

DOI: 10.11931/guihaia.gxzw201903007

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LUO MR. Floral morphogenesis in *Leptopyrum* (Ranunculaceae) with scanning electron microscopy [J]. *Guihaia*, 2020, 40(11): 1645–1652.

蓝堇草属(毛茛科)花形态发生的扫描电子显微镜观察

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摘要: 花的发生和发育过程研究可以发现早期进化的轨迹, 为系统发育的研究提供重要线索。蓝堇草属(*Leptopyrum*)为毛茛科唐松草亚科一单种属, 仅包含蓝堇草一种, 其花的发生和发育过程仍为空白。为了深入理解唐松草亚科乃至毛茛科花发育多样性和演化规律, 该文运用扫描电子显微镜(SEM)观察了蓝堇草各轮花器官的形态发生和发育过程。结果表明: 该属植物所有的萼片、花瓣、雄蕊和雌蕊均为螺旋状发生, 花器官排列式样也为螺旋状; 5枚萼片原基宽阔, 5枚花瓣原基圆球形、位于萼片原基的间隔, 且在后期表现为延迟发育现象, 雄蕊原基较小、为圆球形; 花瓣原基和雄蕊原基连续发生, 无明显的时空间隔, 但与萼片原基有时空间隔; 心皮原基为马蹄形对折, 柱头组织由单细胞乳突组成; 胚珠倒生、具单珠被。该属花器官螺旋状排列、胚珠具单珠被在唐松草亚科中是独有的性状, 花发育形态学证据支持了该属的特殊性。

关键词: 蓝堇草属, 毛茛科, 花, 形态发生

中图分类号: Q944 文献标识码: A

文章编号: 1000-3142(2020)11-1645-08

开放科学(资源服务)标识码(OSID):



Floral morphogenesis in *Leptopyrum* (Ranunculaceae) with scanning electron microscopy

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Abstract: Floral initiation and development can provide important clues for phylogeny for the track of early evolution found in the study process. *Leptopyrum* is a monotypic genus in the subfamily Thalictroideae of family Ranunculaceae. Data on floral initiation and development of this genus are still completely lacking. In order to better understand the floral diversity and evolution of Thalictroideae and Ranunculaceae, the morphological initiation and development of the flowers of *Leptopyrum fumarioides* were studied by using scanning electron microscopy. The results were as follows: Sepals, petals, stamens and carpels of this genus were initiated spirally and the phyllotaxis was

收稿日期: 2019-05-21

基金项目: 国家自然科学基金目(31300158) [Supported by the National Natural Science Foundation of China (31300158)].

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spiral. The five young sepals were broad, crescent-shaped and truncate, but the five young petals were and rounded and between young sepals. After sepal initiation, there was a delay in development, and the plastochron between the last sepal and the first petal was relatively long, but the initiation of petals and stamens was continuous. The petal development was delayed with regard to other floral organs. The carpel primordia were plicate. The stigma was covered with unicellular papillae, and the mature ovule was anatropous and unitegmic. *Leptopyrum* showed similar development features of the sepals, petals and stamens as other members of Thalictroideae, which were also found in other Ranunculaceae. However, spiral floral phyllotaxis and unitegmic ovule were unique characters in Thalictroideae, which support *Leptopyrum* as a distinct genus.

Key words: *Leptopyrum*, Ranunculaceae, flower, morphogenesis

花是被子植物区别于裸子植物和其他孢子植物类群的最显著、最让科学家着迷的关键创新性状,是区分属以上分类群和建立被子植物分类系统的重要依据 (Endress, 2001, 2006; Ronse De Craene & Wanntorp, 2011; Endress & Matthews, 2012)。然而成熟花只是花发育过程中的一个特殊阶段,对花的发生和发育过程的研究可以发现早期进化的轨迹,为系统发育的研究提供重要线索 (Endress, 1994; 孙坤等, 1998)。因此,花的起源和演化一直是探讨被子植物起源和演化的关键问题之一。20 世纪 80 年代,扫描电子显微镜 (scanning electron microscope, SEM) 的应用使科学家可以精细地观察花和各轮花器官的发生和发育过程,极大地推动了植物发育形态学的发展和进步 (Endress, 1994, 2011; Endress et al., 2000)。

毛茛科 (Ranunculaceae) 是一个广泛分布于北温带的大科,全球共有约 59 属,2 500 余种,绝大多数类群为草本 (Tamura, 1993, 1995)。该科是毛茛目 (Ranunculales) 的核心分支之一,对该科花发育过程的深入研究有助于理解基部被子植物和核心真双子叶植物的演化关系 (APG, 2016)。

20 余年来,随着分子系统学的发展,毛茛科的系统发育研究取得了巨大进展 (Hoot, 1995; Johansson & Jansen, 1993; Jensen, 1995; Johansson, 1995; Kosuge et al., 1995; Ro et al., 1997; Wang et al., 2005, 2009, 2010; Zhai et al., 2019)。毛茛科一般被分为 5 个亚科,即 Glaucidoideae、Hydrastidoideae、黄连亚科 (Coptidoideae)、唐松草亚科 (Thalictroideae) 和毛茛亚科 (Ranunculoideae)

(Wang et al., 2009; Cossard et al., 2016)。最新的分子系统学证据表明该科包括 14 个族,代表系统发育研究的 14 个分支,其中 Glaucideae、Hydrastideae 和 Coptideae 是该科早期分化出的三个支系 (Zhai et al., 2019)。

唐松草亚科 (Thalictroideae) 包括了 10 个属,隶属于三个支系:(1) 唐松草属 (*Thalictrum*)、蓝堇草属 (*Leptopyrum*)、*Paropyrum*、拟耧斗菜属 *Paraquilegia*; (2) 尾囊草属 (*Urophysa*)、天葵属 (*Semiaquilegia*)、耧斗菜属 (*Aquilegia*); (3) 人字果属 (*Dichocarpum*)、拟扁果草属 (*Enemion*)、扁果草属 (*Isopyrum*) (Wang & Chen 2007; Wang et al., 2009)。其中蓝堇草属 (*Leptopyrum*) 是 Reichenbach 在 1828 年基于扁果草属 (*Isopyrum*) 的 *I. fumarioides* 建立的。该属仅有蓝堇草 (*Leptopyrum fumarioides*) 一种,在我国分布于新疆、青海东北部、甘肃、陕西、山西、河北、内蒙古、辽宁、吉林、黑龙江等地,在朝鲜、俄罗斯、蒙古、欧洲和中亚等地也有分布,常生于田边、路线或干燥草地 (Wang et al., 2001)。

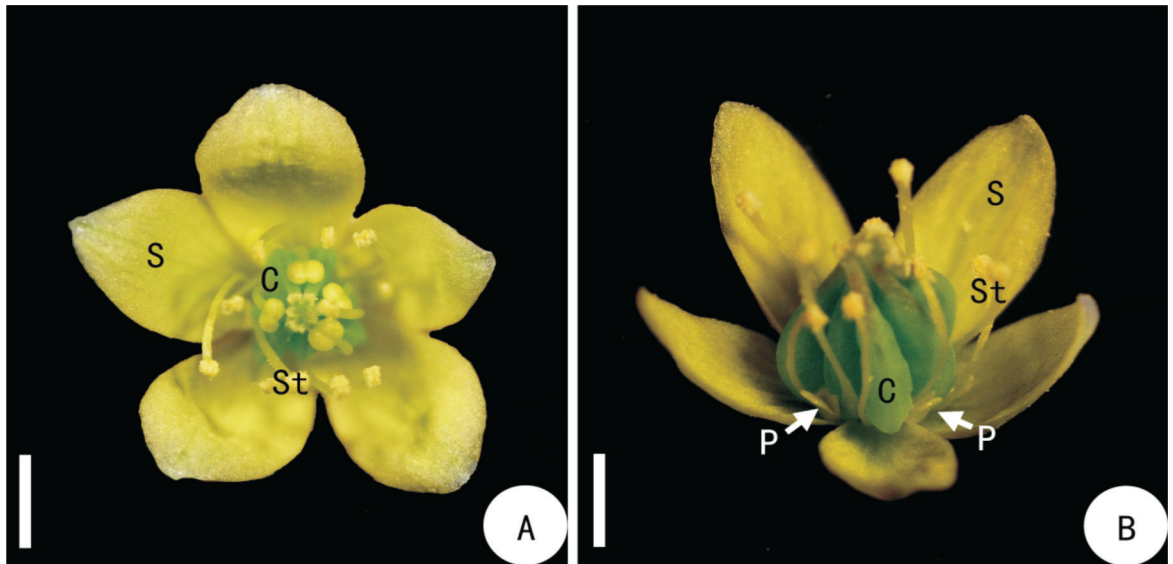
毛茛科植物的花器官发育形态学的研究已有丰富的积累 (如冯旻等, 1995; 常鸿莉等, 2005; 辜天琪和任毅, 2007; 宋萍等, 2007; Endress, 1995; Tucker & Hodges, 2005; Wang & Ren, 2008; Jabbour et al., 2009; Ren et al., 2009, 2010, 2011; Zhao et al., 2011, 2012a, 2012b, 2016; Wang et al., 2016)。在唐松草亚科中,目前已有耧斗菜属 (*Aquilegia*)、天葵属 (*Semiaquilegia*)、拟扁果草属 (*Enemion*)、人字果属 (*Dichocarpum*)、唐松草属 (*Thalictrum*) 和尾囊草属 (*Urophysa*) 等 6 属的花发

育过程被研究(冯旻等, 1995; Tucker & Hodges, 2005; Ren et al., 2011; Zhao et al., 2016)。对于单种属——蓝堇草属的研究主要集中于解剖学(张友民等, 1995)、药理学(Nikolaev et al., 2012; Boldbaatar et al., 2014)和植物化学(Doncheva et al., 2014)等方面, 而花发育形态学研究仍为空白。

本研究拟利用扫描电子显微镜观察蓝堇草的花形态和发育过程, 并与近缘类群进行比较, 以增进对毛茛科、特别是唐松草亚科花形态多样性和花器官演化的理解。

1 材料与方 法

蓝堇草(*Leptopyrum fumarioides*)的花芽于2011至2015年采自东北林业大学的野生个体(凭证标本: LMR2015001, WUK), 材料用FAA(甲醛: 冰醋酸: 70%乙醇=5: 5: 90)固定, 酒精和乙酸异戊酯系列脱水, CO₂临界点干燥, 粘台、喷金镀膜后在日立HITACHI S-3500扫描电镜下观察照相。



A. 顶面观; B. 侧面观. C. 心皮; P. 花瓣; S. 萼片; St. 雄蕊。比例=1 mm。

A. Top view; B. Side view. C. Carpel; P. Petal; S. Sepal; St. Stamen. Scale bars=1 mm.

图1 蓝堇草成熟花

Fig. 1 Mature flower of *Leptopyrum fumarioides*

2 结果与分析

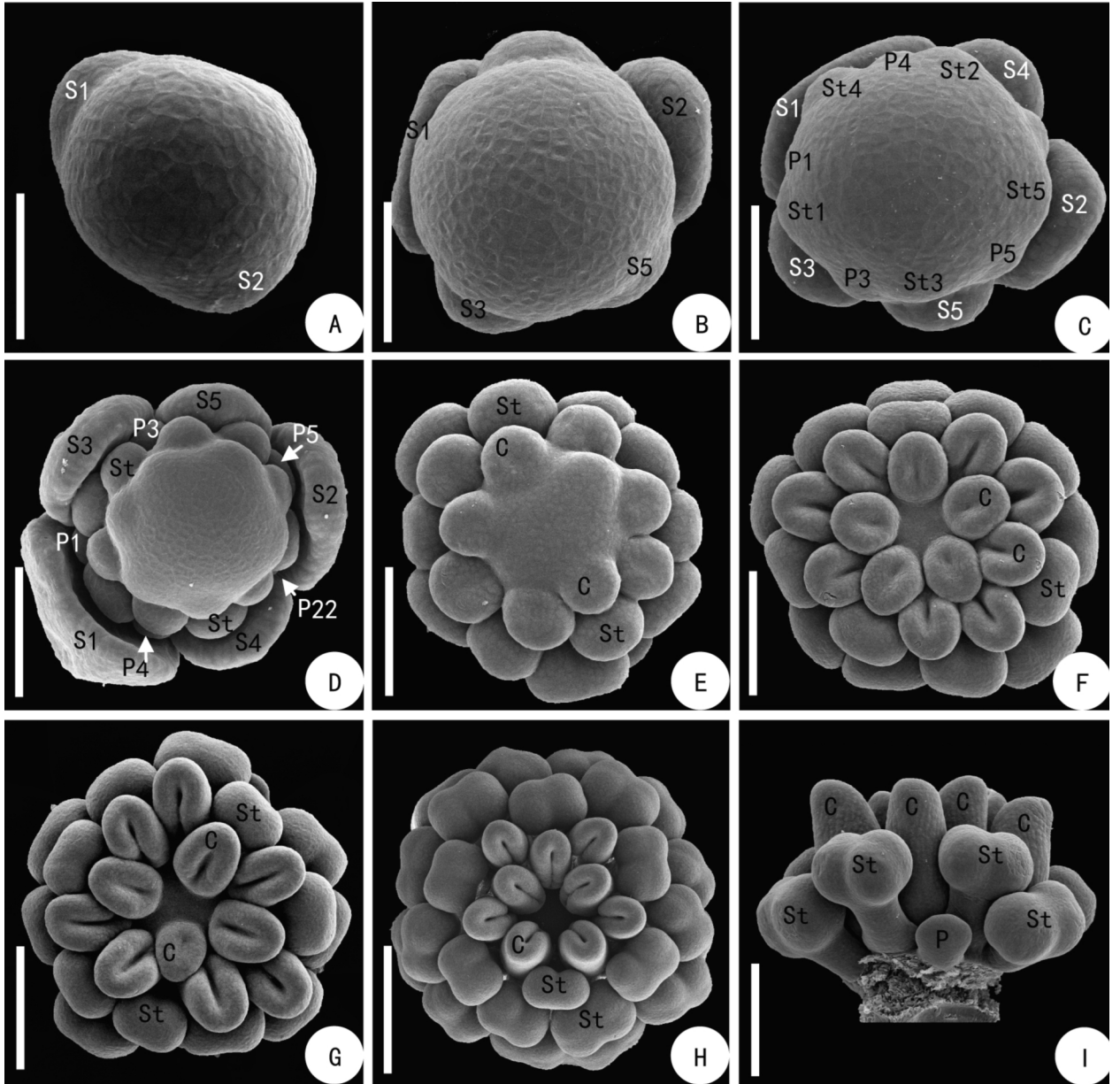
2.1 成熟花的形态特征

蓝堇草为一年生草本, 具简单的单歧聚伞花序, 苞片叶状。花小, 直径约3~5 mm, 辐射对称, 萼片5枚, 椭圆形, 淡黄色; 花瓣5, 黄色, 长约1 mm, 基部管状、上部近二唇形; 雄蕊10~15枚; 心皮6~20枚, 蓇葖果(图1:A, B)。

2.2 花器官的形态发生

萼片原基5枚, 以2/5的顺序螺旋状向心式发

生, 每2个萼片原基之间的夹角约为137°。萼片原基基部宽阔、顶部平截(图2:A, B)。在5枚萼片原基发生后, 有一个相对较长的时间间隔, 然后5枚花瓣原基和雄蕊原基才相继发生(图2:C)。花瓣和雄蕊在发生早期形态相似, 都为半球形, 很难区别(图2:C)。心皮原基也是螺旋式发生, 大小与雄蕊原基相似; 由于雄蕊、心皮数目不固定, 在雄蕊开始分化前, 花瓣原基与雄蕊原基之间以及雄蕊原基与心皮原基之间很难鉴别(图2:E)。心皮原基发生后, 仍然有部分的花托原基的残余(图2:F-H), 这一区域逐步被长大的心皮所覆盖(图2:H)。



A, B. 萼片的发生; C. 花瓣、雄蕊的发生, 示二者原基形状相同而与萼片原基不同; D. 雄蕊继续发生; E-H. 心皮原基的发生与发育, 并逐渐掩盖残余的花托; I. 示花瓣延迟发育。C. 心皮; P. 花瓣; S. 萼片; St. 雄蕊。比例尺 = 100 μm 。

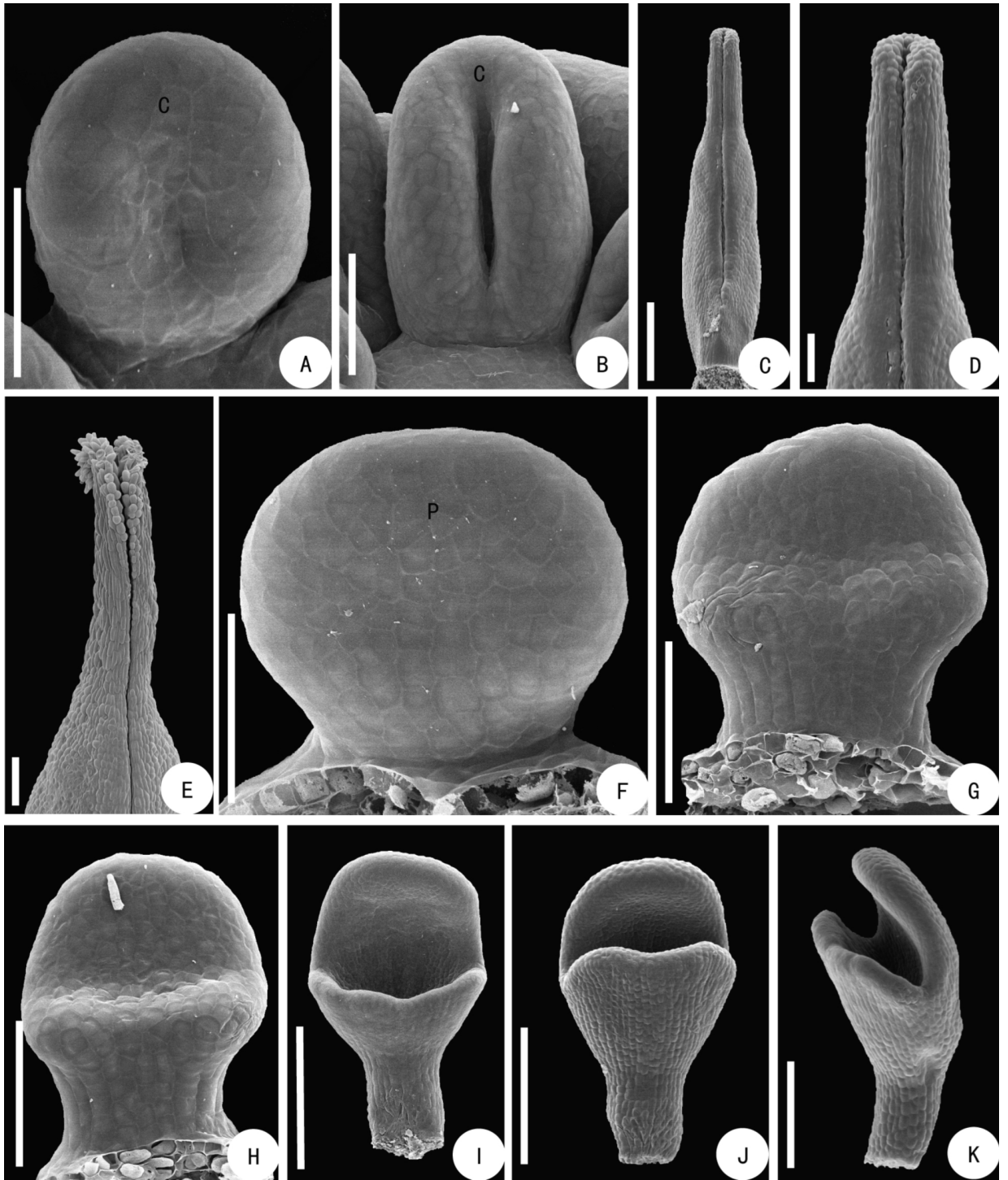
A, B. Initiation of sepal; C. Initiation of petals and stamens, showing their similar shapes but different from that of sepals; D. Initiation of stamens during later stage; E-H. Initiation and development of carpels, which hides the floral apex; I. Showing delayed petal. C. Carpel; P. Petal; S. Sepal; St. Stamen. Scale bars = 100 μm .

图 2 蓝葶草花器官的发生发育

Fig. 2 Floral initiation and development of *Leptopyrum fumaroides*

在后期发育过程中, 萼片原基增大并逐步包围了其他的花器官 (图 2:D)。花瓣原基表现出明显的延迟发育 (图 2:I)。花瓣原基分化为下部较窄的部分和上部较宽的片状结构 (图 3:G)。下部较窄部分逐渐伸长形成花瓣的柄; 上部片状结构

逐渐扁平, 并在腹侧中部形成不明显的凹陷, 在凹陷下方形成两枚突起 (图 3:G, H)。突起逐渐增大愈合, 并和花瓣侧面愈合, 随着凹陷加深, 花瓣逐渐分化出上唇和下唇 (图 3:I-K)。雄蕊原基逐渐地分化出花丝和花药 (图 2:I)。

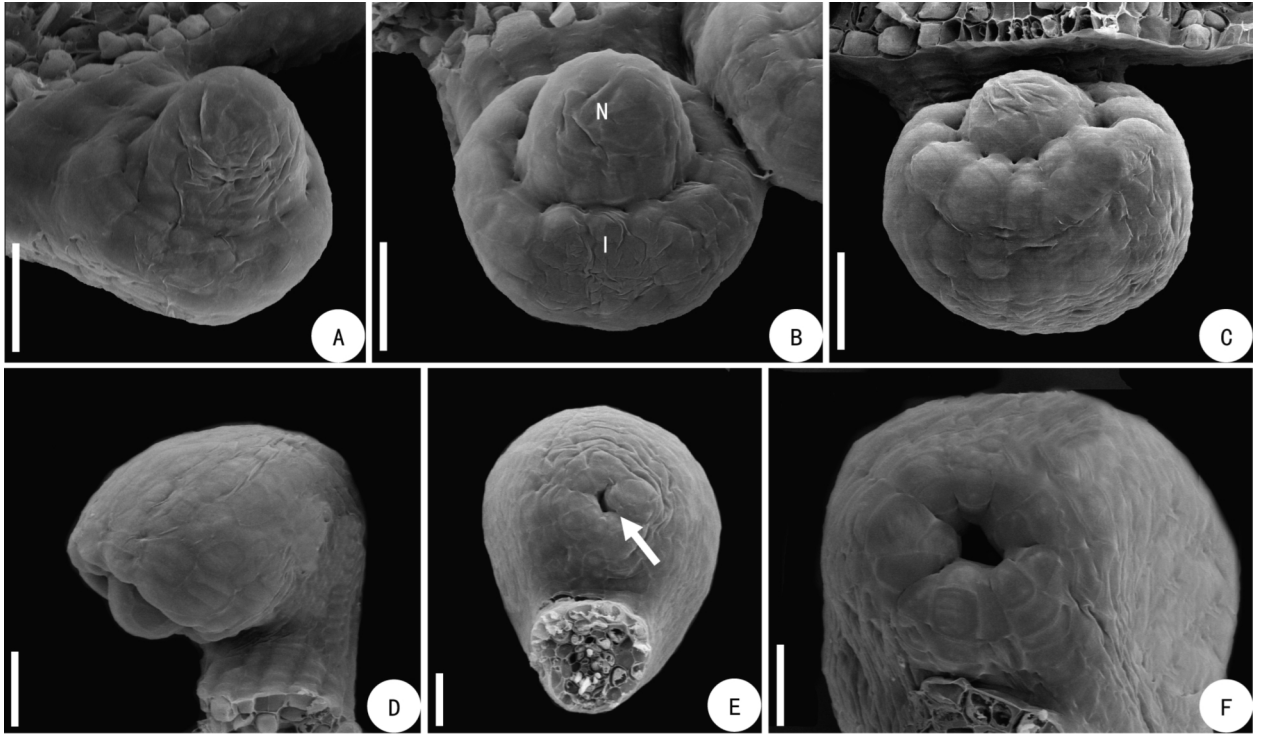


A-E. 心皮原基的发育 A, B. 心皮对折、并逐渐加深; C. 心皮分化出子房和花柱; D. 不成熟的柱头; E. 成熟的柱头组织稍微外翻。F-K. 花瓣的发育 F-H. 花瓣腹侧凹陷,并在凹陷下方产生两个突起; I-K. 两个突起愈合,并和花瓣瓣片愈合,进而形成近二唇形的花瓣。C. 心皮; P. 花瓣。比例尺 = 50 μm 。

A-E. Development of the carpels A, B. Carpels enlarged and become obviously conduplicate; C. Ventral slit formed; D. Immature stigma; E. Upper part of the mature stigma, showing stigmatic tissue consisting of inconspicuous papillae. F-K. Petal development F-H. Petal is differentiated into a lower stalk and an upper blade, and two bulges appear; I-K. Two bulges fuse with each other and with the lamina at the sides and petal becomes bilabiate. C. Carpel; P. Petal. Scale bars = 50 μm .

图3 蓝堇草花器官的发生发育

Fig. 3 Floral initiation and development of *Leptopyrum fumarioides*



A. 胚珠原基; B. 珠被环状发生; C, D. 胚珠逐渐弯曲; E, F. 珠孔。I. 珠被; N. 珠心。比例尺 = 100 μm 。

A. Ovule primordium; B. Initiation of annular integument; C, D. Ovule bends inwards gradually; E, F. Micropyle. I. Integuments; N. Nucellus. Scale bars = 100 μm .

图 4 蓝堇草胚珠的发生发育

Fig. 4 Ovule initiation and development of *Leptopyrum fumarioides*

心皮原基发生后,即发生对折而成为马蹄形(图 2:F,图 3:A)。心皮不断长大,成为明显的对折状(图 2:F-H,图 3:B)。其后,心皮对折的边缘逐渐愈合(图 3:C),分化出下部的子房和上部较短的花柱,心皮基部具心皮柄(图 3:C),在腹缝线顶端向下分化出柱头组织。柱头组织由单细胞乳突组成,沿腹缝线稍下延(图 3:D-E)。

胚珠原基发生后,开始轻微地向内弯曲;伴随着胚珠原基伸长弯曲,珠被在胚珠原基中部环状发生(图 4:A)。珠被逐渐包被珠心,形成珠孔(图 4:B-F)。成熟胚珠倒生,单珠被。

3 讨论

毛茛科植物的花器官有轮状、螺旋状和不规则状三种排列式样(Endress, 1995)。而在唐松草亚科中,花器官排列方式通常为轮状(如耧斗菜

属、尾囊草属、天葵属、人字果属)(冯旻等, 1995; Tucker & Hodges, 2005; Ren et al., 2011; Zhao et al., 2016)或不规则的轮状(唐松草属)(Ren et al., 2011)。本研究中,蓝堇草的花器官为螺旋状发生、螺旋状排列,与唐松草亚科已报道的类群均不同,体现了该属的特殊性。同时,花器官螺旋状发生出现在毛茛科的不同分支中,如黄连亚科的黄连属(*Coptis*)(辜天琪和任毅, 2007),毛茛亚科的罂粟莲花属(*Anemoclema*)、银莲花属(*Anemone*)、白头翁属(*Pulsatilla*)、毛茛属(*Ranunculus*)等(Ren et al., 2011; Zhao et al., 2012a, 2016),这表明毛茛科中花器官螺旋状排列是多次独立发生的(Zhai et al., 2019)。

花瓣是毛茛科植物形态多样性最丰富的器官之一,具有极其重要的分类学价值(Tamura, 1995)。蓝堇草属花瓣原基在发生后,有明显的延迟发育,这与以往报道的毛茛科有花瓣的类群一

致(Zhao et al., 2012a, 2012b, 2016)。唐松草亚科的祖先状态重建表明,花具花瓣为祖先状态,而拟扁果草属、唐松草属中,无花瓣为次生性丢失(Wang & Chen, 2007)。有花瓣的类群其形态结构多样,如天葵属、尾囊草属、耧斗菜属、蓝堇草属花瓣均具短柄,瓣片基部分别为杯状、囊状、距状、近二唇形,而人字果属花瓣多具爪状长柄、瓣片漏斗形(Tamura, 1995; Wang, 2001)。对上述类群花瓣发育过程的研究表明,球形花瓣原基逐渐分化为基部的柄和上部的片状结构以后,片状结构腹侧中部凹陷,进而经过不同程度的生长发育形成各种复杂的立体结构(Tucker & Hodges, 2005; Ren et al., 2011; Zhao et al., 2016; 本研究)。发育中后期不同程度的发育重塑可能在不同类型花瓣形成过程中起到了重要作用(张睿等, 2014)。

尾囊草属、耧斗菜属的雄蕊排列成 10 条规则的直列线,天葵属、唐松草属、人字果属的雄蕊排列成不规则的直列线(Tucker & Hodges, 2005; Ren et al., 2011; Zhao et al., 2016),而蓝堇草属的雄蕊排列成不规则的斜列线。在唐松草亚科中,天葵属-尾囊草属-耧斗菜属分支的雌蕊外往往有 5 枚不育雄蕊,而其他属均未见不育雄蕊(Zhao et al., 2016)。

唐松草亚科植物的心皮数变化较大,人字果属具两枚基部稍合生的心皮,蓝堇草属和唐松草属心皮属较多,为 6~20 枚;其他属多为 3~5 枚(Tamura, 1995; Wang et al., 2001)。具瘦果的唐松草属的心皮原基为囊状,胚珠早期裸露;而蓝堇草属、尾囊草属、耧斗菜属、人字果属等具蓇葖果的类群为对折心皮(Tucker & Hodges, 2005; Ren et al., 2011; Zhao et al., 2016)。毛茛科植物成熟胚珠的珠被层数包括 2 种类型,单珠被和双珠被,胚珠结构在属以上具有极其重要的分类学价值(Wang & Ren, 2008)。从已有报道资料看,双珠被是最毛茛科基本的类型,唐松草亚科的尾囊草属、耧斗菜属、唐松草属、人字果属的胚珠均为双珠被、倒生、具附属物,但是附属物的位置、内外珠被的长度在不同属中表现不同(Wang & Ren, 2008; Zhao et al., 2016)。本研究中,蓝堇草属的倒生胚珠仅具一层珠被,也未见明显的附属物,区

别于唐松草亚科的其他成员,也是该属较特殊的性状。单珠被也出现在铁筷子族、毛茛族和银莲花族(Wang & Ren, 2008),单珠被这一性状独立地出现在毛茛科的不同分支上,表明单珠被是多次发生的次生性状。

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