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Sporeling Development in *Athalamia pusilla*

By

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With 30 Figures

Introduction

Recent contributions on Indian *Sauteriaceae* include the sporeling development and regeneration in *Athalamia pinguis* (UDAR 1958b), its (*A. pinguis*) morphological features along with the details of life history (UDAR 1960), and a report of *A. pusilla* from South India (UDAR & SRIVASTAVA 1965). The species under consideration (i. e. *A. pusilla*) has been earlier reported also from several localities in the Western Himalayas (KASHYAP 1929). Amongst the two Indian species of the genus *Athalamia*, considerably much attention has been laid on *A. pinguis*. The other species (i. e. *A. pusilla*) has not been so far worked out in detail as regards its life history and stages in the sporeling development. A detailed investigation concerning the life history of this plant, which includes the stages in the ontogeny of antheridia, archegonia and sporophyte, is under progress. The present paper deals with the early stages of sporeling development in *A. pusilla* so far undescribed.

Materials and methods

The specimens of *A. pusilla* were collected by one of us (R. U.) from Deoban in the North-Western Himalayas at an altitude of ca 8,000 ft. — 9,500 ft. during the last week of September 1969. This is the time when the plants normally complete their life cycle and many plants show dehisced capsules or intact capsules with mature spores.

The plants of *A. pusilla* grow in extensive mats on thin soils adhering to shaded rocks often in association with the plants of *Exormotheca tuberifera* KASH.

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Complete mature sporophytes were isolated from the plants and washed several times with distilled water. Spores were cultured on January, 14, 1970, in sterilized covered pyrex glass petridishes, containing:

(a) Sterilized tap water

(b) Sterilized full strength Knop's solution

(c) Sterilized half strength Knop's solution

Knop's solution was made with the usual constituents. The cultures received diffused sun light through the north glass window panes of the laboratory at room temperature.

Although the spores germinated in (a), (b) and (c), best growth was observed in (b) and (c). The cultures were kept for about a month and a half, during which time all the stages were obtained.

Spore morphology of *Athalamia pusilla*

The mature spores of *A. pusilla* (Fig. 1) are apolar, globose in outline, dark brown and papillate (or saccate), measuring 48.0—57.6 (—67.2) μ in diameter (including the papillae). Prominant papillate projections numbering 6—8 (in top focus) occur on the surface of spores and perinium or wing is lacking. The proximal and distal faces of the spores are more or less similar in appearance as the triradiate mark is not clearly defined.

Observations

The spores started germination in about ten days (i. e., on January 23, 1970). Like the spores of *A. pinguis* the spores of *A. pusilla* apparently have no obligatory rest period. In *A. pinguis*, however, the spores germinated in five days (Udar 1958b). All the spores proved viable, i. e., spore viability is 100%.

The first sign of spore germination is the absorption of water causing swelling of the spore (Fig. 2). At this stage the chloroplasts and oil drops increase in number and the spore coat becomes light in colour with papillae

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Fig. 1: Mature spore. — Fig. 2: Spore drawn from 7 days old culture. — Figs. 3, 4: Appearance of germ pore at the distal face. — Figs. 5, 6: Emergence of germ papilla (germ tube). — Fig. 7: First transverse wall dividing the germ tube into two-celled filament. — Figs. 8, 9: Three-celled filament. Note the germ rhizoid in fig. 8. — Figs. 10, 11: Appearance of vertical wall in the subterminal and terminal cell of the filaments respectively. — Figs. 12, 13: Four-celled germ plate or germ disc. — Fig. 14: Four-celled filamentous stage. — Fig. 15.: Vertical division in the terminal cell of the four-celled filamentous stage. — Figs. 16, 17: Divisions in the five-celled filamentous stage. — Figs. 18, 19: Organisation of an apical cell (apc). — Fig. 20: Dichotomous growth of the germ disc. — Fig. 21: Multicellular disc formed over a four-celled linear filamentous column. — Figs. 22, 23: Eccentric germ plate formation.

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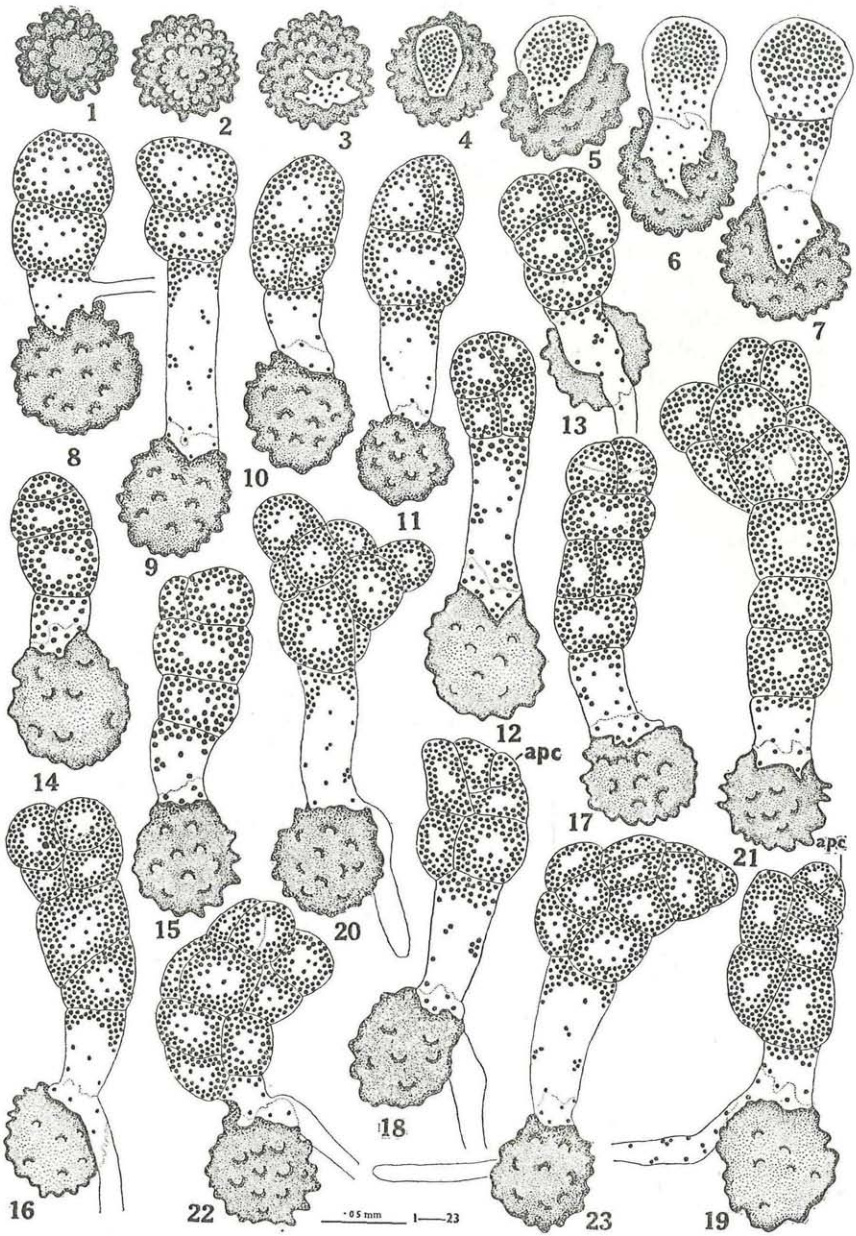

Figs. 1—23

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appearing fainter. The spore coat ruptures at the distal pole forming a germ pore (Fig. 3) as in *Riccia* (UDAR 1958a) and *Exormotheca ceylonensis* (UDAR & SRIVASTAVA 1967). The distal dehiscence of the spore coat in *A. pusilla* is entirely different from the proximal or irregular dehiscence in *A. pinguis*. Other significant differences between the two species are noticeable in the initial stages of sporeling development and the fate of the spore coat in relation to the sporeling. In *A. pusilla*, in hundreds of sporelings observed, there is the formation of a germ tube (Figs. 4—6). The spore coat remains intact and attached to the sporeling even at very advanced stages of development (Figs. 28—30). In *A. pinguis*, on the other hand, the spore germinates while the spore coat is still intact and continued cell divisions form a multicellular globose germ disc exerting pressure on the spore coat which gets torn off in isolated shreds. Rarely a germ tube is formed as in *A. pusilla* but even such stages have the spore coat behaving in a similar manner.

After the dehiscence of spore coat a germ papilla grows to form a germ tube (Figs. 3—6). In this the chloroplasts are aggregated at the terminal portion (Fig. 6). The tube may elongate or remain short.

A transverse wall towards the apex of the germ tube delimits the first cell of germ disc (Fig. 7). A subsequent transverse division, parallel to the first one, gives rise to a three-celled stage (Fig. 8). The formation of first rhizoid (germ-rhizoid) is usually delayed until the germ tube becomes septate, and makes its appearance from the basal cell in its continuation maintaining an internal continuity in both (as in *Stephensoniella brevipedunculata*: MEHRA & KACHROO 1952). In this first rhizoid some chloroplasts also pass from the basal cell but later on these chloroplasts disappear.

In some of the sporelings the germ tube elongates more in length and the transverse walls are laid down afterwards (Fig. 9).

Subsequently vertical walls are laid down in the upper two cells of the filament (Figs. 10, 11) resulting into the formation of a four celled germ plate or germ disc (Fig. 12). In some cases the terminal cell of the filament at a very early stage develops into a quadrant which is organised by the formation of two vertical intersecting walls (Fig. 13) as in *Rebouliaceae* (MEHRA & KACHROO 1951).

Occasionally there is the formation of four-celled filamentous stage (Fig. 14), the terminal cell of which subsequently divides by vertical wall (Fig. 15).

In some of the sporelings the germ tube undergoes four transverse divisions forming a five-celled filamentous stage. The terminal cell further divides by a vertical wall and in the next stage of development the subterminal or even the next lower cell may also be involved in the formation of similar vertical walls (Fig. 17). The terminal cell ultimately becomes four celled (Fig. 16) by subsequent division.

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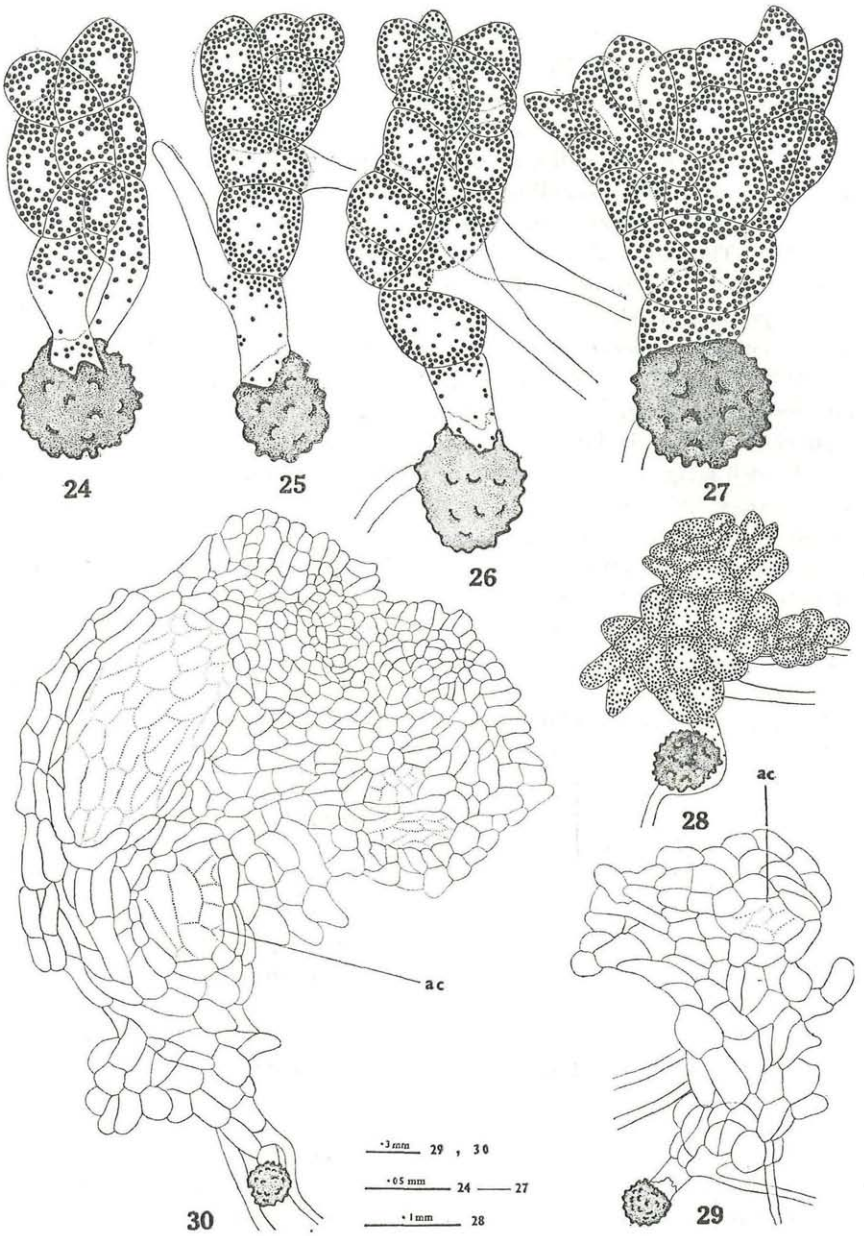

Fig. 24: Development of two germlings from the same spore. — Figs. 25, 26: Multicellular germ disc showing the emergence of primary as well as secondary rhizoids. — Fig. 27. Germ disc in a straight column. — Figs. 28—30: Five weeks old sporelings showing the formation of air cavities (ac) in Figs. 29 and 30. Note the spore coat attachment to the sporeling till late in development.

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In later stages vertical and transverse divisions occur in this germ disc. The apical cell is organised rather early in development (Figs. 18, 19). Further growth of the germ disc takes place by the activity of the apical cell. Some sporelings may show dichotomous growth (Fig. 20).

Two types of germ disc or germ plate formation seem to occur in *A. pusilla*. Some of the sporelings (Figs. 22, 23) show '*Asterella* type' plate formation (INOUE 1960) where the development of the plate is essentially eccentric. The cells of the quadrant undergo tangential and to a lesser degree vertical divisions and form a multicellular germ plate which is mostly peltate and elongated (INOUE 1960). Most of the sporelings, however, form germ plates along the axis of the germ tube (Figs. 24—30) resembling the '*Stephensoniella* type' (MEHRA & KACHROO 1952). Finally an erect multicellular column is formed from the terminal quadrant by a series of transverse and vertical divisions.

In still later stages of development the multicellular column flares up at the apex by a generalised growth in which all the cells in front are involved forming a cellular mass. Within this cellular mass large cavities make their appearance opening through the entire length and breadth (Fig. 30). These cavities give the young sporeling a very spongy appearance. Later on by the activity of four-sided apical cells, formed on one side of flaring mass of cells, the dorsiventral thallus and air pores are formed.

The development of secondary rhizoids may take place in the middle (Figs. 25, 26, 28) of the plate and their formation is similar to that of germ rhizoid formation, i. e., secondary rhizoids are also not separated by any septum.

Some interesting stages of spore germination were also observed. In one case a multicellular disc was formed over a four celled linear filamentous column (Fig. 21), while in some two germlings developed from the same spore (Fig. 24). Thus, it appears that two germ tubes are emerging from a spore as has also been observed by MEHRA & KACHROO 1951 in *Plagiochasma articulatum* and *P. appendiculatum*, in which two or even three germ tubes arise respectively from one spore.

In *A. pusilla* no stages of regeneration were observed in the sporelings although in *A. pinguis* this phenomenon was relatively common.

Conclusions

The sporeling development in *Athalamia pusilla*, outlined in the present communication, appears basically similar to that of *Stephensoniella brevipedunculata* except in the nature of spore coat dehiscence. However, the spore coat dehiscence in the latter species is undoubtedly distal as the tri-radiate mark plays no part in the rupture of the spore (MEHRA & KACHROO 1952). Instead of forming a regular germ pore as in *A. pusilla*, there is the formation of cracks between the pentagonal areas on the convex surface of the spore in *S. brevipedunculata*.

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In the present state of our knowledge there is a stabilized spore morphology in *Sauteriaceae* rather characteristic of the family. All the members or the family have papillate (saccate) spores. However, the early stages of sporeling development in various genera, investigated so far, seem to present a dynamic pattern.

From the data available so far on sporeling development in various genera of the family *Sauteriaceae* variations in spore coat dehiscence, germ rhizoid formation and germ disc formation rather characteristic of the species have been encountered.

Spore coat dehiscence: Amongst the species investigated two clearly defined patterns of spore coat dehiscence have been noticed:

(a) Distal dehiscence: In this type there is the formation of a germ pore at the distal face of the spore, and the spore coat remains intact elsewhere till late in sporeling development as described above for *A. pusilla*. Although the spores are apolar in this species but the formation of a distinct pore is suggestive of the distal dehiscence. Such type of distal dehiscence is known in *Funicularia bischleriana*, *Corsinia coriandrina* (*Corsiniaceae*: Jovet-Ast 1963), *Sphaerocarpos* (*Sphaerocarpaceae*: Goebel 1930; Proskauer 1954), *Riella* (*Riellaceae*: Proskauer 1955), *Riccia* (*Ricciaceae*: Duthie & Garside 1937, 1940; Udar 1958a) and *Exormotheca ceylonensis* (*Exormothecaceae*: Udar & Srivastava 1967). The distal dehiscence of the spore coat is supposed to be an advanced feature because of the fact that this type of spore coat rupture is very common in those forms in which the spores remain adherent in tetrads even at maturity which is also considered to be an advanced character. Adherent spores are found in some species of *Riccia* (e. g. *R. curtisii*, *R. perssonii* and *R. synspora*) and *Sphaerocarpos*.

(b) Irregular dehiscence: In this type of dehiscence described mostly in those genera where the spores are apolar, the spore coat ruptures irregularly and gets torn off into small pieces. *A. nana* and *Sauteria yatsuensis* present a good example of this type of spore coat dehiscence (Inoue 1960). Although in *A. pinguis* the spore coat dehiscence has been described as proximal (Udar 1958b) but it is basically irregular. This type of dehiscence is also found in *Targionia hypophylla*, *Cyathodium* sp. (*Targioniaceae*), *Marchantia polymorpha*, *M. paleacea*, *Dumortiera hirsuta* subsp. *tatunoi* and *Lunularia cruciata* (*Marchantiaceae*: Inoue 1960) suggesting interrelationships between the families *Marchantiaceae*, *Sauteriaceae* and *Targioniaceae*.

Germ rhizoid formation: The germ rhizoid formation is characteristic of species or genera (Inoue 1960). In the family *Sauteriaceae* the germ rhizoid formation is mainly of two types:

(a) *Targionia* type: In this type the germ rhizoid shows distinct polarity being produced in the opposite direction to the germ tube or to the germ disc. *Sauteria yatsuensis* (Inoue 1960) and *A. pinguis* (Udar 1958b)

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show this type of germ rhizoid formation rather characteristic of the family *Targioniaceae* (as in *Targionia hypophylla* and *Cyathodium* sp.: INOUE 1960).

(b) *Stephensoniella* type: In this type the germ rhizoid is produced as an extension of the basal cell of a filament and internal continuity is maintained in both (MEHRA & KACHROO 1952). This type of germ rhizoid formation is characteristic of the family *Exormothecaceae* (as in *S. brevipedunculata*, MEHRA & KACHROO 1952 and *Exormotheca ceylonensis*: UDAR & SRIVASTAVA 1967). Two species of *Athalamia*, *A. pusilla* (as described in the preceeding pages) and *A. nana* (INOUE 1960) fall in this category of germ rhizoid formation. In *A. pinguis* sometimes, when the germ tube becomes prominent, the germ rhizoid formation is of this type as has also been encountered in *Riccia*(UDAR 1958a) and *Monoselenium tenerum* (INOUE 1960).

In *A. pinguis* the germ rhizoid develops early, whereas in those cases where it is of *Stephensoniella* type its development may be delayed as in *A. pusilla* and *A. nana*.

Germ disc formation: The germ disc formation in the family *Sauteriaceae* is also of two types:

(a) The germ tube is highly reduced and the germ disc formation takes place within the ruptured spore coat. *A. pinguis* more commonly represents this type of germ disc formation. However, some of the sporelings of the same crop may show prominent germ tubes (UDAR 1958b). *A. pinguis* therefore shows affinity with *Targionia hypophylla* in having highly reduced germ tube and the germ disc formation within the ruptured spore coat as sometimes occur in *Wiesnerella denudata* (INOUE 1960) also.

(b) The germ tube formation is very prominent as in *A. pusilla*, *A. nana* and *Sauteria yatsuensis*. The germ tube becomes septate (filamentous) and ultimately a quadrant is formed by the division of the terminal cell of the filament. Subsequently an apical cell is organised by the activity of which two distinct types of germ discs may be formed in the family *Sauteriaceae*:

(I) *Asterella* type, occurring in *A. pusilla* and *Sauteria yatsuensis* as well as in *Exormotheca ceylonensis*.

(II) *Stephensoniella* type, occurring in *A. pusilla* and *A. nana* as well as in *Exormotheca ceylonensis*.

Thus from the above account it may be said that *A. pusilla* shows sporeling development very much similar to that of *S. brevipedunculata* and *Exormotheca ceylonensis*.

Summary

The spore morphology and sporeling development in *Athalamia pusilla* has been described. The emergence of the germ tube takes place through the distal face of the spore. The germ-rhizoid formation is of the *Stephensoniella*-type and the germ plate (germ disc) formation is of two types, i. e. *Asterella*-type and *Stephensoniella*-type. Within the family

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Sauteriaceae there is a more or less stabilized spore morphology but dynamic sporeling pattern.

Zusammenfassung

Die Morphologie und das Keimen der Sporen von *Athalamia pusilla* werden beschrieben. Der Keimschlauch tritt an der Vorderseite der Spore aus. Das Keimrhizoid bildet sich nach dem *Stephensoniella*-Typ, die Keimplatte oder Keimscheibe entsteht nach dem *Asterella*- oder nach dem *Stephensoniella*-Typ. Bei ziemlich übereinstimmender Sporenmorphologie besitzen die *Sauteriaceae* eine sehr mannigfaltige Sporenkeimung.

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