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Morphology and Sporeling Development of *Fossombronia wondraczekii* var. *loitlesbergeri* (Hepaticae)

By

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With 55 Figures

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Summary


*Fossombronia wondraczekii* (CORDA) DUM. var. *loitlesbergeri* (SCHIFFN.) K. MÜLLER previously found in southern Europe, Japan and Algeria is being reported from Nandi Hills, Karnataka (South India) for the first time in India’s bryoflora. The morphology is described and the characteristics are compared with other representative species of the genus in India. The sporoderm (under LM and SEM) is reticulate with 5–9 meshes across the diameter, with usually 1–2 wart-like projections in the lumen of almost each mesh. Elaters are narrowly elongate, slender, 2–3 spirate and blunt (at ends). Three ways of sporeling development are observed; filamentous, septate germ-tubes were formed predominantly.

Zusammenfassung


Die bisher aus Süd-Europa, Japan und Algerien bekannte *Fossombronia wondraczekii* (CORDA) DUM. var. *loitlesbergeri* (SCHIFFN.) K. MÜLLER wurde erstmals für

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1. Introduction

SRIVASTAVA & UDAR 1975a in a detailed study of the genus *Fossombronia* reported 7 species from various parts of India and grouped them into three broad categories constructed on the basis of spore morphology and elater characteristics viz. 1. *F. cristula*-type (including *F. cristula* AUST., *F. foreaui* SRIVASTAVA & UDAR), 2. *F. wondraczekii*-type (including *F. wondraczekii* (CORDA) DUM., *F. himalayensis* KASH., *F. pusilla* DUM., *F. kashyapii* SRIVASTAVA & UDAR), and 3. *F. indica*-type (including *F. indica* STEPH). It is noteworthy that the sporoderm ornamentation on the distal face provides tangible features in species recognition while those on the proximal faces show some ornamentation but are of no taxonomic value (SRIVASTAVA 1984). Earlier KNOX 1939 also used the same criteria as a diagnostic marker and categorised the species of *Fossombronia* into three groups.

Recently during a plant collection trip to south India, a territory hosting nearly all the Indian species of *Fossombronia* (except *F. kashyapii*), some fruiting plants of *Fossombronia* with ripe sporogonia were collected from nearly exposed (but partly shaded by the tree canopy) rocky soil at Nandi Hills (53 kms from Bangalore), Karnataka. The plants on detailed investigation revealed characteristic reticulate spores with 5–9 meshes across the distal face of the spore, 1–2 wart-like projections in almost each mesh lumina, and slender, well-developed, 2–3 spirate blunt (at ends) elaters convincingly answering to *F. wondraczekii* var. *loitlesbergeri*, a taxon known so far only from southern Europe, Japan and Algeria. This variety falls under *F. wondraczekii*-type too.

Nomenclatural history: The relevant taxon was recognised for the first time by CORBIÈRE 1903 from France under the specific epithet *F. crozalsii* CORB. (see also BONNER 1965). SCHIFFNER 1909: 195–197 described it as *F. loitlesbergeri* from Dalmatia and regarded it as closely related to *F. wondraczekii* (CORDA) DUM. MACVICAR 1926 reported it (as *F. crozalsii*) from England and suggested its similarity with *F. wondraczekii* too (see also MÜLLER 1954: 538). According to MACVICAR, *F. crozalsii* was more closely connected with *F. dumortieri*-group rather than *F. caespitiformis*-group as mentioned by CORBIÈRE. MÜLLER 1909: 391 admits *F. crozalsii* and presumed affinities to the *F. caespitiformis* group and
to F. dumortieri group; 1916: 732–733 he added F. loitlesbergeri. CHALAUD 1930: 569 made the combination F. cristata LINDB. var. loitlesbergeri (SCHIFFN.) CHALAUD and he also included as a variety the older taxon F. wondraczekii into this species in an illegitimate mode. He put F. cristata together with F. pusilla and his ‘Section III. – Sporae cristatae’. CHALAUD 1937: 127–128 revised a sample labeled F. crozalsii as F. cristata var. loitlesbergeri, maintained the position in the group ‘Cristatae’ and remarked that MACVICAR 1926 and MÜLLER 1916 omitted to represent the projections visible on the sporoderm between the lamellae. MÜLLER 1954: 538, 544–545 retained F. crozalsii, synonymized F. cristata LINDB. with F. wondraczekii correctly and has combined F. wondraczekii var. loitlesbergeri (SCHIFFNER) K. MÜLLER but he ascribed this erroneously to CHALAUD. Recently INOUE & HIBINO 1984 while describing spore morphology of Metzgeriales have treated F. crozalsii as F. wondraczekii var. loitlesbergeri. BOROS 1968: 224 mentioned the occurrence of the latter in S Hungary. STEPHANI 1900 reported F. wondraczekii var. wondraczekii under the misspelled epithet F. crispata STEPH. (= F. cristata STEPH.) from Himalayas.

As our plants were collected in perfect fruiting stage it was thought to provide various details of the generations in the haplophase and in the diplophase. Besides, morphotaxonomic account of the sporoderm pattern (under SEM) and sporeling development has also been provided.

2. Materials and Methods

Fossombronia wondraczekii var. loitlesbergeri was collected by one of us (DS) from the western ghats in Nandi hills (53 kms N from Bangalore) Lat. 13° 22’ N, Long. 77° 41’ E, Alt. ca. 1470 m, Karnataka (south India) during the last week of August, 1991 when the plants normally complete their life-cycle showing ripe or dehisced sporogonia. Fresh as well as specimens preserved in 90% ethyl alcohol were utilised in morphotaxonomic study. For the study of spore germination and sporeling pattern, blackish or dark-brown fully mature capsules were dissected out from the parent plant and repeatedly washed in distilled water. Spores were sown on October 14, 1991 in different grades of Knop’s solution on sterilized cavity slides as well as on corrugated plain slides kept in covered pyrex glass petridishes containing water to maintain humidity. The following constituents (as formulated by INOUE 1960) were used and the culture medium was prepared in 1000 ml of distilled water: KNO₃ (0.25 gm), KH₂PO₄ (0.25 gm), Ca(NO₃)₂ (1.00 gm), MgSO₄ (0.25 gm), Fe₃(PO₄)₂ (0.20 gm) and FeCl₃ solution (1 drop). Four sets of the above experiment containing sterilized 100% Knop’s, 50% Knop’s, 25% Knop’s and distilled water with spores in covered petridishes containing water at the bottom were placed near the North facing window panes of the laboratory. The incidence of diffused light (avoiding a direct exposure to the sun) was available for approximately 10 hrs daily and at a temperature mean range of 33.7°, 27.7°, 26.9°, 23.9°, 24.4° and 31.4° C (maximum) and mean minimum of 17.0°, 12.2°, 9.5°, 8.0°, 9.3° and 13.4° C respectively from October to March.
The glass wares and the medium used in the present investigation were autoclaved at 15–20 lb pressure before use.

For the study of sporoderm architecture the spores were investigated under Scanning Electron Microscope (Philips model 505 SEM, Made in Holland), installed at Birbal Sahni Institute of Palaeobotany, Lucknow. Thoroughly cleaned capsules were taken in small tubes and kept in a hot-water bath for 24 hrs, then dehydrated through usual ethanol series, just after the washing, two ultrasonic treatments (each of 5 minutes) at an interval of 15 minutes were given to the material for ultimate cleaning of the sample. The dehydrated capsules were incised with microneedle and non-acetolysed spores were dusted on the glass stubs affixed by double sided adhesive tape to the aluminium stubs. The samples were then glow discharged and coated with thin layer of Gold Palladium in a PS-2 coating unit equipped with vacuum chamber and pump for about 100–150 seconds. Immediately after coating, the mounted samples were stereoscanned at an accelerating potential of 10–30 KV for different sample and tilt difference of 25°.


3. Morphology

of Fossombronia wondraczekii (Corda) Dum. var. loitlesbergeri (Schiffn.) K. Müller (Figures 1–21, 45–50).

Thallus: Plants are small, green to yellowish-green, differentiated into stem and leaves, usually prostrate or somewhat ascending at apex, growing exposed or under shade on moist soil or rock surface, usually in small patches. Stem is 4–9 mm long, 0.38–0.47 mm wide laterally and 0.28–0.31 mm wide vertically across diameter (in transverse-section), dorsiventrally flattened, dichotomously branched sometimes with tuberous apex. Rhizoids dense, hyaline or pale-yellow. Stem in transverse section (Fig. 1) is undifferentiated. Internal cells parenchymatous, thin-walled, larger (41–56×23–45 μm) towards periphery and smaller (15–34×15–26 μm) in the centre containing mycorrhiza. During winter the plants perrenate by means of apical tubers like all other members of Fossombroniaceae. At the advent of rains the tubers germinate to give rise to a new thallus.

Leaves and leaf-cells: Leaves are simple, succubous and imbricate, closely arranged at apex with cauliflower-like phyllotaxis, oblong to subquadrate (Figs. 2–4), 1.03–1.5 mm long and 1.8–2.5 mm wide, always wider than long, with highly undulate and irregularly angled or lobed margins, with mucilage papillae (26–30×19–26 μm). They are internally
Fig. 1–21. Fossombronia wondraczekii var. loitlesbergeri. – Fig. 1. Transverse section of stem. – Fig. 2–4. Lateral leaves. – Fig. 5. Apical and subapical cells of the leaf. – Fig. 6. Marginal cells of the leaf. – Fig. 7. Median cells of the leaf. – Fig. 8. Basal cells of the leaf. – Fig. 9. Archegonium (fertilized). – Fig. 10. A mature capsule with short seta. – Fig. 11. Outer layer cells of the capsule wall. – Fig. 12. Inner layer cells of the capsule wall (middle region). – Fig. 13. Inner layer cells of the capsule wall ( basal region). – Fig. 14. Transverse section of the capsule wall. – Fig. 15. Spore (equatorial view). – Figs 16–18. Spore (distal view). – Figs. 19, 20. Spore (proximal view). – Fig. 21. Elaters.
unistratose throughout except at the base where more than one (usually 2–3) cell layer thick. Leaf cells (Figs. 5–8) are thin-walled, quadrate to subquadrate or polygonal, occluded with chloroplasts; apical to subapical marginal cells (23-)26–30(-38) × (23-)30–34(-45) μm, basal marginal to submarginal cells broadly subquadrate to polygonal (23-)30–38 (-41) × (41-)45–60(-98) μm, median cells polygonal (30-)41–53(-64) × (30-) 34–41(-53) μm; mid-basal cells large, rectangular or polygonal, (79-) 86–94(-135) × (45-)56–64(-68) μm.

**Sexuality and Pseudoperianth:** This taxon is stated to be monoecious (heteroecious) but Antheridia were not found in the specimen examined which possibly indicate that they are protandrous and the antheridia at the time of sporogonia formation might have already dehisced and disintegrated. Archegonia (Fig. 9) naked and purple, scattered over the flattened dorsal stem near the apex at the proximity of the leaves, up to 186 μm long and 47–62 μm wide, bracts absent. Pseudoperianth campanulate or inverted bell-shaped, margins highly undulate or irregularly lobed, open on one side by means of a longitudinal incision up to the base, calyptra delicate and thin, 2–3 cell layers thick.

**Sporophyte:** The Sporophyte (Fig. 10) is differentiated into a foot, seta and capsule. The foot is multicellular, small and triangular. The seta is short, and massive type, 7–8 cells across diameter with thin-walled and angular cells. The capsule is spherical, up to 908 μm wide, brownish-black at maturity, exserted, dehiscence irregular, capsule wall 2–3 stratose (Figs. 13, 46), with outer layer of cells 23–49 × 26–38 μm, thin-walled, hyaline and without any secondary thickenings (Fig. 11) and inner layer of cells with incomplete (complete) to tangentially dilated subnodular (Fig. 12) or sometimes continuous and sheet-like (Figs. 13, 45) deep-brown thickenings on both longitudinal and transverse walls, in optical section. The secondary thickenings are usually restricted to the radial walls and feebly connected to the tangential walls (Figs. 14, 46).

**Spores:** Spores are tetrahedral, 38–45(-60) μm in diameter, dark-brown, distal face with thick and high (up to 5 μm) lamellae which anastomose to form 5–8 reticulations (or meshes) across the diameter of the spore (Figs. 18, 22, 39, 50). Meshes are sometimes few when the lamellae are somewhat parallel or irregularly forked (Figs. 16, 17) with usually 1–2 wart-like projections in the centre of the mesh-lumina (Figs. 16–18, 22, 39, 50). The lamellae extend up to periphery of the spore (perispore) and project out as narrow, nearly truncate, 19–28, up to 5 μm high spines (Figs. 15, 40). The proximal faces of the spores have papillate to verruform ornamentation consisting of thick and low lamellae scattered throughout in the form of small broken pieces (Figs. 19, 20, 23, 40, 47–49), sometimes they anastomose and form a broken triradiate mark (Figs. 19, 48).
Fig. 22-38. *Fossombronia wondraczekii* var. *loitlesbergeri*. – Fig. 22, 23. Distal and proximal views of the spore respectively. – Fig. 24. Spore with emerging germ tube. – Fig. 25. Formation of first transverse spetum. – Fig. 26-30. Formation of several successive transverse septa and filament. – Fig. 31-33. Formation of germdisc. – Fig. 34. Unusually long and three-celled filament. – Fig. 35. A portion of the same with bulbous and swollen apex (after one week). – Fig. 36. Branched germ filament. – Fig. 37. Germ filament with four-celled disc formed at apex. – Fig. 38. Juvenile gametophyte differentiated into young leaves and stem with rhizoid.
Elaters: The Elaters are 130–230 µm long, 5–8 µm wide, reddish-brown, narrowly elongated, slender, well developed, rarely branched, 2–3 spirate, spirals less pigmented and loosely to compactly twisted with obtuse ends (Fig. 21).

Spores under SEM: The SEM studies of the spore also reveal similar sporoderm pattern as observed under LM (Fig. 39). The basic architectural components of the sporoderm on distal face of the spore are the lamellae (or ridges) which usually anastomose to form angulate meshes or the lamellae become forked and form parallel ridges.

The lamellae are usually broad and gradually taper towards the distal end with 1–2(-3) wart-like blunt projections in the centre of the mesh-lumina or, at times in between the two parallel ridges (Fig. 41). The proximal faces of the spore bears a conspicuous tri-radiate ridge (Fig. 42) which is inconspicuous under LM (Fig. 40). The spines at the periphery of the spore (projections of the lamellae at the spore margin) which are distinct under the LM (Figs. 39, 40) were difficult to locate under SEM (Figs. 41, 42).

3.1. Discussion

The chief characteristics of *F. wondracekii* var. *loitlesbergeri* include monoecious sexuality, tuberous stem apices, presence of mycorrhiza in the central cells of the axis, highly convoluted and irregularly lobed leaves aggregated at the stem apices, campanulate and irregularly lobed pseudoperianth, 2–3 stratose capsule wall with nodular to continuous and sheet-like thickening in the inner layer cells, reticulate spores of 38–45 µm in diameter with 5–9 meshes across the distal face having 1–2 wart-like projections in the mesh-lumina, well developed perispore having 19–28 spines, slender and well developed 2–3 spirate elaters with less pigmented and loosely twisted spirals.

Of the three groups of Indian species of *Fossombronia* categorized by SRIVASTAVA & UDAR 1975a *F. wondracekii* var. *loitlesbergeri* closely approaches *F. wondracekii*-type which includes *F. kashyapii*, *F. wondracekii* var. *wondracekii*, *F. pusilla* and *F. himalayensis*. The plant size (4–10 mm long), hyaline to pale yellow rhizoids, and tuberous apex are by and large identical in all these species. MACVICAR 1926 suggested its similarity with *F. w. var. wondracekii* except for the violet coloured rhizoids in the latter one. *F. w. var. wondracekii* differs in the absence of mycorrhiza which need reinvestigation, while *F. kashyapii* can be easily separated in having more longer than wide (19–163 × 19–53 µm) leaf cells and plicate pseudoperianth (SRIVASTAVA & UDAR 1975a). *F. wondracekii* var. *loitlesbergeri* has more wider than long (23–64 × 24–98 µm) leaf cells and aplicate pseudoperianth.
Another very common species, *F. himalayensis* also shows some affinity with *F. wondraczekii* var. *loitlesbergeri* and both can be easily distinguished.

The other two Indian species, belonging to *F. cristula*-type (*F. foreaui* and *F. cristula*) and *F. indica*-type also resemble *F. wondraczekii* var. *loitlesbergeri* in the above features but the species under *F. cristula*-type differ from the latter in having large leaves, plicate pseudoperianths and reduced elaters. The stem in *F. cristula* and *F. indica* is not tuberous at apex. *F. indica* however differs in having vinous-purple rhizoids.

All the species of *F. cristula*-type are monoecious and *F. indica*-type is dioecious while those of *F. wondraczekii*-type show both monoecious as well as dioecious sexuality. Thus the present variety approaches *F. wondraczekii*-type so far as monoecious/heteroecious sexuality is concerned.

Apart from the vegetative characteristics and nature of sexuality the present variety shows some sporophytic features including the sporoderm morphology which are highly stable and diagnostic. The capsule wall is 2–3 cell layers thick as compared to generally 2-layered in other Indian species (Srivastava & Udar 1975a), *F. longiseta* has however the same thickness of capsule wall as *F. wondraczekii* var. *loitlesbergeri* (Humphrey 1906).

In reproductive structures the present variety shows affinities with *F. cristula* and *F. foreaui* in monoecious sexuality, spore size, and reticulate distal face of the spore. The latter two, however, differ from the former in having greatly reduced elaters, which are usually arched in *F. cristula* and 1–2 celled in *F. foreaui* having 1(–2) spirals or annular rings and also in lacking wart-like projections in the mesh lumina of the sporoderm in contrast to *F. wondraczekii* var. *loitlesbergeri* which possesses narrowly elongate, well-developed, 2–3 spirate elaters and wart-like projections on the sporoderm. They further differ in the number of spines (projections of the lamellae) at spore margin. *F. cristula* reportedly has 12–21(–25) spines (Udar & Srivastava 1969) which are inconspicuous or absent in *F. foreaui* (Udar & Srivastava 1973).

There are no regularly reticulate spores in *F. wondraczekii* type but the elater characteristics in this as well as in *F. indica*-type correspond with *F. wondraczekii* var. *loitlesbergeri* but it is slightly narrower (5–8 μm wide) in the latter and more broader (8–19 μm) in the former two types.

The number of spines at the periphery of the spore in optical section is reported to be 28–32 in *F. w.* var. *wondraczekii*, 14–18 in *F. pusilla*, and 19–28 in *F. wondraczekii* var. *loitlesbergeri*.

*F. indica* shows similarities with *F. wondraczekii* var. *loitlesbergeri* in spore size and lamellae forming reticulations (on distal face) and much developed elaters. However, the former differs from the latter in dioecious
sexuality, thin and low lamellae and absence of wart-like projections on the distal face of the spore.

4. Sporeling development
(Figures 22-38, 51-55)

The spores cultured on October 14, 1991 showed initial stages of germination in all the four sets containing different concentrations of the culture medium.

The spores after a few days of sowing became pale green and showed an increase in size by absorption of moisture which results into the rupture of the spore coat through the proximal face.

The spores started sprouting on 12th day (i.e. on October 26, 1991) in 100% Knop's medium while in 50% and 25% Knop's media the spores germinated only after 17th day (i.e. on October 31, 1991). However, in distilled water it germinated after about 3 weeks (19 days). The lowest germination percentage (ca. 40%) was observed in spores cultured in distilled water. The highest germination percentage (ca. 86.4%) was observed in 50% Knop's medium, however, ca. 83.3% spores germinated in 100% Knop's solution (see also Table I).

<table>
<thead>
<tr>
<th>S.No.</th>
<th>Media used (conc. of Knop's soln.)</th>
<th>Time of Germination</th>
<th>Number of spores Observed</th>
<th>Number of spores Germinated</th>
<th>Germination %</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>100%</td>
<td>12 days</td>
<td>90 ± 10</td>
<td>75 ± 10</td>
<td>ca. 83.3%</td>
</tr>
<tr>
<td>2</td>
<td>50%</td>
<td>17 days</td>
<td>110 ± 10</td>
<td>95 ± 10</td>
<td>ca. 86.4%</td>
</tr>
<tr>
<td>3</td>
<td>25%</td>
<td>17 days</td>
<td>70 ± 10</td>
<td>50 ± 10</td>
<td>ca. 71.4%</td>
</tr>
<tr>
<td>4</td>
<td>0% (distilled water)</td>
<td>19 days</td>
<td>100 ± 10</td>
<td>40 ± 10</td>
<td>ca. 40%</td>
</tr>
</tbody>
</table>

In majority of the spores the rupturing of sporecoat is followed by emergence of a germ-papilla (as in most Marchantiales) from the proximal face, the papillae at this stage contains numerous chloroplasts and oil globules (Fig. 24), and soon these richly supplied chloroplasts migrate towards the tip as the germ-papilla elongates into a germ-tube. The first wall

Fig. 39-44. Fossombronia wondraczekii var. loitlesbergeri. - Fig. 39. Spore (distal view). - Fig. 40. Spore (proximal view). - Fig. 41. Spore (distal view) under SEM. - Fig. 42. Spore (proximal view) under SEM. - Figs. 43-44. A portion of under SEM. - Scale bars equal 10 µm.

Fig. 45-55. Fossombronia wondraczekii var. loitlesbergeri. - Fig. 45. Inner layer cells of the capsule wall. - Fig. 46. Transverse section of the capsule wall. - Figs. 47-50 Spores. - Fig. 51. Young sporeling. - Figs. 51-54. Advanced stages of the sporeling development. - Fig. 55. Juvenile gametophyte differentiated into young leaves and stem. - In Fig. 45-50 scale bars equal 25 µm, in Fig. 51-55 equal 100 µm.
is laid down transversely dividing the short germ-tube into a basal cell and an upper cell, the latter being packed with dense chloroplasts. The upper cell further divides either by a transverse, or a vertical wall. In sporelings where the germ-tube is predominantly formed, there occurs repeated transverse divisions to form a 5–6 celled filamentous sporeling with exospor attached to the basal cell (Figs. 25–30). This type of filamentous sporeling was also observed in other species of the genus viz., *F. pusilla* (LEITGEB 1877, CHALAUD 1926), *F. longiseta* (HUMPHREY 1906), *F. japonica* (INOUE 1959, NEHIRA 1966) and *F. kashyapii* (SRIVASTAVA & UDAR 1975b).

In some sporelings the first wall is laid down at a very early stage (Fig. 25) and subsequent transverse and vertical divisions in the uppermost cell results in the formation of a cell mass or a multicellular germ-disc (Figs. 31, 33). Ultimately an apical cell with two cutting faces is organised (Figs. 31, 33) which initiates further growth in the sporeling and thus well organised sporelings are formed (Figs. 52, 54) which subsequently become differentiated into a juvenile gametophyte with an axis and leaves.

The juvenile leaves develop laterally, and the first leaf is always transversely inserted. The rhizoids are formed as an elongation of the ventral superficial cells of the juvenile axis and maintain the hyaline pale colour even at maturity.

Some sporelings after nearly 3 weeks of sowing in 50% Knop's medium show a fairly long germ-tube up to 373 μm without any septum and ceases to grow after 4 weeks except for the chloroplasts which aggregate towards terminal end forming a swollen and bulbous apex. Some of the chloroplasts, however, remain aggregated in the middle and the sporeling develop a branch thus forming a branched and aseptate germ-tube (Figs. 34–36). Occasionally transverse and vertical walls are laid down, forming 4 to several celled germ-disc (Figs. 37, 52, 53) somewhat similar to that of *Dumortiera hirsuta* and *Ricciocarpus natans* (see also YANG & HSU 1967).

The stages illustrated (Figs. 22-38, 51-55) have been drawn from 142 days old cultures.

### 5. Conclusions

The present study reveals that *Fossombronia wondraczekii* var. *loitlesbergeri* is different from all other taxa of *Fossombronia* known so far from India and it constitutes a new record for the country. Like other species of the genus sporoderm ornamentation is stabilized in this taxon also. The sporeling development follows three patterns (i) where the germ-papilla develops into a long unsegmented germ-tube bearing germ-disc at the distal end (Figs. 34–37, 53), (ii) where the germ-papilla grows and becomes segmented by several transverse division forming a filamentous germ-tube
(Figs. 29, 30, 51), and (iii) where germ-papilla first divides by a transverse
division but later divides by a transverse or vertical divisions forming a
several-celled germ-disc (Fig. 33). There is no prominent germ-tube in the
last pattern.

The overall pattern of the sporeling development nearly corresponds
to those already described in *F. pusilla* (Leitgeb 1877 and Chalauud 1926,
1929, 1930), *F. longiseta* (Humphrey 1906), *F. japonica* (Inoue 1959, Nehira
1966), *F. cristula* (Udar & Srivastava 1972) and *F. kashyapii* (Srivastava &
Udar 1975b). All the above species show a cell mass formation with the
stray occurrence of filamentous stages which are considered to have devel-
oped because of environmental effect, or overcrowding of the spores (Inoue
1959). In *F. wondraczekii* var. loitlesbergeri, however the germ-tube for-
mation and filamentous sporeling are predominant and only a few spor-
elings show cell-mass formation.

The earlier stages of the sporeling pattern of *F. wondraczekii* var.
loitlesbergeri and other species of the genus previously described seem
rather similar to those of the Marchantialean taxa (Mehra & Kachroo
Chandra 1965, Udar & Kumar 1972, Udar & Srivastava 1968, Srivastava
& Udar 1975b, Udar & Singh 1978). Like *F. kashyapii* the predominance of
germtube formation in this taxon further suggests its affinity with March-
antiales (Srivastava & Udar 1975b) than those with predominance of cell
mass formation as observed in *F. cristula* (Udar & Srivastava 1972).

The filamentous sporeling is generally formed in the Jungermanniales
(Nehira 1966). However, the exospore does not remain attached to the ba-
sal cell of the sporeling at the later stage, and the differentiation of the axis
is usually direct from the sporeling. While in *Fossombronia* the sporeling
pattern corresponds with Marchantiales in which the germ-disc itself de-
velops into a thallus (Inoue 1960, Yang & Hsu 1967).

Among the thalloid anacrogynous taxa filamentous sporelings are
formed somewhat like Jungermanniales as reported in *Riccardia* and Metz-
geria (Inoue 1959), but the thallus is formed in direct continuation of the
sporeling which is never so in *Fossombronia*.

The sporeling development pattern in this taxon further strengthens
theory of derivation of Marchantialean thallus from foliose ancestors
(Mehra 1957) as has also been noted earlier (see also Inoue 1959, Udar &

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