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长喙毛茛泽泻的花器官发生* Q344.58王玉国¹ 王青锋¹ 陈家宽² 袁秀平³ Q343.712.5⁽¹⁾ 武汉大学生命科学院植物科学系, 武汉 430072)⁽²⁾ 复旦大学生物多样性研究所、遗传研究所, 上海 200433)⁽³⁾ 中国科学院水生生物研究所, 武汉 430072)

摘要 用扫描电镜对长喙毛茛泽泻 (*Ranalisma rostratum* Stapf.) 的花器官发生进行了观察。该种的花器官发生在泽泻科中既典型又比较特殊。其特殊之处在于从花原基的发生直至最外轮 6 枚雄蕊原基的发生过程都存在单向发育; 3 个萼片原基和 3 个花瓣原基的发生存在次序性, 萼片原基和花瓣原基均为顺时针发生, 邻近花序侧生分支复合芽的萼片原基和花瓣原基倾向于优先发生; 最外轮 6 枚雄蕊的发生是成对的按对萼的形式发生。这是以往对该属花器官发生研究没有注意到的。由雄蕊原基向心皮原基的转变发生在与最外轮 6 枚雄蕊相交替的 6 个位点, 其中一些位点仍可能被雄蕊原基所占据, 最初心皮的发生或多或少地与前一轮雄蕊交替, 而以后的心皮的发生顺序看上去是螺旋状排列的。鉴于花器官发生过程出现的具体情况, 长喙毛茛泽泻花的单向发育可能真正代表着原始螺旋策略的相继发生在花部的保留和花序的两侧对称向花器官的扩展; 最外轮 6 枚雄蕊原基的对萼排列, 不支持花瓣-雄蕊复合原基的存在; 本文还通过花部结构分化的差异对毛茛泽泻属与黄花蔺科的联系进行了讨论。

关键词 泽泻科, 长喙毛茛泽泻, 花器官发生

分类号 Q 944

Floral Organogenesis of *Ranalisma rostratum* (Alismataceae)*WANG Yu - Guo¹ WANG Qing - Feng² CHEN Jia - Kuan² YUAN Xiu - Ping³⁽¹⁾ Department of Plant Science, College of Life Sciences, Wuhan University, Wuhan 430072)⁽²⁾ Institute of Biodiversity, Institute of Genetics, Fudan University, Shanghai 200433)⁽³⁾ Institute of Hydrobiology, The Chinese Academy of Sciences, Wuhan 430072)

Abstract The floral development of *Ranalisma rostratum* Stapf. has been observed under scanning electron microscope (SEM). Floral organogenesis of *R. rostratum* is generally typical in Alismataceae, but it is unique in having unidirectional development up to the stage of initiation of the first six stamen primordia. The initiation of the three sepal primordia and the three petal primordia is in proper order. The former is clockwise and the latter too. The sepal primordia and the petal primordia initiate first towards the side of the flower adjacent to the lateral branch complex of the inflorescence. The transition from stamen to carpel initiation occurs at six sites alternating with the first six stamens, some of them may be occupied by stamen primordia. Initiation of first carpel

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primordia alternate more or less with previous stamen primordia, but the initiation of later carpel primordia appear to be spiral. In view of specific condition occurring on the process of floral organogenesis, floral unidirectional development in *R. rostratum* may really represent reservation of successive initiation of original spiral tactics and continuation of bilateral symmetry tactics of the inflorescence. Antisepalous characteristic of the first six stamens, has even not been paid attention to, provides the evidence that the existence of petal – stamen complex primordia is impossible in *Ranalisma*. Basing on the difference of differentiation floral constructure, the relationship between *Ranalisma* and Limnocharitaceae is still discussed.

Key words Alismataceae, *Ranalisma rostratum*, Floral organogenesis

Ranalisma, a genus of Alismataceae, is a key group connected between Limnocharitaceae and Alismataceae (Posluzny & Charlton, 1993; Charlton, 1991; Charlton & Ahmed, 1973a, 1973b). It comprises two species: *R. rostratum* Stapf., from China, Vietnam and Malaysia, and *R. humile* (Kuntze) Hutch., from tropical Africa. Some morphological, anatomical and embryological studies of *Ranalisma* have been finished (Wang, 1996* ; Charlton, 1991; Charlton & Ahmed, 1973a, 1973b). After investigating floral organogenesis of *R. humile* using epi – illumination light microscopy, Charlton (1991) considered that unidirectional development with the same kind of trimery is special and typical in Alismataceae. He suspected the existence of petal – stamen primordia (CA primordia). The floral development of *R. rostratum* has not been studied so that it becomes difficult to compare floral development of the two species and to evaluate exactly the characteristic of floral constructure in *Ranalisma*. The present paper reports the floral organogenesis of *R. rostratum*. The research aims at making an inquiry into some key subjects and providing reliable evidence for phylogenesis of Alismataceae. The subjects are morphological essence of floral unidirectional development, the possibility of petal – stamen complex primordia (CA primordia) and the relationship between *Ranalisma* and Limnocharitaceae.

1 Materials and Methods

Plants of *Ranalisma rostratum* were collected in 1993 from natural population in Dongxiang, Jiangxi, China and cultivated in the experimental water field of Wuhan University, Hubei, China. All experimental materials are from this water field from 1993 to 1994. Inflorescence of all stages was immediately fixed and preserved in formalin – acetic acid – alcohol (FAA). Voucher specimens were deposited in the herbarium (WH) of Wuhan University, China. Fixed materials were later preserved in 70% alcohol – acetone series. The dissected pieces were critical – point – dried with CO₂ in a DCP – 1 apparatus, mounted on aluminum stubs using double – face glue as adhesive, coated with gold – palladium and micrograph taken with an Hitachi S – 650 SEM at 20kV.

2 Observations

2.1 Organography of the natural inflorescence and flower

The bracts of inflorescence arrange in pairs and the inflorescence develops sympodially in *R. rostratum*. Its flower, usually solitary, is bisexual with three green herbaceous sepals and three white membranous petals. There are 6 ~ 10 stamens, and numerous carpels arranging spirally on a convex receptacle. Each carpel has a single basal anatropous ovule.

* Wang J B, 1996. Conservation biological studies on *Ranalisma rostratum*, an endangered plant in China: Life history traits and mechanisms of endangerment. Ph. D. Thesis. Wuhan; Wuhan Univ. (In Chinese with English abstract)

2.2 The process of floral organogenesis

After the transition from vegetative to reproductive meristem, a first bract of the inflorescence initiates opposite to the last foliage leaf (Plate I : 1) and then a second bract opposite to the first one. Subsequently, the inflorescence meristem broadens and bifurcates. The bifurcation product adjacent to the first bract gives rise to a lateral branch complex bud. It can grow and become a vegetative bud and a floral bud (Wang, 1996); The product adjacent to the second bract becomes a floral meristem (Plate I : 2). The floral meristem grows and begins to differentiate. Initiation of three sepal primordia is in proper order. The first sepal primordium initiates adjacent to the lateral branch complex bud earlier than the others (Plate I : 3, 4). The sequence of initiation of them is clockwise (Plate I : 4, 5). Initiation of three petal primordia is also in proper order, and the sequence of initiation of three petal primordia is same direction, i. e. clockwise (Plate I : 5). Side view of floral bud shows clearly that the petal primordia alternate with the sepal primordia (Plate I : 6 ~ 10). The petal primordium opposite to the first sepal primordium occurs later than the other petal primordia (Plate I : 5, 8). After initiation of the petal primordia, two stamen primordia will initiate at the corner between petal primordia and two adjacent sepal primordia. It is worth noticing that two stamen primordia above the petal primordium close to the first sepal primordium initiate in proper order (Plate I : 6, 7, 10). The stamen primordium near the first sepal primordium initiates prior to the other though the two primordia locate in the position of a same "whorl" at later stage of floral development. Initiation of the two stamens adjacent to the third petal primordium is also in proper order (Plate I : 8). But following later synchronous development they appear to be nearly simultaneous (Plate I : 9). However, initiation of the two antisealous stamens appears nearly simultaneous (Plate II : 11). Initiation of the first six stamen primordia may be considered spiral arrangement if antisealous stamen pair is regarded as a complex unit. Charlton (1991) did not notice it in the process of floral development in *R. humile*. As developmental process goes on, the first six stamen primordia tend to develop synchronously (Plate II : 12). Yet it can be seen that the two stamen primordia adjacent to the first sepal primordium develop prior to the others.

Following initiation of the first six stamen primordia, further stamen primordia occupy the relatively suitable position if they exist (Plate II : 13 ~ 15, 17); One usually orient opposite the second petal primordium (Plate II : 13); Two orient separately opposite the second and third petal primordia (Plate II : 17); Three orient separately opposite the first, second and third petal primordia (Plate II : 14); Four orient separately opposite the first, second and third petal primordia and the second sepal primordium (Plate II : 15); Five further stamen primordia (or more) are not observed in the flower of *R. rostratum*. So initiation of further stamen primordia after the first six can occur in succession. The appearance of successive primordia may be too short to be noticed easily. In mature flowers of *R. rostratum*, there are 6-stamen flowers and 9-stamen flowers for the most part. Although further stamen primordia may be not in any semblance of a trimerous pattern in a few flowers, they conform essentially to trimerous pattern as far as the whole population is concerned.

Initiation of carpel primordia becomes rather variable and there is no clear evidence that the numbers of primordia are regular. The first carpel primordia are small in relation to the circumference of floral meristem and they seem to arise as a rather irregular whorl alternating more or less with the previous stamens (Plate II : 12 ~ 16). Further carpel primordia arise between and above previous ones (Plate II : 12, 13, 15, 16). Even initiation of carpel primordia that appear to locate at the same whorl is not simultaneous. The initiation can not be regarded as a whorl initiation, on the contrary it seems spiral initiation particularly in the later stage of carpel development (Plate II : 17, 18). However, In the last stage of carpel Initiation, every three carpel seemsto be a "whorl" and each has one ovule (Plate II: 19, 20).

3 Discussion

As reported for *R. humile*, floral organogenesis of *R. rostratum* is unidirectional at the earliest stages of floral de-

velopment. However, Charlton (1991) only noticed that this phenomenon occurs in the process of sepal and petal initiation, i. e., both sepal and petal initiation occur first on the same side adjacent to the lateral branch complex of the flower bud. So successive initiation of the first stamen primordia is not been considered. Unidirectional development can continue until initiation of the first six stamen primordia. The two stamen primordia adjacent to the first sepal primordium occur earlier than the others. And the two stamen primordia adjacent to the second sepal primordium occur earlier than the two adjacent to the third sepal primordium. Floral unidirectional development in *Ranalisma*, unique type of Alismataceae, differs distinctly from nearly-whorl alterate initiation of floral primordia in the other genus of Alismataceae, such as *Alisma*, *Sagittaria*, *Echinodorus*, *Caldesia* (Wang & Chen, 1997; Sattler & Singh, 1978; Singh & Sattler, 1977, 1973, 1972). On the contrary, it is similar to spiral initiation in some ways. When antisepalous stamen pair is regarded as a complex unit, initiation of the first six stamen primordia may be considered successive initiation. Analysed unidirectional development from the angle of symmetry, symmetry of the floral bud is radial in the earlier phase of floral meristem before the sepal primordia initiate. When the first sepal primordium occurs, symmetry translates from radial symmetry to bilateral symmetry. Then the floral bud is to maintain a rather asymmetrical appearance because of sequential initiation of the second and third sepal primordia. If only it is explained as continuation of bilateral symmetry tactics of the inflorescence as explained in *R. humile* by Charlton (1991), evidently, the kind of symmetry can not be the case. Later, symmetry can be seen nearly bilateral as a result of synchronous development of the second and third sepal primordia. In matrual flowers, radial symmetry is general but bilateral symmetry can be seen in the non-6 (or 9) stamens' flowers. As far as morphological essence is concerned, floral unidirectional development may be reservation of successive initiation of original spiral tactics in the process of floral development and continuation of bilateral symmetry tactics of the inflorescence.

According to floral organogenesis in *R. rostratum*, petal primordia and first six stamen primordia initiate independently. The existence of petal-stamen complex primordia (CA primordia) should be not only suspected as reported in *R. humile* by Charlton (1991). Antisepalous characteristic of the first six stamens, has even not been paid attention to, provides the evidence that the existence of petal-stamen complex primordia is impossible in *Ranalisma*. Although sometimes there are sites where a petal primordium plus two primordia will occur, a common primordia can not be discerned as reported for *Sagittaria montevidensis* (Ronse Decraene & Smet, 1995). Initiation of these primordia has distinct difference in sequence of time and spatial position. Petal primordium and two stamen primordia occupy separately two different whorls. They occur in different sequence, even the two antipetalous stamen primordia do not occur simultaneously, it is not found (or noticed) in the floral development of *R. humile* by Charlton (1991). Developmental studies indicate that petal-stamen complex primordia are not existing in the process of floral development of *R. rostratum*. Sattler and Singh (1978) considered that antipetalous stamen pairs were general characteristic of floral construture in Alismatales. Evidently, *Wisneria* is an exception as a result of only three stamens, and *Limnocharis flava* is also an exception because three simultaneous stamens replace stamen pair. Wang and Chen (1997) observed that antipetalous stamen pair is exactly not existing in the initiation process of floral organogenesis of *Cadisia parnassifolia*. So this point of Sattler and Singh (1978) is not suitable. Antipetalous stamen pairs should be not regarded as general characteristic of floral construture in Alismatales, even this point narrowed down the scope of Alismataceae, it is in question.

Floral development of *R. rostratum* does not exhibit too much relationship with Limnocharitaceae than development of inflorescence and pseudostolon. Its centripetal development of androecium differs distinctly from centrifugal development of androecium in Limnocharitaceae (e. g. *Hydrocleys*, *Limnocharis*) though it can be interpreted as secondary (Sattler & Singh, 1978; Leins, 1975; Leins & Stadler, 1973). This indicates that the evolution of flower and inflorescence in the two families is not parallel. It may be result from floral development tend toward different directions owing to long-term natural selection in different environments.

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Explanation of Plates

Plate I 1. The inflorescence meristem (I) has grown away from the vegetative bud (V) which is left adjacent to the removed foliage leaf (rL). The vegetative bud has formed a prophyll (Pr) ($\times 480$). 2. The inflorescence meristem has bifurcated, leaving a lateral branch complex meristem (LBC) adjacent to the first bract (B1) and the floral meristem (F) adjacent to the second bract (B2) ($\times 575$). 3. The first sepal primordium (Se1) initiates first at the site of bulge adjacent to the lateral branch complex (LBC) ($\times 380$). 4. Showing successive initiation of the three sepal primordium (Se1, Se2 and Se3) ($\times 340$). 5. Showing successive initiation of the sepal and petal primordium (Se1, Se2, Se3, P1, P2 and P3) ($\times 350$). 6. Showing initiation of the first sepal primordium (Se1) and the third sepal primordium (Se3), the first sepal primordium prior to the third sepal primordium, the first petal primordium has been initiated ($\times 400$). 7. Side view of floral bud with the first sepal primordium (Se1) and the second sepal primordium (Se2) showing initiation of the second petal primordium (P2) ($\times 400$). 8 ~ 9. Side view of the bud with the second sepal primordium (Se2) and the third sepal primordium (Se3) and the third petal primordium (P3) showing successive initiation (in Plate I; 8) and following synchronous development (in Plate I; 9) of the two stamen primordia (S, s) ($\times 385$; (300)). 10. Side view of floral bud with the first sepal primordium (Se1) and the second sepal primordium (Se2) and the second petal primordium showing initiation of two stamen primordia adjacent to the second sepal primordium, the stamen primordium near the first sepal primordium occurs first. ($\times 360$)

Plate II 11. Side view of floral bud showing simulateous initiation of the two stamen primordia (S) adjacent to the first sepal primordium (Se1). ($\times 400$) 12. Showing the floral bud with 6 stamen primordia. The two stamen primordia near the first sepal primordium (has been removed, black arrow puts out its position) are larger than the others ($\times 220$) 13 ~ 17. Showing appearance of 7 ~ 10 stamen (or stamen primordia) and their relative position, the first carpel primordia

(c) arrange in an irregular whorl alternating with the previous stamen primordia, following carpel primordia (c') whorl alternate more or less with the previous stamen primordia and the first carpel primordia (c) in Plate II; 16 ($\times 450$). II: 13, II: 17, II: 14 and II: 15 Show separately the floral bud with 7, 8, 9, 10 stamen primordia ($\times 300$, $\times 165$, $\times 350$, $\times 250$). Black arrow puts out the position of the first sepal primordium removed in Plate II; 13 and 17. 17 - 18. Initiation of carpel primordia (showing by white arrows in Plate II: 17) in the later carpel development seem to be spiral ($\times 165$, $\times 200$). 1920a, b. Showing carpel primordia (c, c') In the later stages of floral initiation, every three carpel seems a whorl (Plate II: 19, 20a, b) and each has one ovule (Plate II: 20b) ($\times 135$, $\times 150$, $\times 110$).

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书评 Book Reviews II

裘维蕃 (主编): 《菌物学大全》, 科学出版社, 1998年, x + 1124页, 图版 11幅, 书号 ISBN 7-03-005598-5, 定价 179.00元。

Qiu, W. F. (Chiu, W. F.) (Editor in chief): *Extensive Mycology*. Science Press, Beijing, 1998, x + Pp. 1124, Pls. 11, in Chinese with English table of contents, ISBN 7-03-005598-5. Price: Chinese Yuan 179.00.

由裘维蕃主编、余永年副主编, 我国菌物学界 14 位著名菌物学家编著的《菌物学大全》已于 1998 年 3 月正式出版并与读者见面。这部权威性巨著是由我国从事多年菌物学研究和教学、具有丰富实践经验的专家教授联合撰写而成的, 它是一部内容较为全面并且又有相当深度的菌物学基础理论性著作。全书共分 10 编, 每编又分若干章节, 主要包括真菌、裸菌(粘菌)、地衣、菌根菌的概念、形态和分类、生理和遗传、生态和地理、菌物毒素、真菌的病毒、寄生于昆虫的菌物、国际菌物学发展史等, 其中不少是新知识、新认识, 有的则全是根据我国学者的多年调查研究成果总结出来的。书中除附有 11 幅精美的图版外, 还有大量插图和参考文献, 书末附有中文索引和拉丁名索引, 便于读者查阅和检索。此书图文并茂, 对读者了解当前国内外菌物学研究水平和主要方面很有帮助, 它是菌物学工作者不可缺少的工具书, 对从事生物学、农学、林学及其它有关学科的人员都是十分重要的参考书。该书对中国菌物学的发展必将产生积极而深远的影响。

由于此书的影响面可能将非常广泛, 为日臻完善, 在将来再版时有必要对其中的少部分插图和个别地方的内容根据最新研究成果稍作修改或补充, 如第 19 页图 1-3-1 中 2 的菌丝横隔上应有锁状联合; 外担菌 (*Exobasidium*) 的担孢子在担子孢梗 (sterigmata) 上的着生方式在担子菌中是十分特别的, 但在第 26 页图 1-3-5 中没有正确反映出来; 第 36 页谈到我国有 *Amanita caesarea* 和其变种, 按现代真菌物种概念和据最近的研究结果, 上述两个“欧洲、北非”的分类群在我国可能没有分布; 第 37 页论及到的鸡枞菌的学名似应为 *Termitomyces eurrhizus* (Berk.) Heim, 而非 *T. albuminosus* (Berk.) Heim (= *Agaricus albuminosus* Berk.)。Pegler 和 Rayner (1969) 研究了 *Agaricus albuminosus* Berk. 的模式标本后发现它是大环柄菇属 (*Macrolepiota*) 的一员 (Pegler, 1972), 后经进一步研究认为它是 *Leucocoprinus cepaestipes* (Sow.: Fr.) Pat. 的异名 (Pegler, 1986)。第 74 页图 2-2-23、第 152 页图 2-3-106B 及第 153 页图 2-3-108A 是转载它书(文)的, 非常重要的细节在多次临摹后已荡然无存, 摆在读者面前的临摹图与最初发表的原图相比似乎已面目全非, 这难免会让读者产生误解。

杨祝良 (中国科学院昆明植物研究所)