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# Floral Organogenesis and Development of Two Taxa in Tribe Hyoscyameae (Solanaceae)—*Przewalskia tangutica* and *Hyoscyamus niger*

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**Abstract:** Floral organogenesis and development of *Przewalskia tangutica* Maxim. endemic to China and *Hyoscyamus niger* L., which belong to the tribe Hyoscyameae (Solanaceae), were studied using scanning electron microscope. They have three common characters of floral organ initiation and development: 1) initiation of the floral organs in the two species follows Hofmeister's rule; 2) the mode of corolla tube development belongs to the "late sympetaly" type; 3) primordia of the floral appendages initiated in a pentamerous pattern and acropetal order. But initiation of the calyx-lobe primordia showed different modes in these two species. The calyx-lobe primordia of *H. niger* have simultaneously whorled initiation, while those of *P. tangutica* have helical initiation, but the five calyx-lobe primordia form a ring after all five calyx-lobe primordia occur. The systematic significance of the present results in the genera *Hyoscyamus* and *Przewalskia* is discussed in this paper.

**Key words:** *Przewalskia tangutica*; *Hyoscyamus niger*; Hyoscyameae; floral organogenesis

Floral development has been studied since the work of Payer and Hofmeister[1]. Plant systematists, geneticists, and reproductive ecologists have paid much attention to the morphology and evolution of flowers[2]. The appearance of scanning electron microscopy has greatly promoted the studies on floral organogenesis and development since the 1970's. The characters of floral development have been used to explain systematic relationships of angiosperms mostly above the genus level[3].

This research is the second of a series of studies on floral development of the tribe Hyoscyameae. Both *Przewalskia* Maxim. and *Hyoscyamus* L. belong to the tribe Hyoscyameae, which is the only tribe of Solanaceae distributed in Eurasia and centered on the Hengduan Mountains (Yangtze-Mekong-Salwin water divides) and the adjacent areas of southwest China. *Przewalskia* endemic to China is a monotypic genus and mainly distributed in sandy and gritty land in dry grassland of the Qinghai-Xizang Plateau. *Hyoscyamus* contains about 20 species. *Hyoscyamus niger* is distributed in southwest Asia, north Africa and Europe.

Plants in this tribe are of great economical and medicinal importance[4]. Taxonomy of Hyoscyameae has been carefully studied and revised[5,6]. Pollen morphology of this tribe and embryology and adaptive ecology of *Przewalskia* were investigated by Lu and Zhang[4], Zhang and Lu[7], and Lu *et al*[8]. Yang *et al*[9] studied the foliar epidermal features of 21 species from seven genera in Hyoscyameae and of two related genera with three species in Solanaceae under the light microscope (LM) and the scanning electron microscope (SEM). For better understanding of the systematic relationship of Hyoscyameae, we carried out a series of studies on the floral organogenesis and development of this tribe. The present paper reports floral organogenesis and development of two species, *Przewalskia tangutica* and *H. niger*.

## 1 Materials and Methods

Flowers of *Przewalskia tangutica* Maxim. were collected from wild plants at Maduo Xian, Qinghai Province, China. The voucher specimens (Jian-Quan Liu 99020) were deposited in the Herbarium of Northwest Plateau Institute of Biology, the Chinese Academy of Sciences (HNWP). Flowers of *Hyoscyamus niger* were collected from the Botanical Garden, University of Nijmegen, The Netherlands. The voucher specimens (Zhi-Yun Zhang 009) were deposited in the Herbarium, Institute of Botany, the Chinese Academy of Sciences (PE). Floral buds at different developmental stages were fixed in formalin-acetic acid-alcohol (FAA). For SEM, dissected buds were dehydrated in a graded series of alcohol-isoamyl acetate and treated with critical point drying in $CO_2$. Materials were mounted on aluminum stubs, coated with gold and photographed under a Hitachi-S800 SEM[10,11].

## 2 Results

### 2.1 Floral morphology of *Hyoscyamus niger*

Flowers are solitary and borne in leaf axils in the middle of the stem, and inflorescence are scorpioid racemes on the upper part of the stem. Flowers are subsessile or pedicels 3 – 5 mm. Calyx tubular-campanulate 1 – 1.5 cm; lobes dentate, unequal, acute. Corolla pale

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yellow, usually with purple veins, campanulate, 2 - 3 cm. Stamens exserted. Fruiting calyx urceolate, (2 - 2.5) × (1 - 1.5) cm; lobes mostly erect, tipped with a sharp tooth[6].

### 2.2 Floral morphology of *Przewalskia tangutica*

The flower buds begin to form in the soil, and generally blossom next to the soil surface only 3 - 4 d after the winter buds appear above the surface[8]. Inflorescences clusters of 1 - 6 axillary flowers, pedunculate or sessile. Flowers, actinomorphic, 5-merous. Pedicel short. Calyx tubular-campanulate. Corolla funnel form; lobes overlapping in bud, spreading at anthesis, with inflexed margins. Stamens equal, inserted in corolla throat, included; filaments very short; anthers dehiscing longitudinally. Disc ringlike. Ovary 2-locular. Fruiting calyx much inflated, with prominent netted veins, completely enveloping fruit, slightly open at apex[6].

### 2.3 Floral organogenesis and development of *Hyoscyamus niger*

The sequence of floral organogenesis is acropetal. Some of calyx-lobe primordia occur firstly, and form a semicircle (Figs.1,2). Later, all five calyx-lobe primordia appear and form a ring inconspicuously (Fig. 3). Then the calyx-lobe primordia ring becomes apparent (Fig.4). When one of the calyx-lobe primordia is bigger than the others, the corolla-lobe primordia appear slightly (Fig.5). When the corolla-lobe primordia are still inconspicuous, stamen primordia appear (Fig.6), and the stamen primordia develop faster than corolla-lobe primordia (Fig.7). Later, when the stamen primordia become dome shape and corolla-lobe primordia are still smaller than stamen primordia, the depression of the gynoecium primordium appears inconspicuously (Fig.8). Then the depression of floral top meristem becomes apparent (Fig. 9). When the corolla-lobe primordia become triangle shape, the gynoecium protrudes apparently (Fig. 10). Corolla-lobe primordia are almost larger than the stamen primordia (Fig. 11). The gynoecium primordium protrudes highly and appears symplicate (Fig.12). Corolla-lobe primordia develop much larger than the stamen primordia and enclose them almost completely (Fig. 13). Later, the five corolla-lobe primordia become connate slightly at the base (Fig.14). Subsequently, the gynoecium enlarges further and a bilobate stigma could be observed (Fig.15).

### 2.4 Floral organogenesis and development of *Przewalskia tangutica*

The sequence of floral organogenesis is acropetal. Five calyx-lobe primordia first initiate spirally and develop at different rates (Figs.16,17). Then the calyx-lobe primordia form a ring when the corolla-lobe primordia occur inconspicuously (Fig.18). The stamens initiate between the corolla-lobe primordia (Fig. 19). When corolla-lobe and stamen primordia appear conspicuously, the depression of floral top meristem can be observed (Fig. 20). The gynoecium protrudes when the stamen primordia become larger than the corolla-lobe primordia (Fig. 21). With the enlarging of the corolla-lobe and stamen primordia, the gynoecium primordium protrudes more and more highly (Figs. 22, 23). When the corolla-lobe primordia are much larger than the stamen primordia, the gynoecium appears symplicate (Fig. 24). Then, five corolla-lobe primordia enclose the stamen and gynoecium completely (Fig.25). Subsequently, the gynoecium enlarges further and a bilobate stigma could be observed (Fig.26).

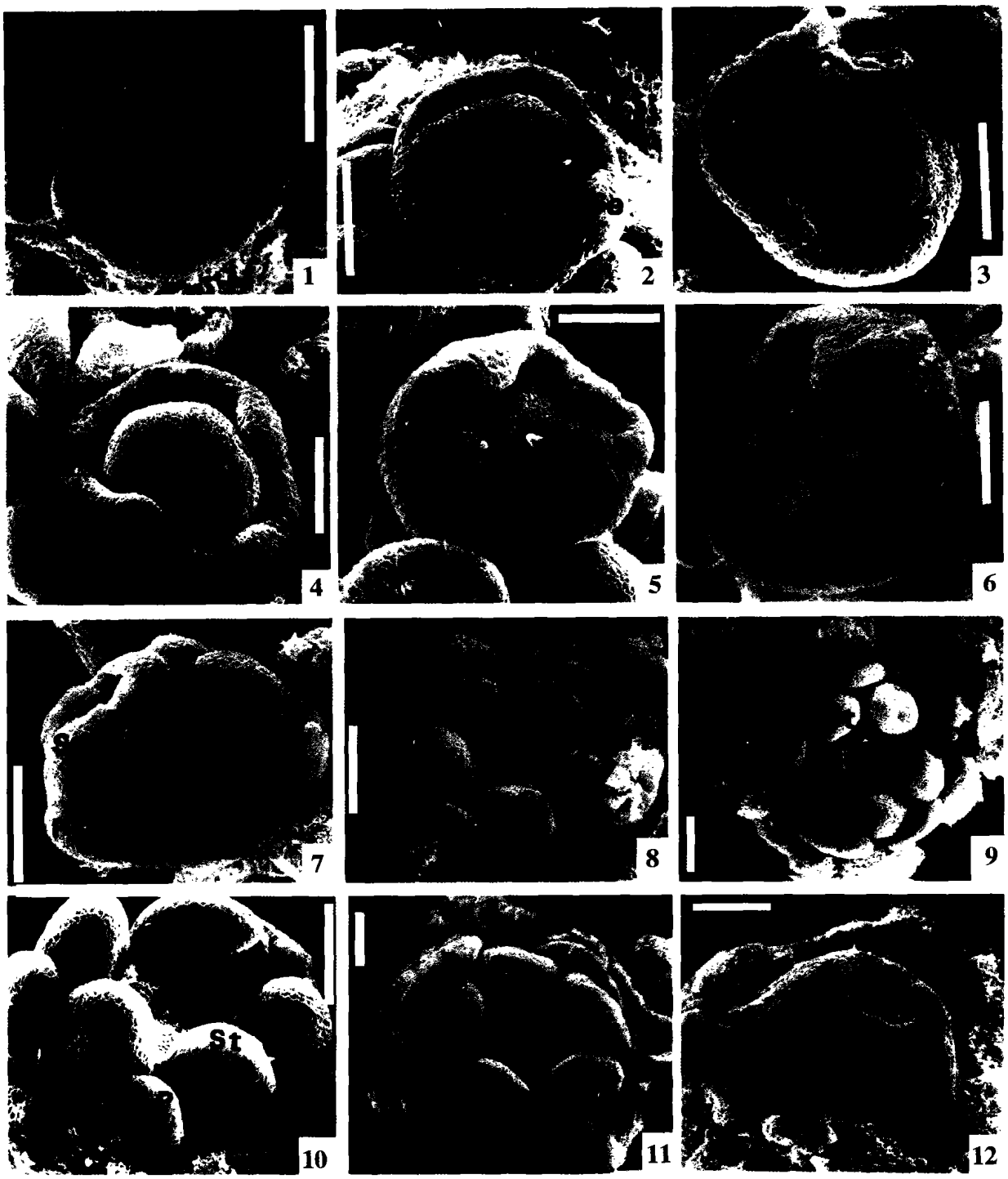
## 3 Discussion

There are different viewpoints of the systematic position of *Przewalskia*. Lu and Zhang[4] regard that *Przewalskia* is more advanced than *Anisodus* Link et otto based on the morphological and palynological characters. However, this genus occurs at the base of the clade in one cladistic study[12]. This study tries to provide some valuable evidence about the systematic position of *Przewalskia*.

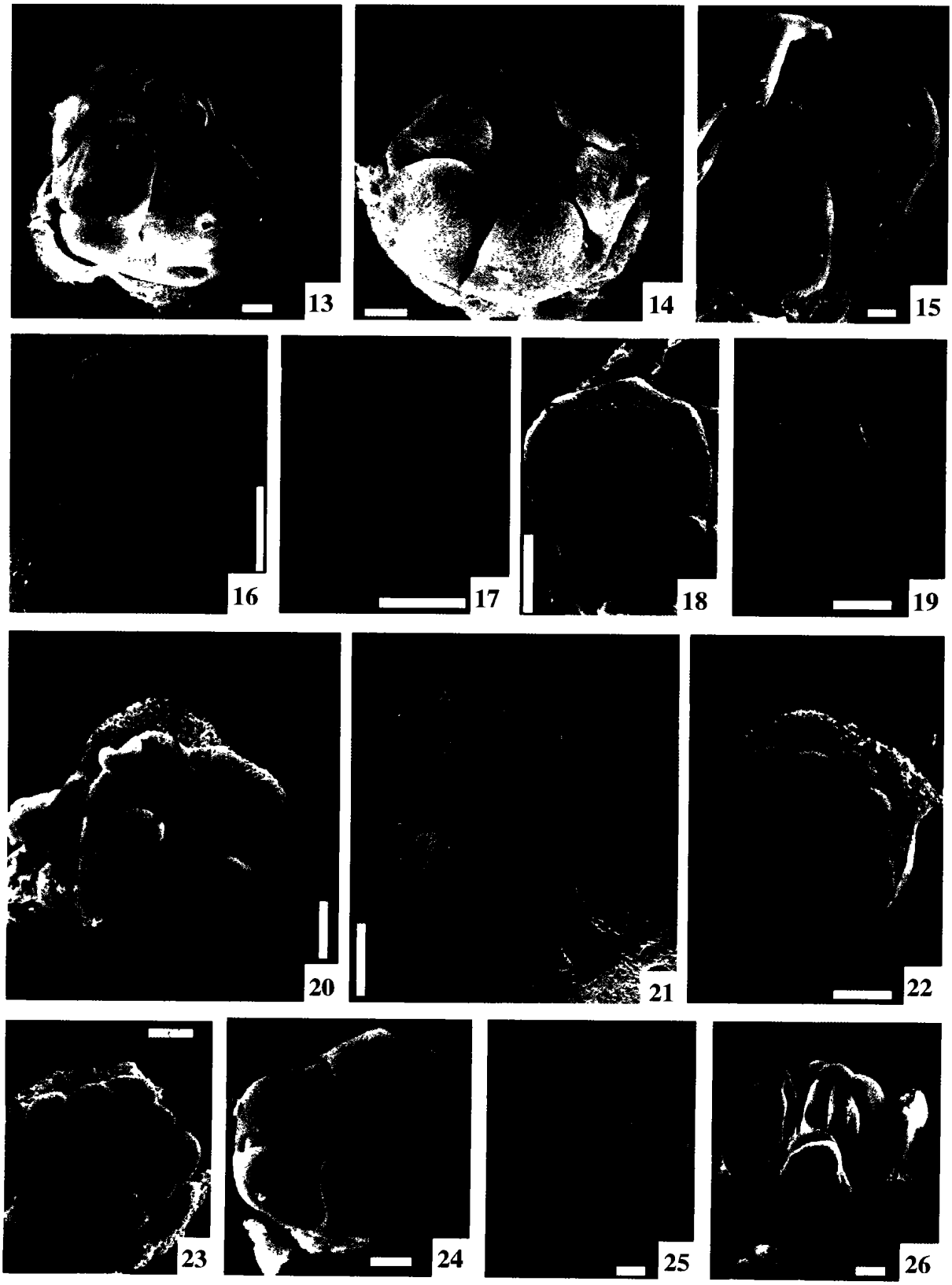
The present study shows that *Hyoscyamus niger* and *Przewalskia tangutica* share the same three common characters in floral development as *Anisodus tanguticus* and *Atropa belladonna*. The three common characters are: 1) The floral appendages initiate in a pentamerous pattern and in acropetal order; the calyx-lobes initiate first, corolla-lobes next, followed by the stamens and the carpels. 2) The whorl of five stamens is formed more or less simultaneously and originates opposite to the calyx-lobe. Thus, the initiation of floral organs follows Hofmeister's rule[1]. 3) The mode of development of the corolla tube is "late sympetaly"[13], namely the corolla-lobe primordia initiate separately and later become joined by fusion of their basal meristem, then rise together and form a corolla tube[14].

The differences of floral organogenesis and development between *Hyoscyamus niger* and *Przewalskia tangutica* are mainly in the patterns of initiation and development of the calyx-lobe. For example, in *Hyoscyamus niger*, some calyx-lobe primordia first protrude simultaneously with inconspicuous connections between them (Fig. 1). Then calyx-lobes become connate at the base more and more conspicuously and form a semicircle (Fig.2). Later, all five calyx-lobe primordia have appear and form a ring when the corolla-lobe primordia still can not be observed (Figs. 3, 4). Apart from that, the five calyx-lobe primordia maintain a ring after all five calyx-lobe primordia have appeared. In contrast, in *Przewalskia tangutica*, the five calyx-lobe primordia obviously initiate spirally but form a ring after the five calyx-lobe primordia have appeared (Figs.16 - 18).

The initiation pattern of the calyx-lobe primordia of *Przewalskia tangutica* is intermediate between the initiation pattern of *Atropa belladonna* and those of *Anisodus tanguticus* and *Hyoscyamus niger*[14]. The initiation pattern of the calyx-lobe primordia of *Hyoscyamus niger* and *Anisodus tanguticus* is whorled, that of *Atropa belladonna* is spiral, and their calyx-lobe primordia are separated when the five calyx-lobe primordia appeared. Only when the center of the gynoecium primordium becomes




**Figs. 1 – 12.** *Hyoscyamus niger* floral organogenesis and development. Scale bar = 100 μm. **1**. Some of calyx-lobe primordia occur firstly and form a semicircle. **2**. The semicircle of calyx-lobe primordia become larger. **3**. All five calyx-lobe primordia appear and form a ring inconspicuously. **4**. The calyx-lobe primordia ring becomes apparent. **5**. When one of the calyx-lobe primordia is bigger than the others, the corolla-lobe primordia appear slightly. **6**. When the corolla-lobe primordia are still inconspicuous, stamen primordia appear apparently. **7**. And the stamen primordia are larger than corolla-lobe primordia. **8**. When the stamen primordia become dome shape and corolla-lobe primordia are still smaller than stamen primordia, the depression of floral top meristem appear inconspicuously. **9**. The depression of floral top meristem becomes apparent. **10**. When the corolla-lobe primordia become triangle shape, the gynoecium protrudes apparently. **11**. Corolla-lobe primordia are almost larger than the stamen primordia. **12**. The gynoecium primordium protrudes highly and appears symplicate.
Abbreviations: C, carpel primordia; Dg, depression of floral top meristem; G, gynoecium primordium; P, corolla-lobe primordia; Se, calyx-lobe primordia; SeR, calyx ring primordia; St, stamen primordia; Stg, stigma.



depressed inconspicuously, do the five calyx-lobe primordia fuse at the base[14]. Whereas, the calyx-lobe primordia of *Przewalskia tangutica* first initiate spirally and develop at different rates (Figs. 16, 17). Then the calyx-lobe primordia form a ring when the corolla-lobe primordia occur inconspicuously (Fig. 18). The spiral initiation of calyx-lobe primordia is a rather primitive character[15]. Therefore, our research supports that *Przewalskia* is more primitive than *Hyoscyamus* and *Anisodus* but more advanced than *Atropa*. It might be a basal clade in the tribe Hyoscyameae and its systematic position is between *Atropa* with *Hyoscyamus* and *Anisodus*.

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**Figs. 13 – 26.** **13 – 15.** *Hyoscyamus niger* floral organogenesis and development. **16 – 26.** *Przewalskia tangutica* floral organogenesis and development. Scale bar = 100 μm. **13.** Corolla-lobe primordia develop much larger than the stamen primordia and enclose them almost completely. **14.** Five corolla-lobe primordia become connate slightly at the base. **15.** The gynoecium enlarges further and a bilobate stigma could be observed. **16.** Five calyx-lobe primordia first initiate spirally and develop at different rates. **17.** Calyx-lobe primordia become larger. **18.** The calyx-lobe primordia form a ring when the corolla-lobe primordia occur inconspicuously. **19.** The stamens initiate between the corolla-lobe primordia. **20.** When corolla-lobe and stamen primordia appear conspicuously, the depression of floral top meristem can be observed. **21.** The gynoecium protrude apparently when the stamen primordia become larger than the corolla-lobe primordia. **22, 23.** With the enlarging of the corolla-lobe and stamen primordia, the gynoecium primordium protrudes more and more highly. **24.** When the corolla-lobe primordia are much larger than the stamen primordia, the gynoecium appears symplicate. **25.** Five corolla-lobe primordia enclose the stamen and gynoecium completely. **26.** The gynoecium enlarges further and a bilobate stigma could be observed.

# 茄科马尿泡和天仙子的花器官发生

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**摘要:** 利用扫描电镜研究了茄科(Solanaceae)天仙子族(Hyoscyameae)中国特有属马尿泡属(*Przewalskia* Maxim.)马尿泡(*Przewalskia tangutica* Maxim.)和天仙子属(*Hyoscyamus* L.)天仙子(*Hyoscyamus niger* L.)的花器官发生和发育,研究结果表明:马尿泡和天仙子花器官的发生和发育具有以下3个共同特征:1)符合Hofmeister规律,即新器官的发生首先出现在花顶已经存在的器官之间;2)花冠的发育模式符合茄科植物所具有的"后合瓣"("late sympetaly")现象,即花瓣单独发生但后来又通过它们基部分生组织的融合而连合起来;3)花被五基数且花器官原基发生顺序为向心发育。但是它们的花萼原基具有不同的发生方式。天仙子花萼裂片原基的发生方式为环状发生;马尿泡花萼裂片原基的发生方式为螺旋状发生,但5个花萼裂片原基在都出现后就连成了一个环。马尿泡是介于天仙子属和山莨菪属之间的类群,它比天仙子属原始但较山莨菪属进化。

**关键词:** 马尿泡; 天仙子; 天仙子族; 花器官发生

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