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Systematic Studies Regarding the Order of Cell Division in Jungermanniales

I. The Mode of Cell Division in the Gametophyte of Jungermannia

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Abstract The mode of cell division at the stem-apex in *Jungermannia tsukushiensis* (AMK.)AMK. is observed, and it is found that Segment **I** and Segment **II** undergo the division of **F**-type, and that Segment **III** undergoes the division of **E**-type.

Examining the models of cell division in three segments (Segment **I**, Segment **II** and Segment **III**), the modes of cell division in the stem-apex of Jungermanniales are classified into six types (Tab. 4). The relationship among such modes of division can be shown as in Figure 9, if we suppose the segments have six predetermined division walls, and if some of them make an appearance in step with the development.

Moreover, whether there are two periods in the gametophytic generation, the sporeling period and the gametophytic period, seems to be an important problem for morphogenesis.

Introduction

In the gametophyte of the Bryophyta, it seems that all species have their own specific modes of division in which to form their own specific organization out of a single cell. It seems important to the systematic study that such specific modes of cell division are confirmed.

In the Bryophyta the gametophyte develops from the apical cell of the stem. The gametophytes of the Bryophyta are morphologically classified into three types: the dorsiventral-thallus, the dorsiventral-cormus and the erectile-cormus. The material used for this research is a species of the order Jungermanniales with the gametophyte whose form is dorsiventral-cormus.

The mode of division in the apical cell of the stem is observed, and through the observation, investigation of the position the species occupies in Jungermanniales is attempted.

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Materials and Methods

The samples, *Jungermannia tsukushiensis* (AMAK.) AMAK. (Herbarium of Kanazawa Univ. No. 39067) used for this research have been collected by the roadside of Hakuchooro Street in Kanazawa City.

Preparations are made by the method of using synthetic resin embedding, and by cutting with a JUM ultra microtome.

Observation and Discussion

(1) Earlier stages in the ontogeny of the stem

The apical cell of the stem is tilted toward the dorsal side of the stem and the apical portion of the stem is curved upward, so that the following planes of sections, A-, B-, and C-planes, are utilized (Fig. 1, 2, 3, 4 and 5). The apical cell of the stem cuts off segments on three sides — two lateral (Segment I- and Segment II-series) and one ventral (Segment III-series). Each segment is a polyhedron with five surfaces — three rectangular surfaces and two triangular surfaces (Fig. 6)

Through observation of the sections along the A-, B- and C-planes in Segment I and Segment II, the following diagram is prepared (Tab. 1). The procedure of cell division is as follows: the division wall first formed is anticlinal running from the free surface to one of the side surfaces of the segment. This division is followed by a periclinal division from the surface on the other side of the segment to the middle of the first division wall (Tab. 1-1,2). As a result of the two divisions, the segment divides itself into three cells — two larger outer cells and one smaller inner cell of the segment. Through further periclinal division, each of the outer cell is divided into two cells (Tab.

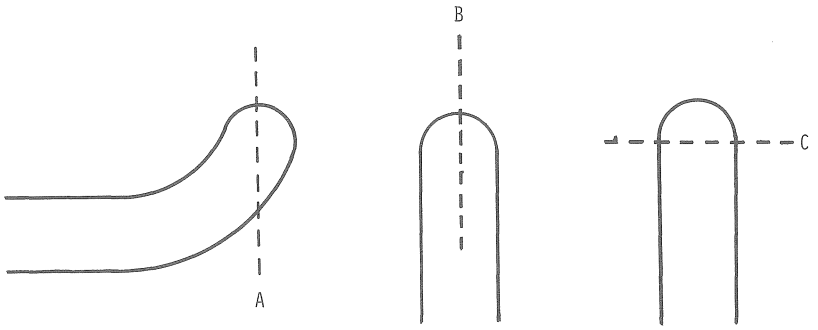


Fig. 1 Three planes of the sections
A-plane: Horizontal longitudinal section of the stem (extending from side to side)
B-plane: Vertical longitudinal section of the stem (extending from dorsal to ventral)
C-plane: Transverse section of the apical portion of the stem

1-3). These five cells are stratified; two cells in the outermost, one cell in the innermost part, and two cells in the mediate between them. This series of four divisions was termed **PGS** (Perklinal geneigt geschnittenen Furchungsgesichter)-Type by KAWAI (1974).

The two outermost cells are the initials of a lateral leaf, and give rise to a lateral leaf through several periclinal and longitudinal divisions. The two mediate cells are the cortical initials and through a transverse anticlinal division, these cortical initials give rise to the epidermal tissue and the cortical tissue (Tab. 1-4). The innermost cell is the initial of the central tissue, and give rise to the central tissue which can be observed in two rows on the A-plane (Tab. 1-5).

Fig. 2 Observation of the sections along the A-plane in the apex of stem ×300

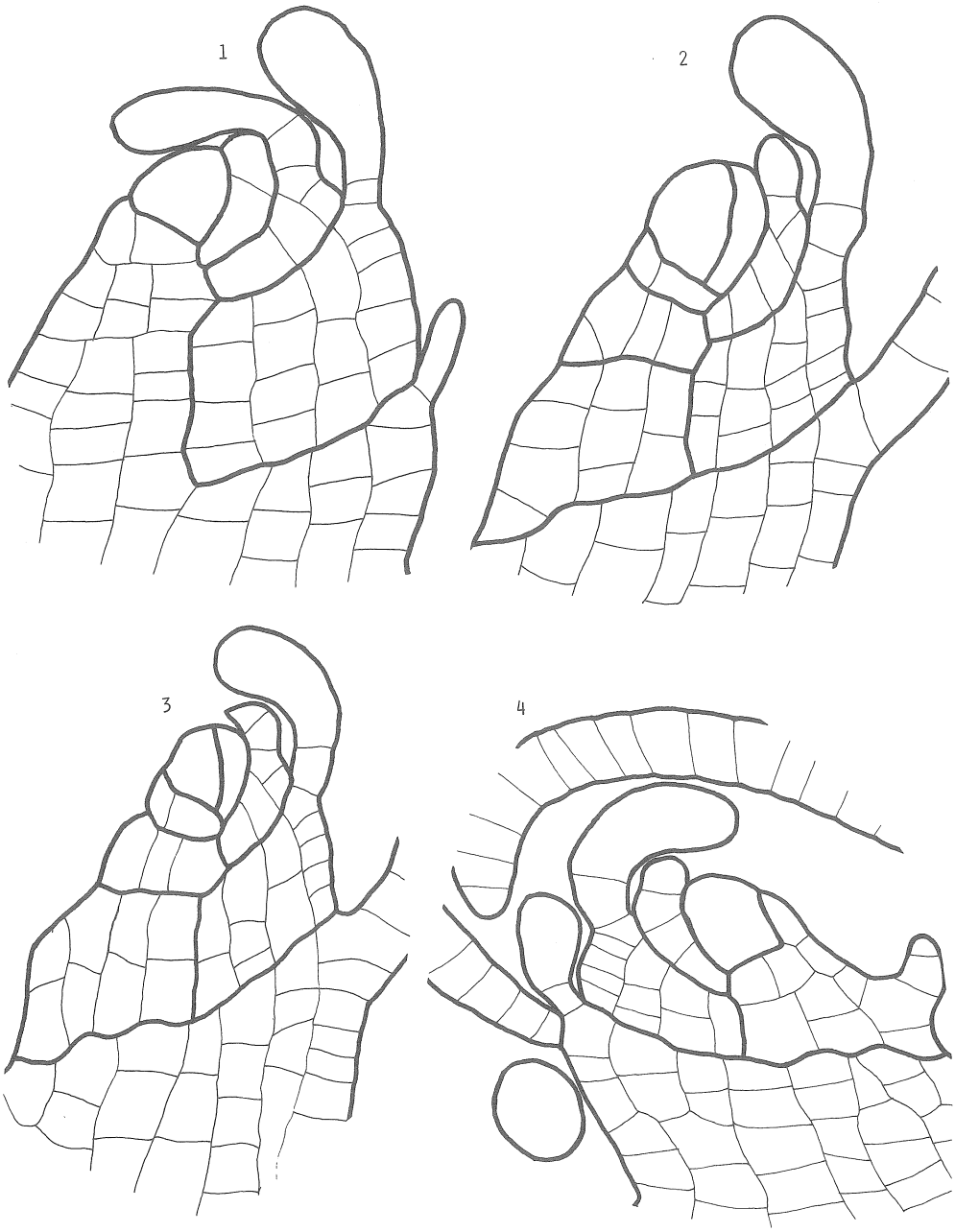


Fig. 3 Observation of the sections along the B-plane in the apex of stem ×300

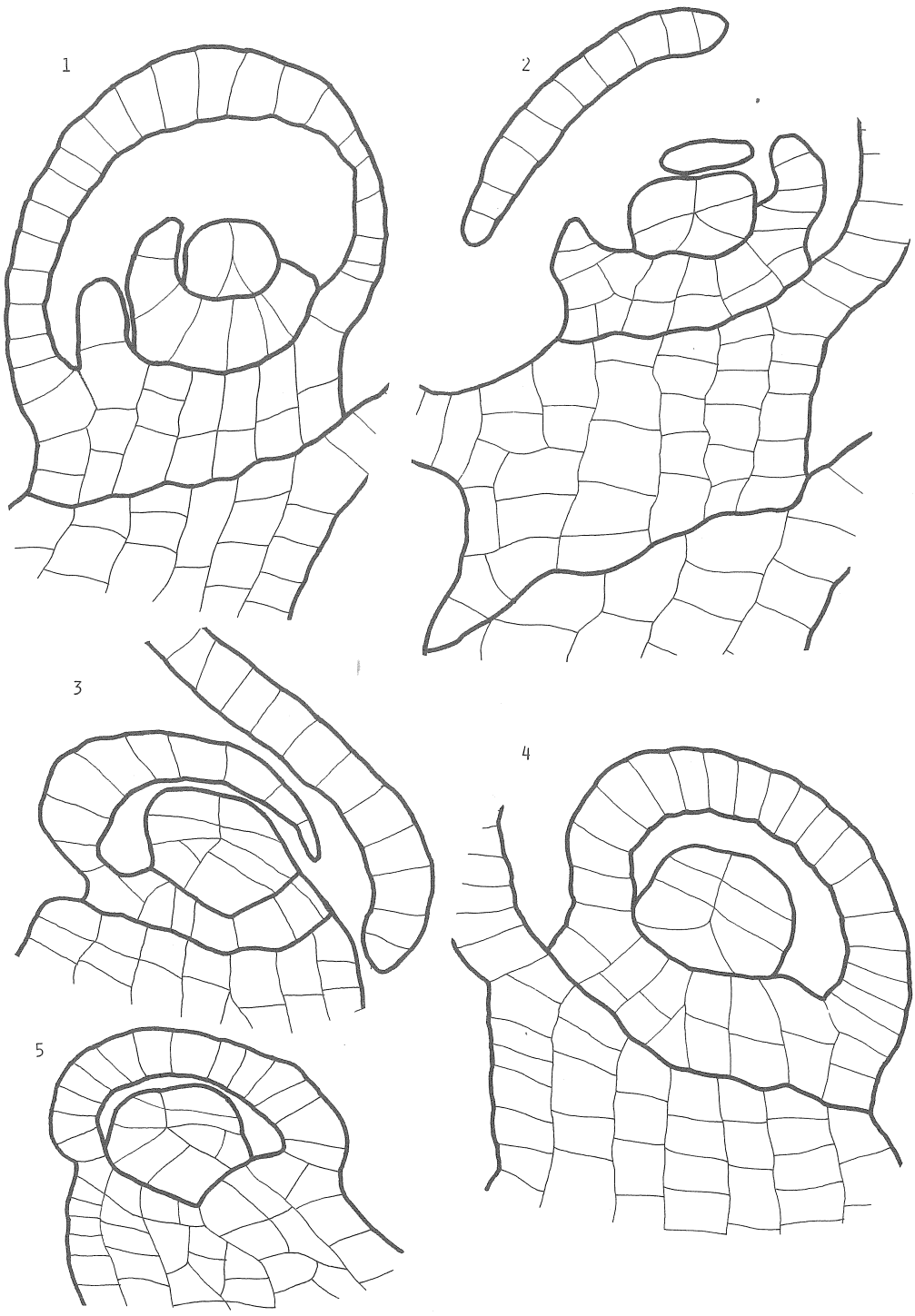


Fig. 4 Observation of the sections along the B-plane in the apex of stem ×300

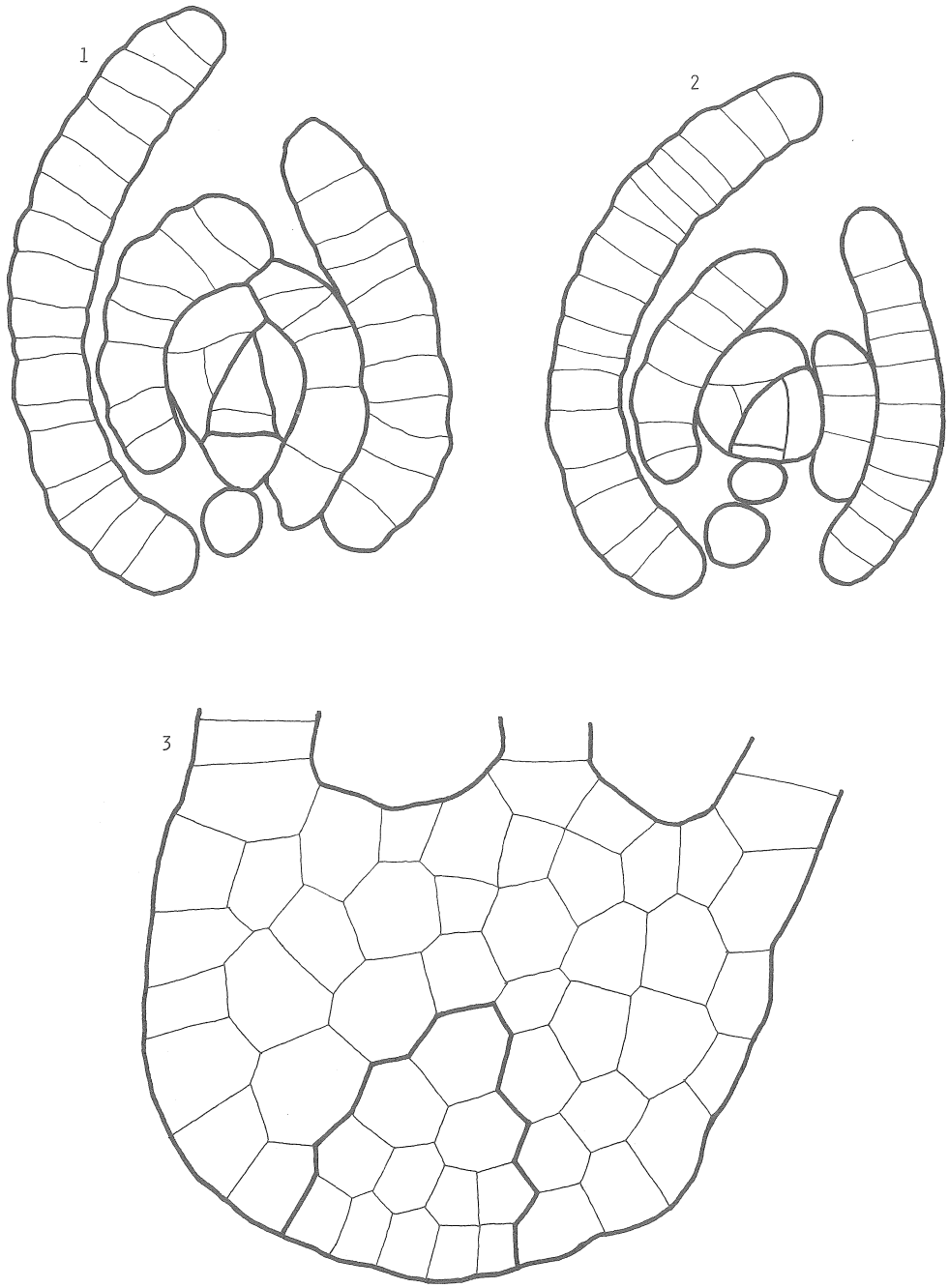


Fig. 5 Observation of the sections along the C-plane in the apex of stem ×300

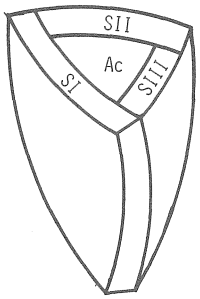


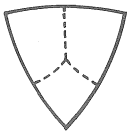
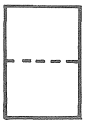
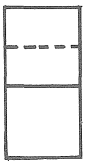
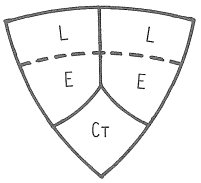
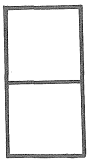
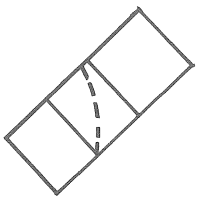
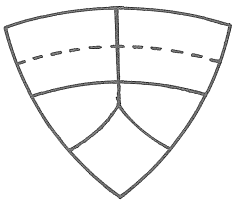
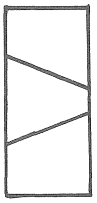
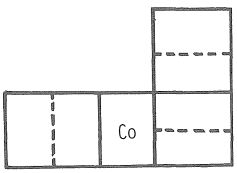
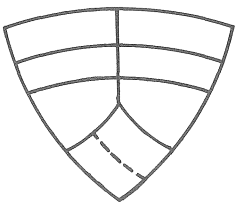
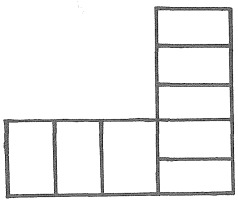
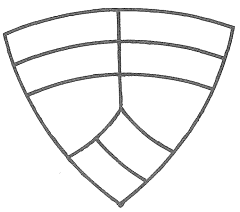
Fig. 6 Diagram of the apical cell with three segments
Ac : Apical cell SI : Segment I
SII : Segment II SIII : Segment III

In Segment **III** through the observation of the sections along the **A**-, **B**- and **C**-planes, the following diagram is made (Tab. 2). The procedure of cell division is as follows: the division wall first formed is periclinal, running from one of the side surfaces to the other side surfaces of the segment (Tab. 2-1, 2). Next, the segment undergoes a few more divisions, and the underleaf-, epidermal-, cortical- and the central tissue-initials are formed (Tab. 2-3, 4). The underleaf initial gives rise to a specialized underleaf, of which the uppermost cell is quite large compared with the other cells. The epidermal- and the cortical-initials respectively turn into the epidermis and the cortex of the stem (Tab. 2-5). The initial of the central tissue gives rise to the central tissue (Tab. 2-6).

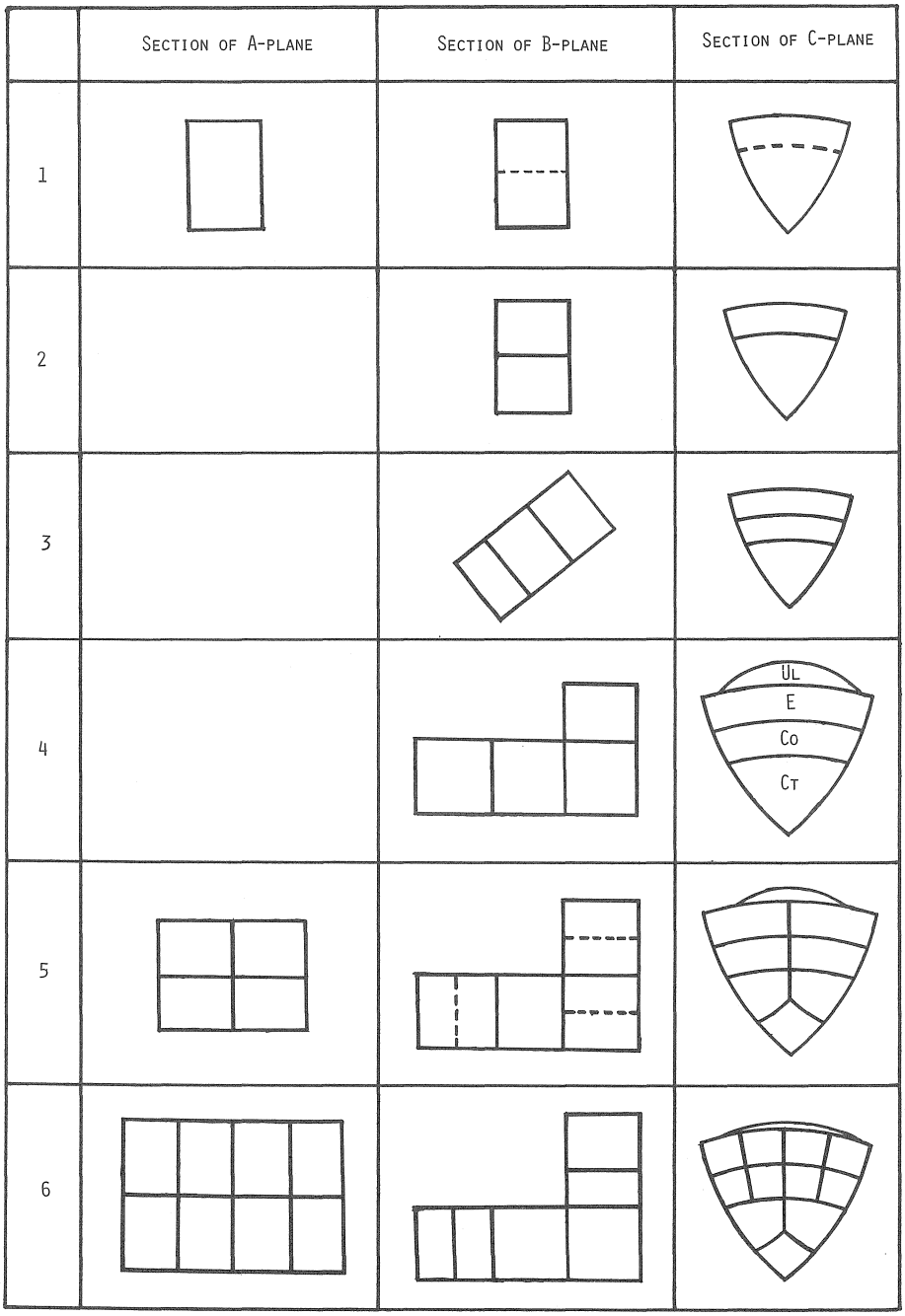
(2) Discussion

In the genus *Jungermannia* the earlier process of division in the apical cell of the stem is similar to that in the other genera of Jungermanniales. That is, the process of division in Segment **I** and Segment **II** is different from that in Segment **III**. And then the cutting faces of Segment **I** and Segment **II** are much broader than that of Segment **III**. These characteristics resemble the ones indicated in *Radula*, *Scapania*, *Tylimanthus, Perssoniella* and *Pleurozia* by CRANDALL (1969). As mentioned above, in the stem of *Jungermannia* the mode of division for Segment **I** and Segment **II** is named **PGS**-type. The mode of **PGS** has been seen in *Pleurozia*, *Radula*, *Scapania*, *Perssoniella*, *Tylimanthus*, *Frullania* and *Bazzania* of Jungermanniales (CRANDALL 1969). In *Jungermannia* the periclinal division of Segment **III** is similar to the pattern of development in *Radula*, *Scapania*, *Tylimanthus*, *Perssoniella* and *Pleurozia*. However, the underleaf initial, which is observed in *Jungermannia*, does not develop in these genera (CRANDALL 1969).

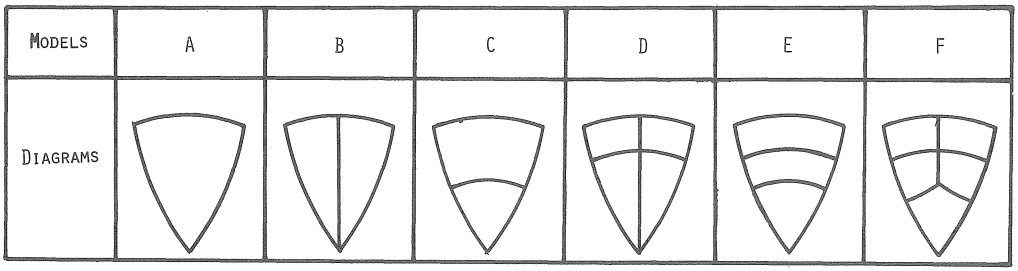
The models of cell division in all segments are illustrated in Table 3. In Model **A**, the segment is only one cell. In Model **B** the segment undergoes a longitudinal division forming two cortical initials. In Model **C** the segment undergoes a periclinal division forming an inner central tissue initial and an outer cortical initial. In Model **D**, the segment undergoes a longitudinal division and a periclinal division forming two cortical initials and two leaf initials. In Model **E**, the segment undergoes two periclinal divisions

	Section of A-plane	Section of B-plane	Section of C-plane
1			
2			
3			
4			
5			

Tab. 1 Diagrams of the manner of cell division in Segment I and Segment II
L : Leaf initial E : Epidermal initial
Co : Cortical initial Ct : Central tissue initial



Tab. 2 Diagrams of the manner of cell division in Segment III
UL : Underleaf initial E : Epidermal initial
CO : Cortical initial CT : Central tissue initial



Tab. 3 The six models of cell division
Model A: The segment is only one cell.
Model B: The segment undergoes a longitudinal division forming two cortical initials.
Model C: The segment undergoes a periclinal division forming an inner central tissue initial and an outer cortical initial.
Model D: The segment undergoes a longitudinal division and a periclinal division forming two cortical initials and two leaf initials.
Model E: The segment undergoes two periclinal divisions forming an innermost central tissue initial, a middle cortical initial and an outermost leaf initial.
Model F: The segment undergoes PGS-divisions forming an innermost central tissue initial, two middle cortical initials and two outermost leaf initials.

forming an innermost central tissue initial, a middle cortical initial and an outermost leaf initial. In Model F, the segment undergoes PGS-divisions forming an innermost central tissue inital, two middle cortical initials, and two outermost leaf initials.

Considering the matter with respect to the models of three segments (Segment I, Segment II and Segment III), the modes of cell division in the stem-apex of Jungermanniales are classified into six types.

Type I: Segment I and Segment II are first divided longitudinally and then periclinally (Model D). Segment III is divided by a wall parallel to the free surface of the segment; an initial of the central tissue is formed in the inner side, and the cortical initial in the outer.

Type II: The same manner of cell division as Type I occurs in Segment I and Segment II, but Segment III develops by a series of two periclinal division into an underleaf initial, cortical initial and an initial of the central tissue.

Type III: Segment I and Segment II undergo PGS divisions. Segment III consists of single cell (Segment III is left undivided).

Type IV: Segment I and Segment II undergo PGS divisions, and Segment III is divided periclinally.

Type V: Segment I and Segment II undergo PGS divisions, and Segment III begaves the same way as Type II.

Type VI: Segment I, Segment II and Segment III undergo PGS divisions (Tab. 4).

Judging from these six types, Segment I and Segment II first undergo a longitudinal division, and then in some genera each segment-half undergoes a periclinal division. In some other genera, Segment I and Segment II undergo PGS divisions. Segment III, however, undergoes a periclinal division or a series of two periclinal divisions in some genera, and in some other genera Segment III undergoes PGS divisions.

Type	Segment I	Segment II	Segment III	Genus name	Observer
1	D	D	C	Cololejeunea	B.J.Crandall(1969)
2	D	D	E	Colura Diplaiolejeunea	B.J.Crandall(1969)
3	F	F	A	Pleurozia	B.J.Crandall(1969)
4	F	F	C	Radula Scapania Perssoniella Tylimanthus	B.J.Crandall(1969)
5	F	F	E	Jungermannia	K.Tomioka(1978)
6	F	F	F	Frullania	B.J.Crandall(1969)
				Bazzania	R.E.Stotler(1969)

Tab. 4 The manner of cell division at the early stage of the gametophyte in the genera of Jungermanniales

In comparing the mode of cell division in Segment I and Segment II with those of Segment III, cann't we illustrate the relationship between them as in Fig. 7? In Jungermanniales, the relationship among the modes of division of Segment I and Segment II may be A–B–D–F, and the relationship among the modes of division of Segment III may be A–C–E–F.

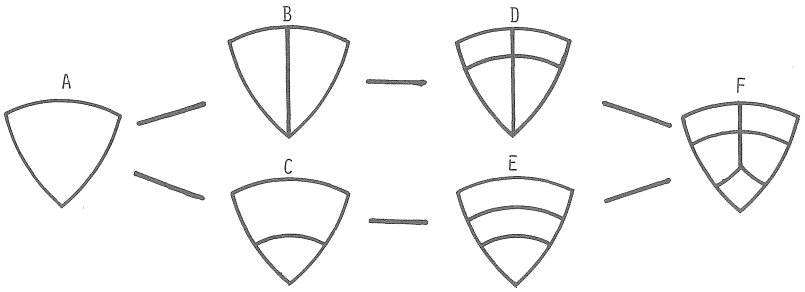


Fig. 7 Relationship between Segment I and II and Segment III in the manner of cell division
Segment I and II : A—B—D—F Segment III : A—C—E—F

The six predetermined division walls built up at the division stage of a segment are shown in Figure 8. If these division walls truly exist, a segment would have six predetermined division walls ($\mathbf{a}_1$, $\mathbf{a}_2$, $\mathbf{b}_1$, $\mathbf{b}_2$, $\mathbf{c}_1$, $\mathbf{c}_2$, and $\mathbf{c}_3$,) and some of them would make appearance in step with the development. And if this supposition is valid, it seems that the six models of cell division in Table 3 are reduced to those of cell division in Table 5, and that the relationship among the segments in Figure 7 is appreciated as that in Figure 9. And the relationship between the **A-B-D-F** and **A-C-E-F** described in Fig. 9 may be more readily understood than that in Fig. 7.

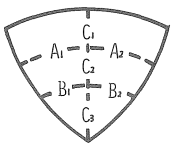
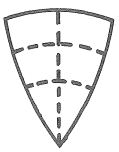
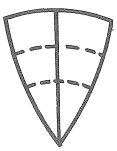
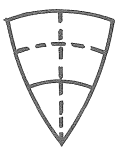
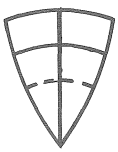
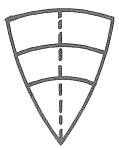
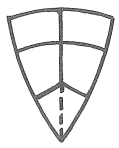


Fig. 8 Six simplified models of cell division
A_1, A_2 : The periclinal division walls separated the leaf initials
B_1, B_2 : The periclinal division walls separated the cortical initials
C_1, C_2, C_3 : The radial division walls symmetrically divided into the leaf initial, cortical initial and the central tissue initial

MODELS	A	B	C	D	E	F
DIAGRAMS						

Tab. 5 Diagrams applied the predetermined division walls to the Table 3
Model A: There is no differentiation yet.
Model B : There are C_1, C_2, C_3 differentiations.
Model C : There are B_1, B_2 differentiations.
Model D : There are C_1, C_2, C_3 and A_1, A_2 differentiations.
Model E : There are B_1, B_2 and A_1, A_2 differentiations.
Model F : There are C_1, C_2, B_1, B_2, A_1, and A_2 differentiations but the C_3 division wall which symmetrically divides the central tissue is not differentiatd.

There have been some reports that the mode of cell division at the early period of the gametophyte is different from that of the following later period (CRANDALL 1969). The pattern of development that occurs in the sporeling, after the formation of the apical cell with three cutting faces, appears to be basically the same in many genera of Jungermanniales. The lateral segments (Segment **I** and Segment **II**) undergo a longitudinal division, and one or both of the cells are periclinally divided. The ventral segment (Segment **III**) is divided by a wall parallel to the free surface of the segment, and in some stems which possess primitive underleaves, an underleaf is produced by a periclinal division (Tab. 6). In some genera of Jungermanniales the Segment **I** and the

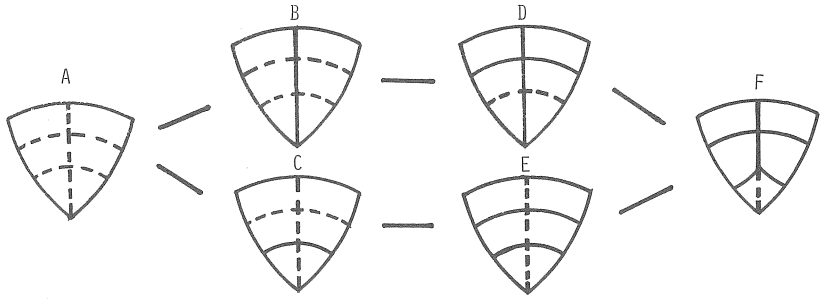
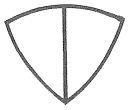
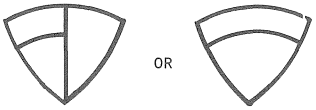
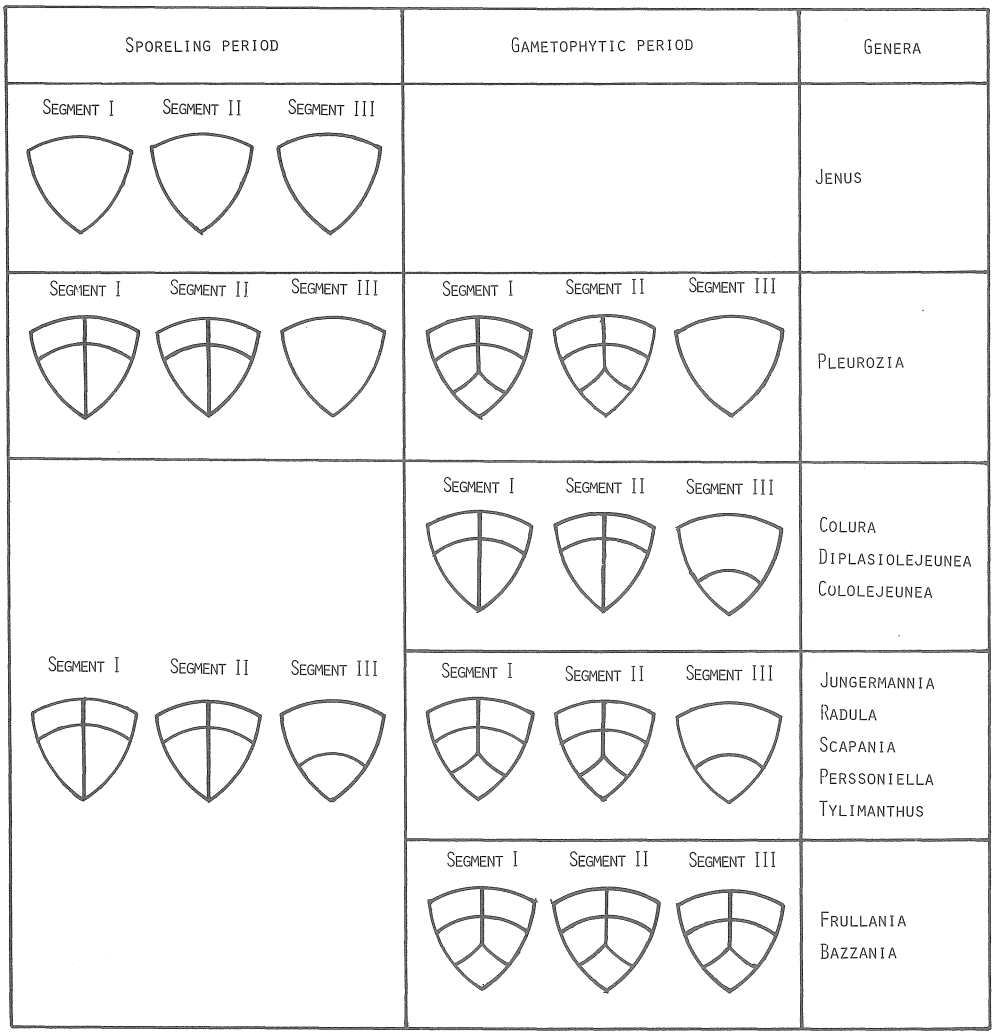


Fig. 9 Diagrams applied the predetermined division walls to Figure 7
The soil lines show the actual division walls and the dotted lines show the predetermined division walls

	SEGMENT	FIRST DIVISION	SECOND DIVISION
LATERAL SEGMENT			 OR
VENTRAL SEGMENT			

Tab. 6 The manner of cell division in the sporeling period
Lateral segments: Segment I and Segment II
Ventral segment: Segment III
This diagram is made on the basis of the observations made by CRANDALL (1969).

Segment **II** undergo divisions of **A**-, **B**- and **D**-types, and the Segment **III** undergoes divisions of **A**-, **C**- and **E**-types in the sporeling period. The Segment **I**, Segment **II** and the Segment **III** for the sporeling period in their modes of division resemble those for the gametophytic period. However, is there not a distinguishable difference between the sporeling period and the gametophytic period ? Judging from this point of view, the affinity regarding the mode of division for the sporeling period and the gametophytic



Tab. 7 A tentative mutual relationships among the patterns of cell division in Jungermanniales

period in some genera of Jungermanniales is proposed as in Table 7.

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