Floral organogenesis of *Potamogeton distinctus* A. Benn. (Potamogetonaceae)

**Abstract** The floral organogenesis of *Potamogeton distinctus* A. Benn. was observed under the scanning electron microscope (SEM). The floral buds are first initiated on the lower portion of inflorescence in alternating whorls of three. Each of the floral buds is subtended by a bract primordium during the early stages. The primordia of the floral appendages arise on the floral bud acropetally. Two lateral tepals are first initiated and then two median ones soon after. Stamens are normally initiated as elongate primordia opposite the tepals, with the two lateral stamens preceding the median ones. The two carpel primordia arise alternating with the stamens. In some flowers, one of the two gynoecial primordia becomes inactive soon after they are initiated, or only one carpel primordium is initiated. The present observation of the gynoecial development supports the viewpoint that the evolution of flower in *Potamogeton* involves a reduction in number of parts. The existence of bract primordium during the early stages in many species of *Potamogeton* indicates that the absence of bract in mature flowers should be the result of reduction.

**Key words** *Potamogeton distinctus*; Floral organogenesis

The interpretation of the flower of *Potamogeton* has been controversial for a long time (Sattler, 1965). The perianth segments were sometimes interpreted as stamen connectives, bracts, or as a true perianth in this genus (Tomlinson, 1982; Sattler, 1965). On the other hand, some of the floral features in *Potamogeton* have led to suggestions that they may be pseudanthia (Miki, 1937).

Although most authors have agreed that the flower of *Potamogeton* is generally tetrahermous, recent studies indicate that a high percentage of variation occurs in the flower structure of *Potamogeton* (Charlton, Poslusnzy, 1991). Based on the observations of floral development, Poslusnzy & Charlton (1993) and Poslusnzy & Sattler (1974) considered that the flowers of *Potamogeton* exhibit features of both flower and inflorescence in the traditional sense. However, floral developmental studies have been mainly concentrated on the species of tetracarpellate or unicarpellate flowers. The bicarpellate flowers in *P. distinctus* have provided an opportunity to make a comparison of its floral d-
development with that of the species previously studied. The present paper describes the development of the inflorescences and flowers of this species for a better understanding of the development of the bicarpellate flower and the floral structure in *Potamogeton*.

1 Materials and Methods

The material of *P. distinctus* was collected in May 1996 from Wuhan, Hubei, China, and grown in the pond for aquatic plants culture in Wuhan University. Floral buds were fixed and preserved in formalin-acetic acid-alcohol (FAA). For scanning electron microscopy, material was washed in 70% alcohol, dehydrated in 95% alcohol, dissected, and further dehydrated in an ethanol-acetone series. The material was then critical point dried with CO₂. Inflorescences mounted on metal stubs were coated for 2–3 min with gold-palladium and were observed under a Hitachi S-800 SEM.

2 Observations

2.1 Organography

The flowers are borne on spikes and arranged in alternating whorls of three. Each flower is composed of four bract-like perianth members or tepals which are affixed in the region of the stamen connective. The four nearly sessile stamens are directly opposite the tepals and have large, extrorse anthers. Generally each flower has two separate carpels in the centre. Flowers with only a single carpel were occasionally noticed, but none with three or four carpels were observed.

2.2 Organogenesis

The inflorescence is initiated from the vegetative apex. The narrow apical meristem broadens at first (Plate I : 1), then the young inflorescence bud (1) elongates rapidly and forms pedicel at the base (Plate I : 2). As enlargement continues, the floral buds (F) are first initiated on the lower portion of the inflorescence axis (Plate I : 3–5), and are arranged in alternating whorls of three on the axis (Plate I : 4, 6). Each floral bud is associated with a bract primordium (B) which is initiated at the same time as the floral primordium (Plate I : 5, 7). The bract, which is prominent during the early stages, later becomes inactive (Plate I : 8, 9).

The young floral bud increases in size and gradually becomes dome-shaped (Plate I : 7–9). All primordia of the floral appendages initiate in acropetal sequence. The first floral appendages to arise on the floral bud are two lateral tepals (P1) (Plate II : 1). They (P1) are initiated almost simultaneously, and grow out as broad elongate primordia (Plate II : 1, 2). The two median tepals (Pm) appear soon after in the same way (Plate II : 2, 3). Immediately afterwards, the two lateral stamens (A1) arise as elongate primordia opposite to the primordia of the lateral tepals (Plate II : 2, 3). Soon after initiation, more rapid upgrowth occurs at the lateral portions of the stamen primordia, thus beginning the differentiation of the anther thecae. Immediately afterwards, the two median stamens (Am) are initiated at the position opposite to the primordia of median tepals in a manner similar to that of the lateral stamens (A1). After initiation the stamen primordia grow rapidly, while the development of tepal primordia is relatively slow (Plate II : 3–5).

With the development of the perianth segments and stamens, the floral apex, which has become flattened and almost square in the horizontal plane (Plate II : 2, 3), becomes slightly dome-shaped again (Plate II : 4). The two gynoecial primordia arise at about the same time in the position slightly near to one side of the floral apex (Plate II : 4, 5), and they are alternating with the primordia of stamens (Plate II : 4, 5). After that, the gynoecial primordium becomes peltate through the rapider upgrowth at its periphery (Plate II : 6). And then, the carpel wall grows up as an open-ended tube, and one ovule primordium is initiated on the carpel wall (Plate II : 7). After ovule initiation, the carpel wall grows more rapidly, enveloping the young ovule primordium (Plate
At the same time, the tepals enlarge rapidly (Plate II: 7, 8). The upgrowth beneath the stamen and the tepals results, at maturity, in the tepals appearing to be inserted on the stamen connective between the pairs of microsporangia (Plate II: 9). In some flowers, there is only one carpel; this is because only one gynoecial primordium is initiated, or soon after the two primordia initiated, one of them becomes inactive (Plate II: 10 – 12).

3 Discussion

The interpretation of the sterile appendages in Potamogeton has been controversial for many years. Markgraf (1936) pointed out that the sterile appendages were only outgrowths of the stamen connectives (see Poslusnzy, Sattler, 1974; Sattler, 1965). Sattler (1965) suggested they were initiated like perianth members. A detailed examination on the sterile appendages was carried out by Poslusnzy and Sattler in 1974. They further confirmed Sattler's view based on the fact that the primordia of these appendages are initiated at the flanks of the floral apex slightly before those of the stamens. They also pointed out that if the flower was considered as a monoaxial organ system, the sterile appendages would be referred to as tepals or perianth members, and that if the flower was interpreted as a condensed inflorescence, they might be referred to as bracts. The floral development in P. richardsonii has shown that the flower of Potamogeton is a structure much closer to a true flower, and that the sterile appendages should be referred to as tepals rather than as bracts (Poslusnzy, Sattler, 1974; Sattler, 1965). The sterile appendages are homologous to perianth members rather than the stamen connectives (Poslusnzy, Sattler, 1974, 1973; Sattler, 1965). The present observation on P. distinctus also indicates that the sterile appendages are homologous to perianth members. Therefore, we suggest that the sterile appendages should be interpreted as tepals.

In Potamogeton, stamen initiation has different ways. According to the floral developmental studies of Poslusnzy (1981) and Poslusnzy & Sattler (1973), each of the lateral stamens in P. zosteriforme and P. densus is initiated as two separate primordia which only later become connected by interprimordial growth. This phenomenon was considered by Poslusnzy & Sattler (1973) to be supportive of Miki's (1937) viewpoint that the stamens of Potamogeton flower were derived from an inflorescence. However, floral developmental studies of other species in this genus indicate that each of the lateral stamens arises as elongate primordium in the same way of the median stamens inception (Charlton, Poslusnzy, 1991; Poslusnzy, Sattler, 1974; Sattler, 1965). This was considered to be a normal manner of stamen initiation in Potamogeton (Charlton, Poslusnzy, 1991). Our observation shows that the stamens of P. distinctus are also initiated in this normal manner.

According to our observation, only two gynoecial primordia develop in this species. They are initiated respectively at the same time and alternating with the primordia of stamens. When initiation, the primordia are slightly near to one side of the floral apex. This implies that the bicarpellate flower of P. distinctus is probably the result of primordial omission of tetracarpellate flower. None of tetracarpellate flowers have been found in materials observed here. But in some floral apex, soon after the two gynoecial primordia are initiated, one of them becomes inactive or only one primordium is initiated. Unicarpellate flowers have been seen in almost every inflorescence. These results support the viewpoint of Charlton and Poslusnzy (1991) that the evolution of flower in Potamogeton usually involves a reduction in number of parts.

In some species of Potamogeton, such as P. zosteriforme (Poslusnzy, 1981), P. richardsonii (Poslusnzy, Sattler, 1974; Sattler, 1965), P. lucens and P. epiphydus (Charlton, Poslusnzy, 1991) as well as P. distinctus (the present paper), each floral bud is subtended by a bract primordium which is prominent during the early stages of floral inception but later becomes inactive. This suggests the absence of bract in Potamogeton flower at maturity should be the result of reduction.
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References

Explanation of plates

摘要  运用扫描电镜观察了眼子菜的花器官发生过程。结果表明，花原基从花序轴的基部开始以三数交互轮状的方式发生，在花原基发生的早期具有明显的苞片原基形成。花器官是以向心的方式发生的，二枚侧方花被片原基首先形成，紧接着产生二枚中间花被片。四枚雄蕊分两轮分别在与侧方花被和中间花被相对的位置发生，四枚雄蕊原基在发生时均呈长条形。上述四轮花被和雄蕊虽然在时间上以二数轮状的方式发生，但在空间上花被片和雄蕊各自分别排成一轮。最后，二个心皮原基在花原基顶端略偏于一侧并与雄蕊相间的位置同时发生。有些花的二枚心皮原基发生后其中一枚很早即停止生长或仅有一枚心皮原基形成。本文结果支持了眼子菜属心皮数目逐渐向简化的方向演化的观点。在花原基早期发育的过程中苞片原基的存在表明眼子菜属植物成熟花中缺乏苞片是简化的结果。

关键词  眼子菜；花器官发生

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See explanation at the end of text
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