing in the Cairo region, including *Fissidens crassipes* subsp. *warnstorfii* (M.Fleisch.) Brugg.-Nann. Many samples of this subspecies were collected over a period of 12 months, more or less regular every two weeks. The first sample was peculiar as it bore an apogamous sporophyte. We describe this sporophyte and comment on the phenomenon known as apogamy in bryophytes.

MATERIAL AND METHODS

A population of *F.crassipes* subsp. *warnstorfii* was found growing, under low light intensity conditions, on the surface of a vertical red-brick wall covered by cement in a greenhouse in the garden of the Botany Department of the Faculty of Science of Ain Shams University. The population covered an area of about 30×100 cm extending to reach the ground. Water from excessive irrigation of ornamental flowering plants, growing in pots placed on top of the vertical wall kept the *Fissidens* population sufficiently wet all the time and the closed greenhouse environment highly humid and warm.

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A sample of about 1 cm² of the population was collected on 4 April 1999. About 20 individuals were randomly picked from the sample. Each individual was hydrated on a microscope slide and gently cleaned under a binocular stereoscopic microscope with critical care not to overlook, detach or damage any organ or structure. Permanent slides maintaining whole plants, excised organs and cross-sections of stems and leaves were prepared for critical examination and photography. Specimens were mounted in glycerin jelly on clean glass slides and refrigerated to solidify as described by Johansen (1940). Specimens and mounted slides are kept in the Botany Department, Faculty of Science, Ain Shams University.

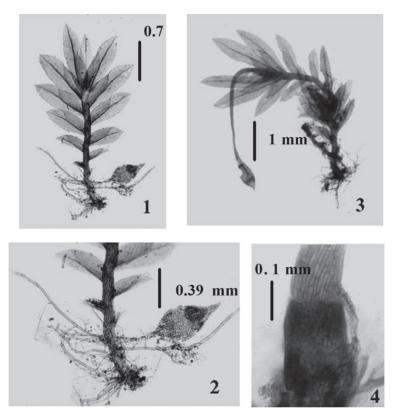
DESCRIPTION

An apogamous sporophyte (Figs 1, 2) was recorded in the sample of April 1999 and only once over the course of the study. It differed from normally recorded sporophytes in both position and structure. It was found in a lateral position near the plant's base (Figs 1, 2). Due to extreme rarity any examination procedures that involve dissection or analytical work were not taken in order to preserve such unique example of naturally occurring apogamy. However, due to its light colour, its structural details were easy to discern through ordinary examination by the light microscope. It was entirely exposed; it lacked a calyptra, a vaginula (compare Fig. 2 with Fig. 4) and a foot, the seta was reduced (0.48 mm long) with delicate cell walls, stomata were lacking, while the capsule was intact and without any developed spores (0.69 mm long, 0.35 mm wide), peristome teeth could be recognized even though the operculum was still intact. The size of the gametophyte that carries it is comparable to attached or detached branches of the adult and old plants (compare Fig. 1 with Fig. 3).

The studied *Fissidens* seems to be well established in the greenhouse environment. Nevertheless, it appears that sexual reproduction is not relied upon for its propagation, and asexual reproduction prevailed through the formation and germination of rhizoidal gemmae, and deciduous branches. Although the population developed normal sexual sporophytes only over the period from May to September 1999, there had been continuous production and obvious overlapped maturation cycles of the gametangia throughout the year of the study. However, normal sexual sporophyte production was relatively rare and the rather different single lateral sporophyte was observed one month before the beginning of the recorded limited normal sexual sporophyte production, which started in May 1999. It is worth mentioning that no lateral gametangia were observed along the stem in all examined individuals of this population.

DISCUSSION

This is a sporophyte (it has a peristome and a detachable lid) and we believe it to be of apogamous origin because no gametangia, calyptra, vaginula or a sporophytic foot were found. We do not know what triggered this apogamous development, however, low light intensity (see Lal, 1963; Knoop, 1984) and



Figs 1-4. 1. Gametophyte carrying an apogamous sporophyte. 2. Close up on the apogamous sporophyte. 3. Normal sporophyte, the capsule being partly grazed and spores totally consumed by insects. 4. Vaginula and lower part of seta of a normal sporophyte.

quality of irrigation water (probably contaminated with chemicals from nearby chemistry labs) are among the conditions that characterize the habitat of this population and may be linked to this development. Among factors, hitherto, known to induce apogamy in bryophytes are: light, hydration, sugars, chloral hydrate, growth regulators, inorganic nutrients, and endogenous factors, however, as stated by Cvetic *et al.* (2005) there are no generalizations for bryophytes.

Formation of apogamous sporopytes is a very rare phenomenon, both in nature and under *in vitro* conditions (Cvetic *et al.*, 2005). The present apogamous sporophyte represents, therefore the most striking discovery, not only for this particular *Fissidens* population under investigation but also for mosses in general. Such a report on naturally occurring incidence of apogamy is only the second since a century when Marchal & Marchal (1911) observed club-shaped outgrowths on leaves and stems of diploid gametophytes but interpreted them as asexual reproductive structures which were later, however, described in detail and properly interpreted by Springer (1935) as apogamous sporophytes, developed on the leaf and stem tips of naturally growing diploid gametophytes of the moss *Phascum cuspidatum* Hedw., which was justifiably regarded since then as "a lucky chance" (Lal, 1984).

Unfortunately the apogamous sporophyte was recorded in the first sample (*i.e.* there is no previous information about the population and the prevailing conditions causing this apogamy), thus any explanation of this apogamy incidence would then be only speculative. However, we tried our best to figure out and conclude the most plausible and possible ones, particularly that no cytological evidence is available.

Since no lateral gametangia were recorded at all along the stems (throughout the year of study) in individuals of the present *Fissidens* population, the lateral position of the discovered apogamous sporangium was regarded as an abnormality confirming its apogamous origin. However, another abnormality, indicating that Fissidens might be particularly susceptible to peculiarities in morphology was reported quite recently by Nour-El-Deen (2011) when she discovered long-stalked gametangia that are borne individually and laterally along one or both sides of the stems of gametophores of a population of this same subspecies of Fissidens, that was found growing on mud overlaying a red-brick wall saturated with sewage water in Nile Valley, Egypt. These gametophores possessed also sessile gametangia, without aberrations, borne normally in terminal heads as is typical for this subspecies (Nour-El-Deen, 2011). It is likely that the abnormalities, as mentioned by Nour-El-Deen (2011), stemmed from the highly contaminated substrate. No sewage water reaches the Fissidens plants under investigation but it is not improbable that water flooding the *Fissidens* population in the greenhouse was contaminated with chemicals originating from nearby chemistry laboratories, which might have caused the development of this single apogamous sporogonium. The low light intensity in the greenhouse sustaining this population of *Fissidens* is also a suspected cause favouring the production of sporophytes in general, whether normal sexual, or abnormal apogamous ones (see Lal, 1963; Knoop, 1984). The apogamic nature of the discovered sporogonium, if not discerned from its lateral position, would be unequivocally evidenced from the absence of a gametophytic calyptra, a vaginula as well as the lack of a sporophytic foot. The development of archegonia laterally as single organs, though rare in mosses, is known in *Takakia*, some Sphagna and some Splachnobrya (Goffinet et al., 2008; Nour-El-Deen 2011) and is known to be normal in these mosses. The single lateral gametangia of Fissidens were, however, regarded by Nour-El-Deen (2011) as abnormalities because their development is a deviation from the norm of this sub-species and the suspected cause is the highly contaminated substrate.

The lack of spores in the present apogamous sporogonium may be due to incomplete ontogenesis (Goffinet el al., 2008) being developed unprotected by a calyptra (Chopra, 1988) or because it had been collected before meiosis took place. It is less probable, however, that this apogamous sporophyte lacked spores because it could be haploid since truly monoploid gametophytes seem to lack the ability to develop apogamous sporogonia (Chopra, 1988). A knowledge of chromosome number or DNA content of the cells, therefore, seems essential to determine the ploidy of an abnormal or a normal gametophyte, sporophyte or even certain tissues or cells of the former. For example, according to Knoop (1984), Hallet (1972) states that hydroids and cortex cells in *Polytrichum* become endopolyploid during the course of differentiation while Nagl & Ullmann (1973) state that in *Drepanocladus*, the leaf lamina cells are endopolyploid. Knoop (1984), likewise, states that chloronema cells of a protonema may remain haploid whereas the caulonema cells (not very stable in the face of disturbances) of the same protonema become diploid. The assumption, therefore, that gametophore cells are haploid may not always be correct (Paolillo, 1984) and a filamentous precursor of calli and apogamous sporophytes cannot, therefore, necessarily be classified as haploid (Knoop, 1984).

Accordingly the reported apogamous sporogonium and the gametophyte carrying it may both be haploid or diploid or the gametophyte haploid while the sporophyte diploid. Polyploidy and aneuploidy are known to occur in the genus *Fissidens* and are believed (Chopra & Kumar, 1981) to have played a definite role in its evolution and speciation.

Regarding factors causing apogamy in mosses Knoop (1984) states "from our present knowledge, we cannot deduce any common molecular mechanism that is valid for both apogamous and sexual sporophytes induction". Lal (1963) adds (according to Knoop, 1984) "possibly there exists a sporophytic factor permanently produced by conditioned tissues and in balance with a gametophytic factor produced in high light only". This could explain the occurrence of sporophytes in the dark or in low light and that of gametophores in high light (Lal, 1963). Knoop (1984) adds that these internal factors remain speculative.

It may be said in conclusion that careful microscopic investigation of large numbers of moss gametophytes may lead to the spotting of more instances of apogamous sporophytes (which would allow for better studies necessitated to throw more light on this phenomenon), particularly that polyploidy is very common in many mosses (Wyatt & Anderson, 1984), that only mosses whose genome is truly monoploid seem to lack the ability to develop apogamous sporogonia on vegetative plants (Chopra, 1988) and that apogamous sporophytes are readily induced to develop *in vitro* by various factors which are not exclusively artificial (such as low light intensity, increased sugar content in the medium, or growth hormones) (Chopra, 1988).

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