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西南獐牙菜的胚胎学及其系统学意义*

薛春迎[1,2], 何廷农[2], 李德铢[1]
(1 中国科学院昆明植物研究所, 云南 昆明 650204; 2 中国科学院西北高原生物研究所, 青海 西宁 810001)

摘要: 报道了西南獐牙菜的大、小孢子发生及雌、雄配子体发育过程, 并以此讨论了獐牙菜属宽丝组和多枝组的分类等级和系统演化关系。西南獐牙菜花药四室; 药壁发育为双子叶型; 绒毡层二型起源、腺质型; 中层细胞 2 层; 药室内壁纤维状加厚, 药壁表皮宿存。小孢子母细胞减数分裂为同时型; 小孢子四分体的排列为四面体形; 成熟花粉为 3 - 细胞型。子房为 2 心皮, 1 室, 胚珠 12 列, 故为超侧膜胎座。薄珠心、单珠被, 倒弯生胚珠。大孢子母细胞减数分裂形成 4 个大孢子呈直线形排列, 合点端的大孢子具功能。胚囊发育为蓼型。两极核在受精前融合为次生核。3 个反足细胞次生增殖为 5 ~ 8 个, 宿存。比较宽丝组和多枝组的胚胎学性状表明宽丝组从多枝组中分出是合理的, 在系统位置上宽丝组较多枝组进化。

关键词: 西南獐牙菜; 龙胆科; 胚胎学; 系统关系
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Embryology of *Swertia cincta* (Gentianaceae) and Its Systematic Value

XUE Chun - Ying[1,2], HE Ting - Nong[2], LI De - Zhu[1]
(1 *Kunming Institute of Botany, Chinese Academy of Sciences*, Kunming, 650204, China;
2 *Northwest Plateau Institute of Biology, Chinese Academy of Sciences*, Xining, 810001, China)

Abstract: This paper reports the mega-, micro-sporogenesis and female-, male-gametogenesis of *Swertia cincta* for the first time, with the aim of discussing the systematic position of section *Platynema* and section *Ophelia* of *Swertia*. Anthers are tetrasporangiate. The development of anther walls conforms to the dicotyledonous type. The tapetum cells have dual origin and are similar to the glandular type. There are two middle layers. The endothecium and epidermis persist. Cytokinesis in the microsporocyte meiosis is simultaneous type and the microspore teads are tetrahedral. Pollen grains are 3-celled. The ovary is bicarpellum and unilocular. The placentation is of suparietal placentation with 12 series of ovules. The ovule is unitegmic, tenuinucellar and ana-campylotropous. The embryo sac originates from the single-archesporial cell. The one chalazal megaspore in linear tetrad becomes the functional megaspore. The development of embryo sac is of the *Polygonum* type. Before fertilization, two polar nuclei fuse into one secondary nucle-

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作者简介: 薛春迎 (1969 -) 女, 博士, 现在中国科学院昆明植物所博士后流动站工作, 主要从事植物系统与进化生物学的研究。

us. Three antipodal cells persisted and divided into 5 – 8 cells. A comparison between two sections indicates that section *Platynema* is better treated as distinct section and is more advanced than section *Ophelia* according to the evolutionary trends of embryological characters.

Key words: *Swertia cincta*; Gentianaceae; Embryology; Systematic relationships

Swertia cincta Burk. belongs to *Swertia* section *Platynema* T. N. Ho et S. W. Liu (Gentianaceae). The section *Platynema* was split off from *Swertia* section *Ophelia* (D. Don ex G. Don) Benth. et Hook. f. ex Gilg by Ho & Liu (1980) on the basis of morphological characters: filaments connate into a short tube surrounding ovary; nectary horseshoe-shape, naked and style filiform. According to the evolutionary trends of morphological characters, Ho (1994) regarded section *Platynema* is more advanced than section *Ophelia*. The section *Platynema* has never been investigated embryologically. The aims of the present paper are to report the observations results of embryology of *S. cincta* and to discuss systematic implications of the embryological data.

1 Materials and Methods

Materials investigated were collected from Lijiang, Yunnan province, China. The voucher (Liu Jian-quan 206) was deposited in the Herbarium of Northwest Plateau Institute of Biology, Chinese Academy of Sciences, China (HNWP).

Anthers and ovules at different stages of development were fixed in the formalin-acetic-alcohol (FAA). After being stained in Ehrfich s hematoxylin, the material was embedded in paraffin by the conventional method and sectioned at the thickness of 5 – 10 μm. Sections were stained with safranin-fast green. Observation and photographs were taken under Olympus BH2 microscope.

2 Observations and Results

2.1 Microsporangia, Microsporogensis and Male Cametogenesis

Flowers of *Swertia cincta* were bisexual and protandrous. Anthers were tetrasporangiate. At an early stage of development, 4 rows of archesporial cells differentiated below the epidermis of the anthers. Archesporial cells were recognizable by their dense cytoplasm and conspicuous nuclei. These cells divided periclinally forming outer primary parietal cells and inner primary sporogenous cells. The primary parietal cells divided periclinally and anticlinally forming two layers of the secondary parietal cells. The inner secondary parietal cells gave rise to the tapetum, which partly came from the ground tissue near the connective tissue. Thus, the tapetum was of dual origin (Plate Ⅰ: 1). The outer secondary parietal cells formed a subepidermal endothecium and two middle layers by periclinal and anticlinal division. Anther wall was composed of five layers: epidermis, endothecium, two middle layers and tapetum (Plate Ⅰ: 3). Endothecium and middle layers originated from the primary parietal cells. The development of microsporngial wall thus conformed to the dicotyledonous type (Davis, 1966).

Cells of tapetum on the connective side showed radial elongation or periclinal division and intrud-

ed into the anther locule. All the tapetal cells degenerated at their original sites and degenerating tapetum unclei in the middle of the anther locule were from the early differentiation protruding of the tapetum (Plate Ⅰ: 3); therefore, the tapetum is similar to the glandular type.

The middle layers were crushed during meiosis of microsporocytes.

As the anther matured, the epidermis of the anther wall persisted and the cells of the endothecium became pillar and fibrous (Plate Ⅰ: 5).

Simultaneous changes took place in the wall of microsporangia. The primary sporogenous cells underwent mitosis, forming secondary sporogenous cells, which microsporocytes were derived. Meiosis in each microsporocyte resulted in a microspore tetrad. The cytokinesis was the simultaneous type. Microspore tetrads were tetrahedral (Plate Ⅰ: 2). Microspores were separated from the tetrad as a uninucleate pollen grain (Plate Ⅰ: 3). Each microspore had a dense cytoplasm with a prominent and centrally placed nucleus. As the central vacuole developed, the nucleus took a peripheral position. The first division of the microspore nucleus resulted in the formation of two unequal cells, a large vegetative one and a smaller generative one (Plate Ⅰ: 4). The generative cell gave rise to two sperms by mitosis. Pollen grains were 3-celled at time of anther dehiscence (Plate Ⅰ: 6).

2.2 Megasporogenesis and Female gametogenesis

2.2.1 Macrosporangium and macrosporogensis

The ovary was superior, bicarpellary, syncarpous and unilocular with parietal placentae. There were 12 rows of ovules in the transection of ovary (Plate Ⅱ: 16). The integument initiated by periclinal and oblique division at the base of nucellus. The ovule of *S. cincia* was unitegmic. The integument reached the top of nucellus and formed a micropyle by continued division. The type of ovule was anacampylotropous (Plate Ⅱ: 17).

At the stage of microsporocyte, a single hypodermal archesporial cell differentiated in the young nucellus and functioned directly as the megasporocyte (Plate Ⅱ: 7) which was characterized by a large nucleus and dense cytoplasm. Thus, the ovule of *S. cincia* was tenuinucellate. The megasporocyte underwent meiosis, forming a linear tetrad of megaspores (Plate Ⅱ: 8, 9). Three micropylar megaspores eventually degenerated, in which the chalazal one became functional (Plate Ⅱ: 10 – 11).

2.2.2 Embryo sac and female gametophyte

A 7-cells and 8-nucleate female gametophyte of *Polygonum* type formed by three meiosis divisions of functional megaspore (Plate Ⅱ: 12). Three micropylar nuclei became the egg and two synergids, they formed the egg apparatus. The two nuclei became the polar nuclei. The chalazal nuclei became the three antipodals (Plate Ⅱ: 13 – 14). The polar nuclei fused at the center and the resulted secondary nucleus then moved close to the egg apparatus (Plate Ⅱ: 15).

In the mature 8 – nucleate embryo sac, the egg cell was recognized by nucleus at the chalazal end and a large vacuole at the micropylar end, two synergids was recognized by their nuclei at the micropylar end and a large vacuole at the chalazal end.

Three antipodal cells of *S. cincia* were not ephemeral as observed in most angiosperms (Hu, 1982). They persisted at the mature embryo sac stage (Plate Ⅱ: 13 – 14). Afterward, three cells

divided into 5 – 8 cells with enlarged and multiseriate nuclei and persisted like a layer of "out endosperm" around embryo sac.

3 Discussion

According to our recently study (Liu *et al*, 1998), the embryological characters of *S. franchetiana* in section *Ophelia* are summarized: tetrasporangium anthers; dicotyledonous type of microsporangium development; dual tapetal origin; placenoids formed by division of tapetal cells; glandular tapetum; 2 middle layers; persistent epidermis in the mature anther; simultaneous cytokinesis at meiosis of microsporocytes; tetrahedral microspore tetrads; 2-celled pollen; superior, bicarpellary and unilocular ovary with typical placentae; anatropous, unitegmic and tenuinucellar, ovules 8 in number; *Polygonum* type of megagametophytes, antipodal cells 5 – 8. Although there are numerous similar embryological characters between *S. cincta* and *S. franchetiana*, *S. cincta* is different from *S. franchentiana* in the embryology: (1) *S. cincta* has ana-campylotropous ovules, while *S. franchetiana* has anatropous ovules, and (2) *S. cincta* has 12 rows of ovules and superficial placentae, whereas *S. franchetiana* has 8 rows of ovules and typical parietal placentae.

From above comparision of embryological characters between section *Platynema* and section *Ophelia*, the result indicates that they are significantly different in embryology. The embryological characters confirm the treatment that section *Platynema* should be separated from section *Ophelia*.

The evolutionary trends of embryological characters have been elucidated by many authors (e.g. Johri *et al*, 1992; Tobe, 1989). The embryological features of ana-campylotropous ovules and superficial placentae in section *Platynema* are advanced characters, while anatropous ovules and typical perficial placentae are primitive characters. Thus, section *Platynema* is more advanced than section *Ophelia* according to evolutionary trends of the embryological characters.

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Explanation of Plates

AC: Antipodal cell. DM: Degenerating megaspore. E: Egg. En: Endothecium. Ep: Epidermis. FM: Functional megaspore. M: Middle layer. Pn: Polar nucleus. Sp: Sperm. Sy: Synergid. SN: Secondary nucleus. Sy: Synergid.

Plate I 1. Anther wall at early stage of microspocyte. 2. Tetrahedral tetrad. 3. Five layers of anther wall cells: epidermis, endothecium, 2 middle layers and tapetum. 4. Anther wall of two-nucleate pollen grain. 5. Anther wall before releasing pollen, showing fibrous thickened endothecium and persisted epidermis. 6 3-celled pollen grains. (1×634, 2. 6×1200, 3－5×452)

Plate II 7. A unitegmic ovule and megasporocyte. 8. Anaphase I of meiosis in megasporocyte. 9. Linear megaspore tetrad. 10－11. Consecutive transactions showing the functional chalazal megaspore, with other three degenerating. A one-nucleate embryo sac and showing the other three degenerated megaspores. 12. The two-nucleate embryo sac. 13－14. Consecutive transactions of mature embryo sac, showing an egg, two synegids, two polar nuclei and 5－8 antipodal cells. 15. Showing egg apparatus and secondary nucleus. 16. Transverse section showing 12 rows of ovules. 17. Showing ana－campylotropous ovule. (7－14×768, 15×1128, 16×136, 17×86).

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Cao CY（曹成有），Kou ZW（寇振武），Jiang DM（将德明），*et al*，2000. Interdune Duccession in the Kerqin Sandy Region. *Acta Phytoecologica Sinica*（植物生态学报），24 (3)：262－267

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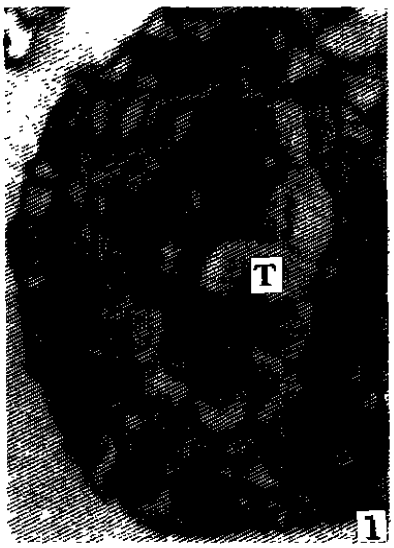
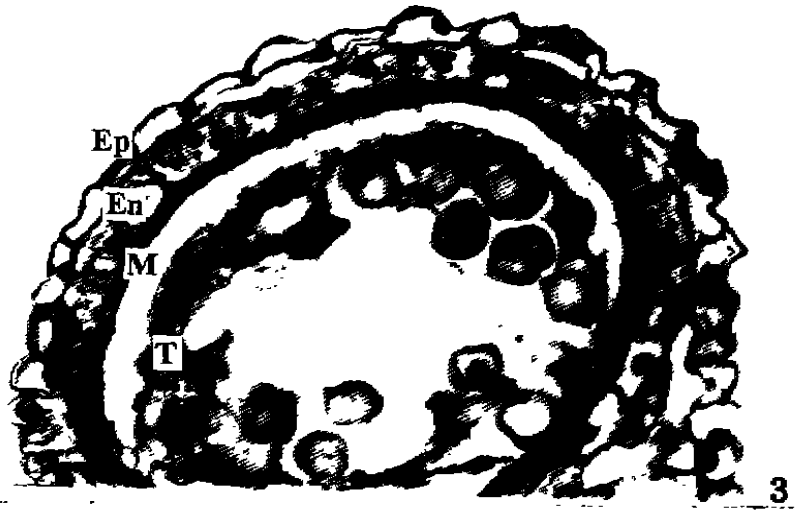
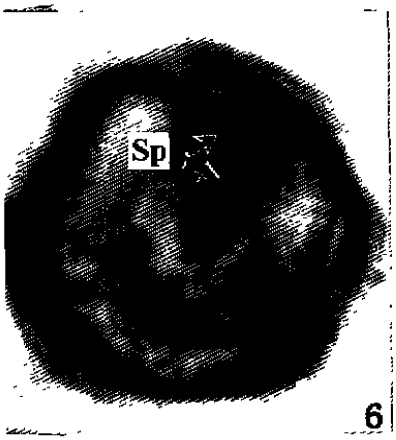
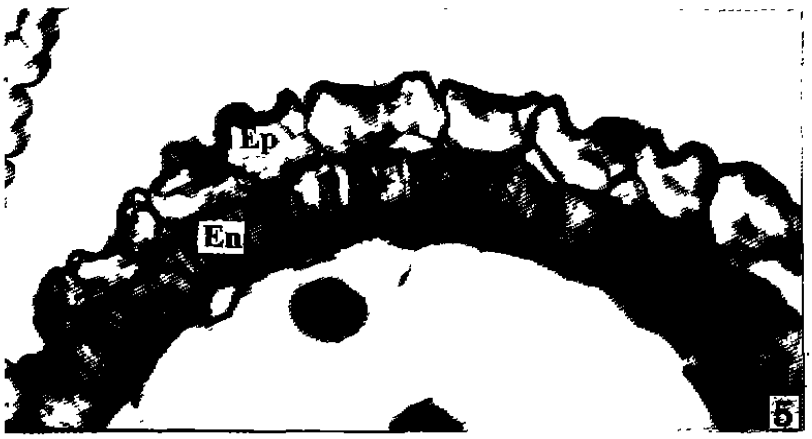


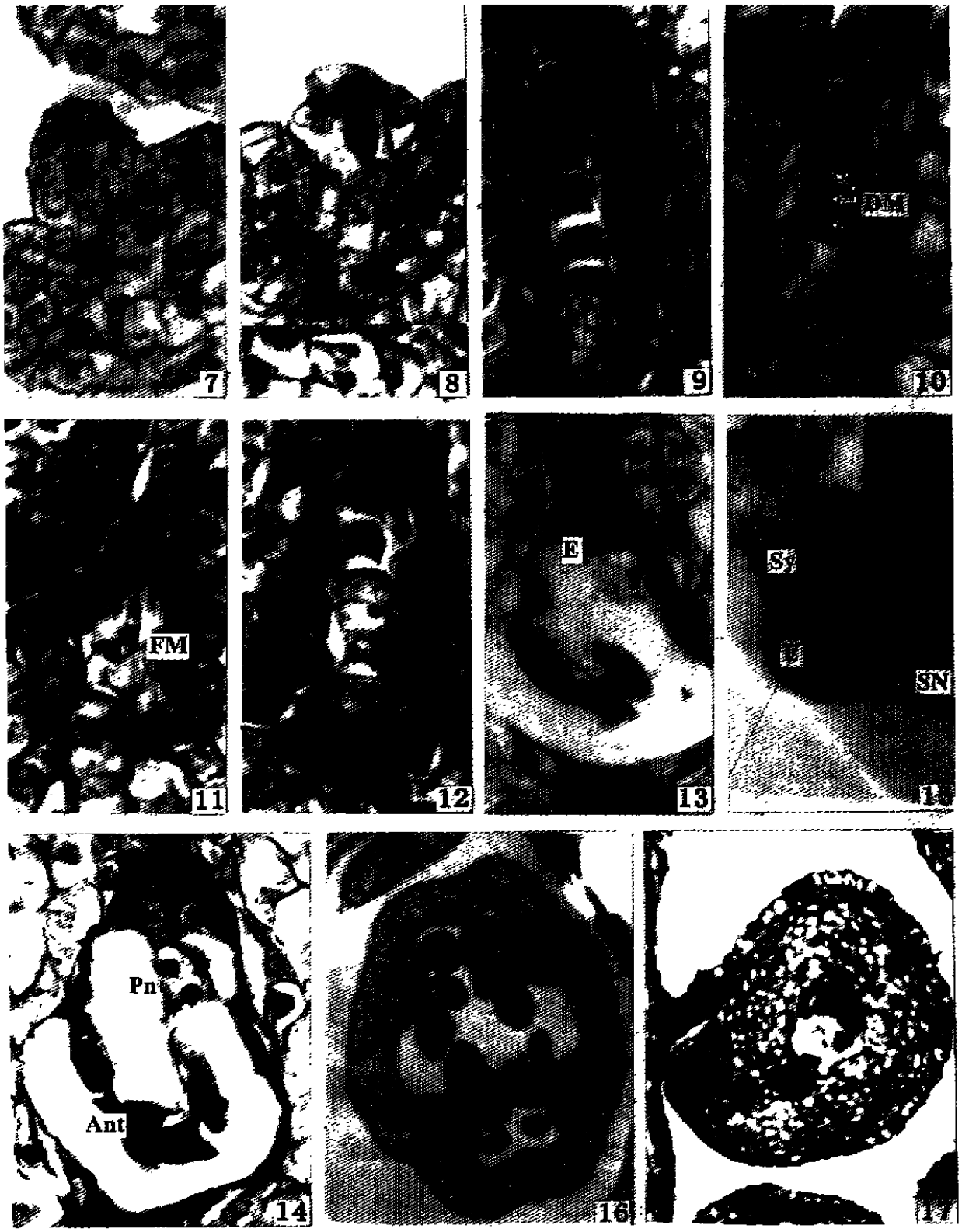






薛春迎等： 图版 I

XUE Chun – Ying *et al*: Plate I



薛春迎等： 图版Ⅱ XUE Chun – Ying *et al*: Plate Ⅱ