湖北双蝴蝶小孢子发生及雄配子体发育

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摘 要：首次报道了湖北双蝴蝶小孢子发生和雄配子体发育。主要结果如下：花药四室；药壁发育为双子叶型；绒毡层异型起源，属腺质型绒毡层，药隔处的绒毡层细胞形成类胎座，其余部位的绒毡层细胞仍为一层细胞；花药成熟时，药室内壁纤维状加厚且柱状伸长，表皮细胞减缩退化，纤维状加厚不明显。小孢子母细胞减数分裂为同时型，四分体排列方式主要为四面体形，少数为十字交叉形；成熟花粉多为 2-细胞型，偶见 3-细胞型，具三萌发孔。

关键词：湖北双蝴蝶；小孢子；雄配子体；龙胆科

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Genesis of microspore and the development of male gametophyte in *Tripterospermum discoideum*

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Abstract: The present paper firstly reports the microsporogenesis and the development of male gametophyte in *Tripterospermum discoideum*. The main results can be concluded as follows: Anthers are tetrasporangiate. The development of anther walls conforms to the Dicotyledonous type and comprises of epidermis, endothecium, one or two middle layers and tapetum at the mature stage. The tapetal cells have dual origin and belong to the glandular type. The tapetal cells on the connective side show radial elongation or periclinal division and intrude into the anther locule to form placenoids; The endothecium persists and its cells become pillar and fibrous, and the epidermis degenerates. Cytokinesis at meiosis of microsporocytes is of the simultaneous type and most of microspore tetrads are tetrahedral, there are still a few other types, such as dilateral. Pollen grain is mainly 2-celled type when shed, occasionally 3-celled type, and has three apertures.

Key words: *Tripterospermum discoideum*; microspore; male gametophyte; Gentianaceae

Tripterospermum discoideum belongs to *Tripterospermum* of Gentianaceae. This twining perennial herb distributes primarily in Hubei, Shanxi and Hunan province, and the west of Hunan is the mostly station (He *et al.*, 1988). *T. discoideum* has been widely used in curing furuncle, mastitis, trauma, bleeding, and fracture at civilian of some provinces that in the middle and west of China, such as Hunan, Hubei, Shanxi and Guizhou. In recent years, the wild resources decrease annually with the rising collections by some medical factories in the east area. Many factories in the west of Hunan province have been trying to cultivate *T. discoideum* by artificial introduction. However, it is always defeated at last on account of having little knowledge about its life history, sexual reproduction and asexual reproduction. Though there are lots of

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studies on embryo of Gentianaceae in present (Zhu *et al.*, 1989; Li *et al.*, 1994, 2006; Liu *et al.*, 1996a, b, 1997, 1998; He *et al.*, 1999a, b, 2000; Xue *et al.*, 1999a, b, 2002a, b; Xue, 2005), but there are little investigations on *Tirpterospermum* in China (Chen *et al.*, 1999; 2000) and this genus has never been embryologically investigated. The objective of the present paper is to accumulate embryological data of *Tirpterospermum* in order to offer evidence for systematic taxonomy and conservation biology by studying on the microsporogenesis and the formation of male gametophyte of *T. discoideum*. Furthermore, it will provide basic data that is beneficial for introduction and artificial cultivation of this genus.

1 Materials and Methods

Material investigated for the present study was collected from Gaowangjie Forestry Centre of Guzhang County of Xiangxi Tugia and Miao Autonomous, Hunan province, China (110°04′E, 28°38′N, Alt: (792±13) m). The voucher (Long hua178) is deposited in the Herbarium of Biological Resources and Environmental Science Department of Jishou University. Specimen identifier is Zhang Dai-Gui (Biological Resources and Environmental Science Department of Jishou University).

Flower buds and flowers at different stages of development were collected and fixed in the modified FAA (50% alcohol : glacial acetic acid : formaldehyde =89 : 6 : 5). The fixed materials were stained in Ehrfich's hematoxyfin. The materials were embeded in paraffin after being washed with water, dehydrated in ten grades of alcohol and transparentized with five grades of xylene, and serially sectioned at the thickness of 5 — 8 μm by Microm. Sections were mounted on slides in Neutral balsam, observed and photographed with Leica DM2000.

2 Observations

2.1 Microsporogenesis

Flower of *Tirpterospermum discoideum* is bisexual and has five stamina. Anthers are tetrasporangiate. In the early phase of budding, the primordium of flowers forms perianth and staminate primordium in sequence. From observations in the transverse section of a young anther derived from staminate primordium, the surface of anther is a layer of epidermal cells, inside which there are a group of cells which divided actively. With the development of anther, four patches of tissue are differentiated from the main mass of cells. The archesporial cells in each patch, which are differentiated below the epidermis, are recognizable by their large size, conspicuous nuclei and radial elongation. These cells divide periclinally (Plate Ⅰ: 2) to produce primary parietal cells towards outside and primary sporogenous cells towards inside (Plate Ⅰ: 3).

2.1.1 The formation and differentiation of the anther wall　The primary parietal cells undergo periclinal division to produce outer layer and inner layer forming three layers including the epidermis. The outer cells formed a subepidermal endothecium and one middle layer by periclinal division (Plate Ⅰ: 4). At the time when secondary sporogenous cells appear, the mature anther wall consists of four layer cells: epidermis, endothecium, one middle layer and one tapetum (Plate Ⅰ: 5), but a few (about 5%) consists of five layer cells: epidermis, endothecium, two middle layers which are both from the outer cells and one tapetum (Plate Ⅰ: 6). It indicates that the outer layer derived from primary parietal cells to produce endothecium and middle layer by divisions whereas the inner layer directly matures into tapetum. According to Davis's (1966) compartmentalization, the development of microsporangial wall conforms to the Dicotyledonous type.

The innermost layer of anther wall is tapetum with dual origin that mainly from the inner cells and partly from the connective cells. Tapetum starts to differentiate at phase of early sporogenous cells and its cells gradually augment while its protoplasm gradually manifold in the course of development of microspore mother cells. The tapetal cells increase attaining the maximal development at phase of microsporocytes with the feature of glandular cell. Here, the tapetal cells are much larger than those of the outer and present close

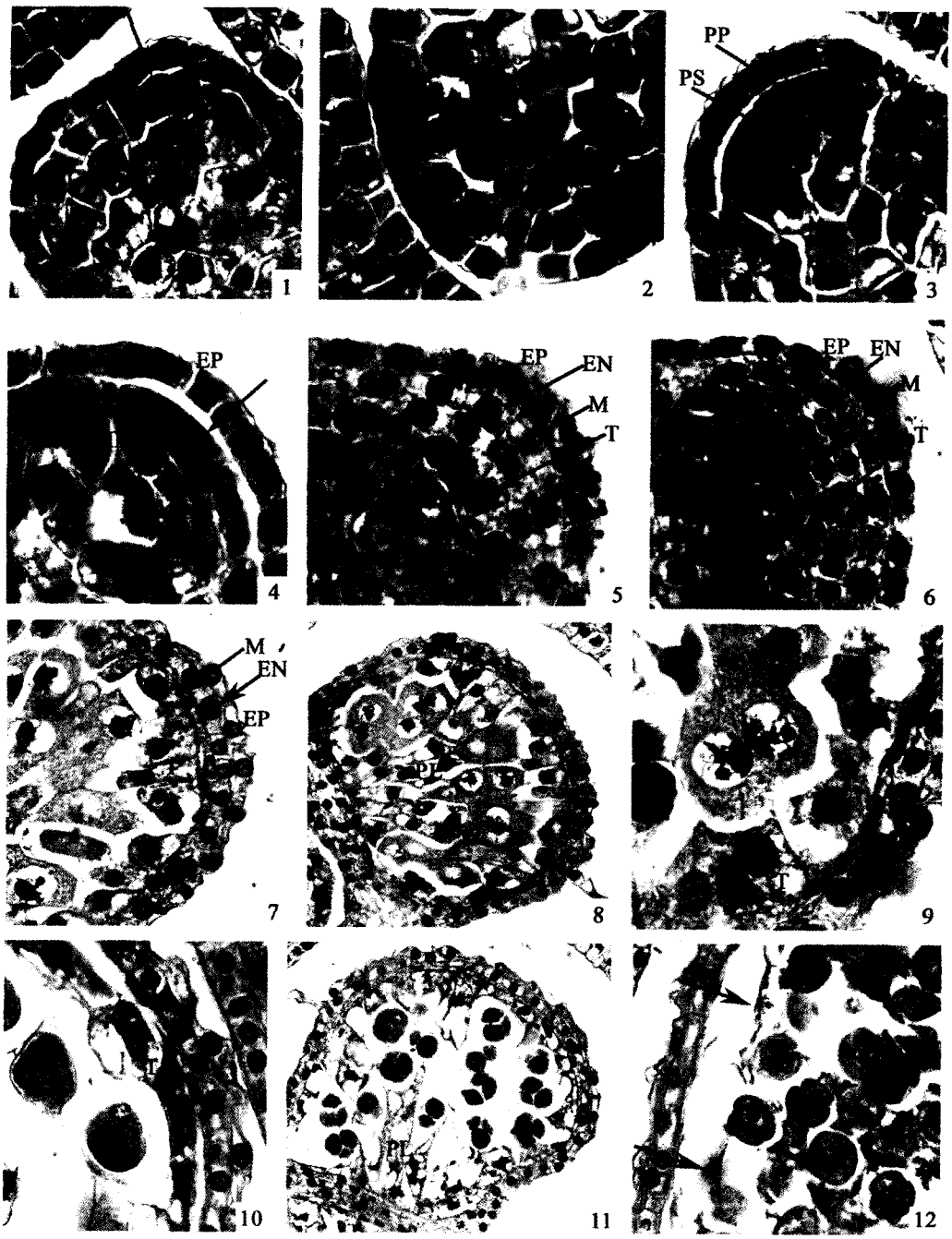

Plate I **EP.** Epidermis; **EN.** Endothelium; **M.** Middle layer; **PL.** "Placentoid"originating from the tapetum cells; **PP.** Primary parietal cell; **PS.** Primary sporogenous cell; **SS.** Secondary sporogenous cell; T. Tapetum. **1.** Male archesporium(↑)×1000; **2.** Microspore archesporial cells dividing(↑)×1000; **3.** Primary parietal cells(PP)and primary sporogenous cells(PS)×1000; **4.** Primary parietal cell dividing(↑)×1000; **5.** Four layers anther wall in the time of secondary sporoginous cell×1000; **6.** Five layers anther wall in the time of secondary sporoginous cell×1000; **7.** Tapetum cells in the time of microspore mother cells(T)×1000; **8.** Tapetum cells protruding the anther chamber in the time of microspore mother cells ×400; **9.** Tapetum cells with two nuclei(T)×1000; **10.** Disintegrating tapetum cells at the telophase Ⅱ of meiosis×1000; **11.** Stage of microspore tetrads,disintegrated tapetum×400; **12.** Trails from disintegrated tapetum(↑)×1000.

squareness(Plate Ⅰ: 7). Cells of the tapetum on the connective side show periclinal divisions and intrude into the anther locule. At this region where division occurs,the tapetum becomes two or more layers and appears as"quasi-placenta"or"cross-grid"(Plate Ⅰ: 8). It is observed that most of tapetal cells are uninucleate,

while it is also observed that minority are binucleate (Plate Ⅰ:9). Tapetal cells start to separate from each other when the development of microsporocytes are approximately over, degenerate obviously when miosis of microsporocytes are approximately over (Plate Ⅰ: 10) and disaggregate intensively at their original site in the time of tetrads. The degenerated nuclei of tapetal cells in the anther chamber are formed by the same layer cells that enter it at early time but they are not formed by degenerated tapetal cells of circumference that enter it(Plate Ⅱ:11). It is not found that amalgamation occurs and periplasmodium appear when tapetal cells disaggregate from large numbers of sections. The tapetal cells are single till disappearing. At late period of uninucleate microspore, there are only few degenerated vestiges left (Plate Ⅰ: 12). Therefore, the tapetum is similar to the glandular type.

The middle layer accomplishes differentiation at time of secondary sporogenous cells, including one or two layers, of which cells are of smaller size, bigger nucleus and flat rectangle(Plate Ⅰ:5,6). The middle layer gets degenerated during meiotic division of microsporocytes(Plate Ⅱ:13).

The endothecium comes into being at time of secondary sporogenous cells while cells arrange close and present strip shape (Plate Ⅰ: 5). The endothecial cells are most developed when microsporocytes formed (Plate Ⅰ:7) and develop fibrous thickenings from their inner tangential walls anatony and ectad in mature anther at late period of the uninucleate pollen. At time of pollen grains, the fibrous thickenings is very obvious while the outer tangential thin wall is persist(Plate Ⅱ: 14) and this characteristics of the endothecium are helpful for anther dehiscence. The anther wall dehisces and the mature pollens emit when shed with the cells keep on losing water. The reason is that the outer tangential wall without thickening of the cells of endothecium shrinks and caves in.

The epidermis only includes single-layer cells that arrange closely. At time of secondary sporogenous cells, the epidermal cells reach the highest level of development(Plate Ⅰ: 5) and they begin to degenerate at time of microsporocytes(Plate Ⅰ:8). The epidermis only leaves the vestiges at time of anther dehiscence(Plate Ⅱ:15).

2. 1. 2 Microsporogenesis　The primary sporogenous cells undergo mitosis resulting in secondary sporogenous cells(Plate Ⅰ:5,6). In comparing with surrounding wall cells, the secondary sporogenous cells have larger size, greater nuclear-cytoplasmic ratio, dense cytoplasm, and deeper color; moreover, they arrange closely and don't have obvious vacuoles and present polygon. The polygonal secondary sporogenous cells turn into circular microspore mother cells with development (Plate Ⅰ:9). The microsporocytes show distinct difference from the other anther wall cells around, which have larger size and cell nucleus, dense cytoplasm; Moreover, they arrange closely and don't have obvious vacuoles. The microsporocytes undergo meiosis I without cytokinesis (Plate Ⅱ: 16-18), but cytokinesis take place in meiosis Ⅱ of the microsporocytes and the callose wall form simultaneous(Plate Ⅱ:19-21). Most of microspore tetrads are tetrahedral(Plate Ⅱ:22), there are still a few other types, such as dilateral(Plate Ⅱ:23).

2. 2 Male gametophyte

Because of the callosal dissolution, four microspores separate respectively and are released to anther chamber that permeate secretion of tapetum. The microspore just formed has a central nucleus and dense protoplasm, but the cell wall has not been thickened and there is no obvious vacuole in the cytoplasm. With the development of microspores, many small vacuoles appear in the protoplasm(Plate Ⅱ:25), which get together to form a large central vacuole pushing the nucleus to a peripheral position(Plate Ⅱ:26). The microspores divide mitotically so as to form two daughter nuclei. Before long, cytokinesis between the two nuclei follows, results in the formation of a smaller lenticular generative cell closed to pollen wall and a larger vegetative cell with a large central vacuole by a vaulted cell plate(Plate Ⅱ:27). At the time, the germinal aperture and germ furrow of the pollen wall appear which shows that extine starts to be thickened. The generative cell which is close to the pollen wall at the early stage, moves into the cytoplasm of vegetative cell and becomes a naked cell incursion in its cytoplasm with

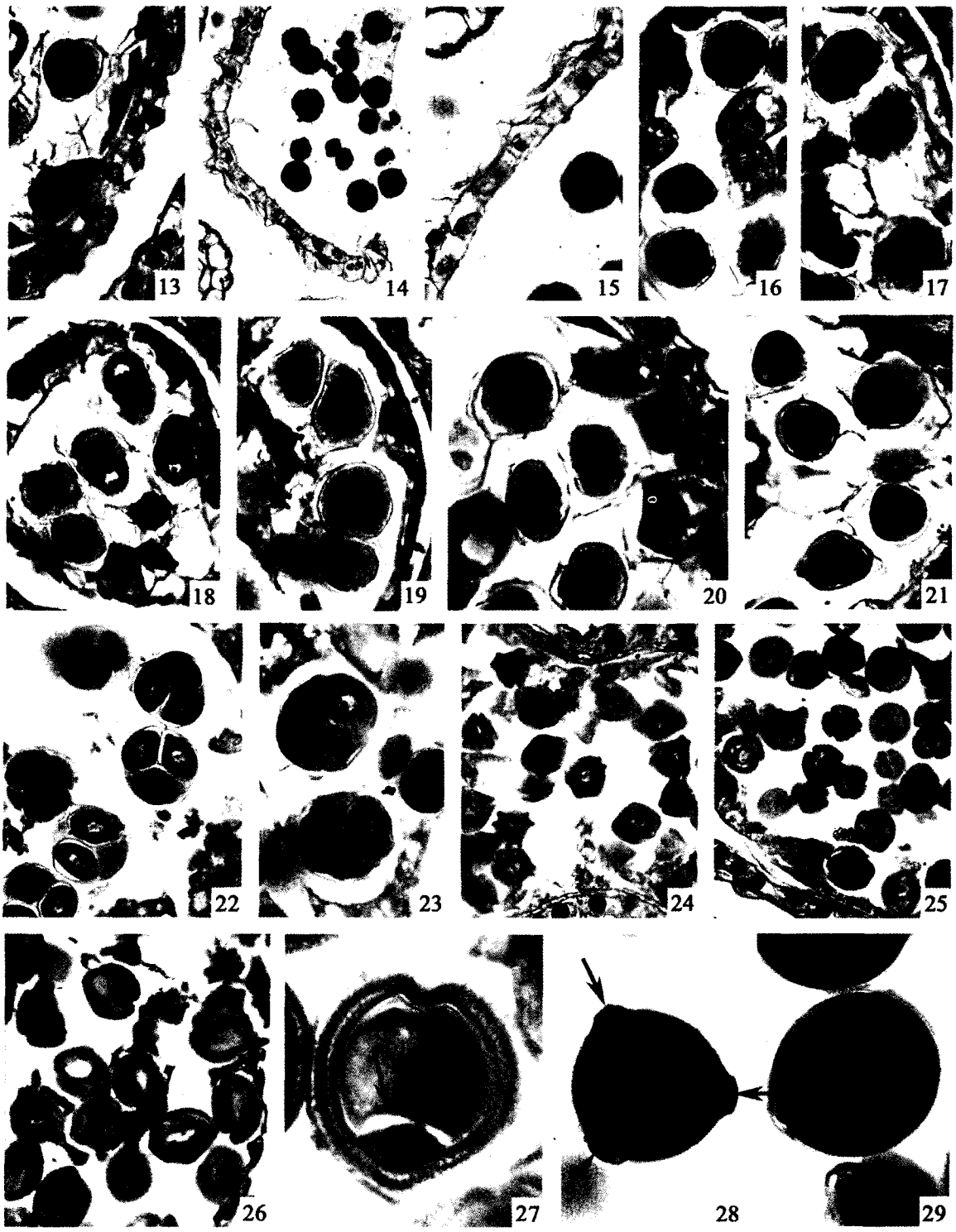

Plate Ⅱ **13.** Degraded middle layer at the telophase of meiosis×1000; **14.** Anther wall of the pollen spread×400; **15.** Anther wall of the time of pollen spread×1000; **16.** Microsporocyte at the metaphase Ⅰof meiosis×1000; **17.** Microsporocyte at the anaphase Ⅰ of meiosis×1000; **18.** Microsporocyte at the telophase Ⅰ of meiosis×1000; **19.** Microsporocyte at the metaphase Ⅱof meiosis ×1000; **20.** Microsporocyte at the anaphase Ⅱ of meiosis×1000; **21.** Microsporocyte at the telophase Ⅱ of meiosis×1000; **22.** Tetrahedral microspore tetrads×1000; **23.** Dilateral microspore tetrads ×1000; **24.** Microspore had just formed from microspore tetrads ×1000; **25.** Some small vacuoles appear, entering the middle of microspore ×1000; **26.** Vacuolate period of uninucleate microspore ×1000; **27.** Early 2-celled pollen, showing obvious cell wall ×1000; **28.** Mature 2-celled pollen and three apertures bourgeoning(↑)×1000; **29.** *Mature 3-celled pollen×1000.*

the cell wall disappears, in a few minutes, generative nuclear moves towards the vegetative nuclear. Up to now, development of the mature 2-celled pollen grains is over(Plate Ⅱ:28). But there are also a few generative nucleuses of pollen grains that give rise to two sperms by further division at time of anther dehiscence. In that case, pollen grains are 3-celled(Plate Ⅰ: 29).

3 Discussion

Tripterospermum is classified to two groups according to the types of fruit, sect. *Platyspermum* and sect. *Tripterospermum* (He *et al.*, 1988; Wu, 1984). The two groups can be differentiated from each other merely at the stage of fruit and can not be differentiated at the stage of flowers. The table 1 shows the comparision of embryological characters between *T. discoideum* and *T. chinense* (Chen *et al.*, 1999) of sect. *Platyspermum* and *T. cordatum* (Chen *et al.*, 2000) of sect. *Tripterospermum*. There are many similar embryological characters from table 1: tetrasporangiate anthers; Dicotyledonous type of anther walls development; glandular tapetum; pillar and fibrous endothecium and degenerated epidermis in the mature anther; simultaneous cytokinesis at meiosis of microsporocytes; tetrahedral microspore tetrads; but there are also some differences in embryology: (1) in the middle layer, most of *T. discoideum* has only one layer, which is similar to *T. chinense*, while there are also minorities have two layers, which is the same as *T. cordatum* of sect. *Tripterospermum*; (2) pollen grain is mainly 2-celled type when shed in *T. discoideum*, but 3-celled in *T. chinense* and *T. cordatum*.

A series of behaviors of anther wall, such as

Table 1　Comparison of embryological characters between *T. discoideum* and some species of *Tripterospermum*

Items	*T. discoideum*	*T. chinense*	*T. cordatum*
Number of anther	Four	Four	Four
Type of anther wall	Dicotyledonous	Dicotyledonous	Dicotyledonous
Epidermis	Underdevelopment	Underdevelopment	Underdevelopment
Endothelium	Derdevelopment and persist	Derdevelopment and persist	Derdevelopment and persist
Layers of middle layer	One or two	two	One
Type of tapetum	Glandular	Glandular	Glandular
Type of cytokinesis	Simultaneous	Simultaneous	Simultaneous
Type of pollen grain	2-celled	3-celled	3-celled

Table 2　The relationships between the development of antheral walls and the microspores

Term of development	Structure of anther wall			
	Epidermis	Endothecium	Middle layer	Tapetum
Term of archesporial cell(s) under epidermis	Rectangular	No	No	No
Term of secondary sporogenous cell	Rectangular	Rectangular	Rectangular, development entirely	Rectangular, uninucleate
Term of microsporemother cell	Start to degenerate	Rectangular, thickening	Start to degenerate	Polygon, binuclear, mild vacuolization
Term of microspore mother cell at metaphase	Degenerating	Rectangular	Degenerating	Start to degenerate
Term of tetrad	Degenerating	Rectangular, mild vacuolization	Degenerate greatly	Degenerating greatly, remnant in anthesac
Term of monokaryotic microspore	Degenerating	Rectangular, vacuolization	Degenerate entirely	Remnant in anthersac
Term of two-cellced pollen	Degenerate entirely	Oblong, antilinal walls are fibrous thickening	—	Degenerate entirely, No remnant in anther sac
Term of anther sac cracking	—	Oblong, antilinal walls are fibrous thickening	—	—

Note: "—" indicates that the structure has degenerated and disappeared.

formation, development, disaggregation and disappearance, shows great physiological value in *T. discoideum*. Disaggregation of each layer is beneficial for the development of other layers. Table 2 shows the relationships between the development of anther walls and the microspores, from which we know that at time of sporogenous cells, the four layers of anther wall differentiate obviously. Before long, cells of the middle layer have started to be used and disappeared until the formation of microspores. Foster *et al.* (1963) indicated that as one or more layers of anther wall went further development, it was stretched and spewed generally. When the anther dehisced, it always was destroyed and difficult to distinguish. However, the other layers of the anther wall are not stretched or spewed when middle layers are disappearing, why? What's more, it is observed that cells of the middle layers reduce and degenerate gradually. Thus, we believe that degenerations of the middle layers are not only the result of stretching and spewing, but also supply nutrition for development of other layers of anther wall, which proved that its behaviors have a great of physiological value.

In recent years, with the help of electron microscope and histochemical method, many authors have proved that there is a cell wall formed between the generative cell and the vegetative cell after mitosis of microspores. But it has been reported differently in various plants on the characters of the wall. In some genus, the cell wall is composed of cellotetrose or pectin (Maruyama *et al.*, 1965; William *et al.*, 1968; Sanger *et al.*, 1971), while it has been considered as callose in some other genus (Heslop-Harrison, 1968; Blackman, 1983; Liu *et al.*, 1997). Similar to other genus of Gentianaceae, *T. discoideum* has a cell wall composed of callose when generative cell is formed, but it will disappear when the generative cell moves into the cytoplasm of vegetative cell. It can be considered as a barrier to isolate the generative cell and the vegetative cell in short time for their development in different ways. Callose makes great contributions not only to the formation of the male gametophyte, but also to microsporogenesis. Wang Fuhsiung (1993) considered that, in the term of sporogenous cells, there were plasmodesmi existed both between each layers of the anther (wall, tapetum, and sporogenous tissue) and neighbouring cells in the same layer. But those connections were cut off gradually when microsporocytes were formed and started to undergo meiosis. At the same time, there was callose collected around the microsporocytes. The later make the microsporocytes separated from the cells of anther wall. It ensures that there are no diploid cells disturbing in the process of the translation from diploid cells to monocaryotic cells by meiosis. With collections of callose, the primary parietal of microsporocytes begins to degenerate, and forms cytoplasmic channels among microsporocytes, cytoplasm and organelles can pass these channels freely. As a result, exchanging of substances and genetic message among the microsporocytes can be more convenient. All of the microsporocytes surrounded by callose remain together to form a symplasm.

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本刊外文刊名"Guihaia"的注释

本刊用"Guihaia"作为外文刊名，是取自"桂海"的汉语拼音，并予拉丁化缀以"a"字尾而成。

"桂海"一词，较早出现在我国南朝梁文学家江淹的<杂体诗・袁太尉>："文轸薄桂海"诗句中。以"南海有桂，故曰桂海"，桂海是泛指南方近海地方。其后，南宋诗人范成大曾任静江府(府治今桂林市)和广南西路(今广西)地方长官，就其见闻，追述广西山川、风物、花、果、草木的名著《桂海虞衡志》，亦用"桂海"一词，概指广西地区。

本刊采用书写简便的"Guihaia"为外文刊名，仅为学术交流时，在外文文献上便于引用而已。

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