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孟仁草的花序发育研究

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摘要: 在光学显微镜和扫描电镜下观察了禾本科(Poaceae)虎尾草属(*Chloris* Sw.)孟仁草(*Chloris barbata* Sw.)的花序发育过程,以寻找适于虎尾草群(*Chloris* group)分支分析的发育性状。结果发现了未见于成熟花序的23个发育性状。阐明孟仁草花序的本质是二级长侧枝包围平截的主轴构成指形花序。该类型花序仅见于单子叶植物和少数高度特化的双子叶植物。涉及花序分枝的分子遗传机制研究亟待开展。

关键词: 孟仁草; 花序; 发育; 性状; 禾本科
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Inflorescence Development of *Chloris barbata* (Chloridoideae, Poaceae)

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Abstract: In order to look for developmental features for future cladistic studies of *Chloris* group (*Chloris*, *Cynodon*, *Eleusine*, *Dactyloctenum*, and *Microchloa* etc.), digitate inflorescence development in *Chloris barbata* had been examined under light and scanning electron microscope. Twenty-three developmental features indiscernible in the mature inflorescence were found. The structure of digitate inflorescence of *Chloris barbata* show that several secondary long axes circle the truncated main axis in the branch system. This type of inflorescence branch system has been reported only in monocotyledons and few highly specialized dicotyledonous group. To clarify whether the branch primordia are derived from a part of the shoot apical meristem and/or axillary meristems, studies on the genetic control of grass inflorescence architecture involved in branching are imperative.

Key words: *Chloris* barbata; Inflorescence; Development; Characters; Poaceae

Poaceae is one of the largest and most widely distributed families of vascular plants and dominant in many ecosystems. The genus *Chloris*, having c. 50 species and characterized by digitate inflorescence (Fig. 1A, B), belongs to subfamily Chloridoideae which are distributed in tropical and subtropical region with arid and semiarid habitats[1]. One of these species, *Chloris barbata* Sw., commonly occurs in SE China[2].

Mature inflorescence morphology of the family has been intensively studied by previous workers[3-5]. Mature inflorescences can be seen as a specific stage of development, which is not enough to understand their morphological diversification and relationships[6]. Therefore, it may be preferable to look for homologies at the different developmental stages of inflorescences

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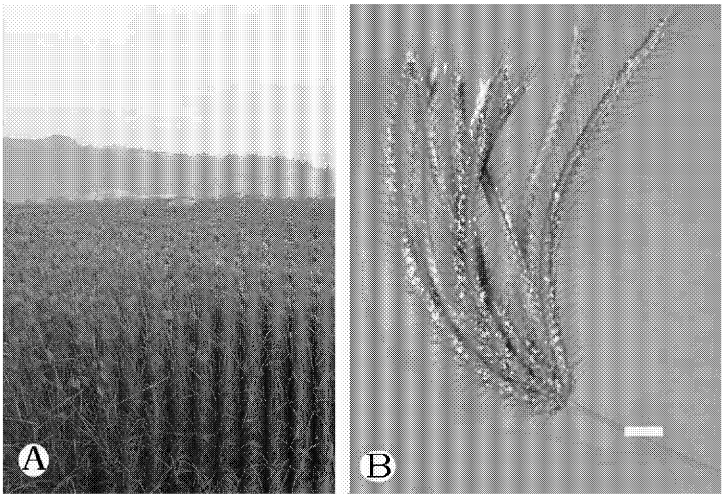

Fig. 1 *Chloris barbata*

A. Habit; B. Morphology of the mature infloresnce.

Scale bar = 10 mm.

rather than only at the mature inflorescences[7].

The analysis on inflorescence development of *Chloris barbata* may also help to understand of the nature of digitate branches. Branch system has been viewed as one of the long paraclades being the main axis[8], or as several long paraclades circling the truncated main axis[5,9]. The observation of inflorescence development will allow the question to be properly formulated.

The present study aims to: (1) explore the precise developmental sequences and clarify the nature of branch system of the digitate inflorescences in *Chloris barbata*; and (2) search for features in the development of inflorescences that could be used in future cladistic studies on the finger grass clade.

1 Materials and methods

Field work *Chloris barbata* was collected in bushland c. 20 km from Sanya to Anyou, Hainan, Qing LIU 02026 (SCIB); around dry steppe in Yuanmou, Yunnan, Qing LIU 05026 (SCIB); near the coast in Dongfang, Hainan, Zhonglun WU 546 (SCIB).

Experiment work Approximately 40 inflorescences in various developmental stages of *Chloris barbata* were collected and preserved in FAA (formaldehyde-ethanol-glacial acetic acid), dissected under the Nikon SMZ645 Stereo Microscope (NIKON, Tokyo, Japan). Then the representative samples were fixed overnight in 2% (V/V) glutaraldehyde in phosphate buffer at 4℃, rinsed three times, five minutes each and 2 h in 1% osmium tetroxide (OsO_4, pH = 6.8) at room temperature. Samples were dehydrated in a series of ethanol solutions (50%-70%-90%-100%-100%-100%), critical point dried in an Eiko DX-1 critical-point dryer (Eiko Engineering, Hitachi, Japan) and sputter coated with gold in a JFC-1100 sputter coater (JEOL, Tokyo, Japan). Examination and photography of inflorescences were done under a Jeol JSM-6360V scanning electron microscope (SEM) (JEOL, Tokyo, Japan) at 10 kV. Polar axis diameter (P) and equator axis diameter (E) were measured using SEM to obtain the data. The proporation of P/E corresponding different shapes follows Erdtman[10].

2 Results

The beginning of inflorescence development in *Chloris barbata* can be identified by the elongation of the shoot apex meristem as it undergoes the transition from vegetative to reproductive growth (Plate I: A). For the purposes of description we here define the main inflorescence axis as the first (1°) axis, the major branches as secondary (2°) axes, branches on these as tertiary (3°) axes, and so on.

Inflorescence development of *Chloris barbata* starts with the formation of suboblate (100 · P/E = 79.34) 1° axis primordium (P = 44.15 μm, Plate I: A). It stops elongation (P = 80.99 μm, Plate I: B) until the initiation of 3 ~ 9 2° axis primordia in 25° angle. These 2° axis primordia are arranged verticillate surrounding the arrested 1° axis (Plate I: C ~ D). When these 2° axis primordia elongate to nearly 630.00 μm, the suboblate (100 · P/E = 83.59) 3° axis (spikelet) primordia initiate basipetally on the 2° axis (Plate I: E). The proximal spikelet primordium (P = 22.45 μm, Plate I: F) is 50% smaller than the distal one (P = 51.25 μm, Plate I: G).

Spikelet differentiation on the 2° axis of *Chloris barbata* is basipetal (Plate I: H). It starts with the inception of two alternate concave glume primordia. The first formed primordium develops into a lower glume and the second one into an upper glume (Plate I: I). The glume arrangement of spikelets on the 2° axis is similar in all samples examined, the lower glume of spikelet is near the center of the abaxial surface of 2° axis, in contrast to the upper glume of spikelets on the lateral of the abaxial surface of 2° axis. In *C. barbata*, the lemma primordia of the four florets (f_1, f_2, f_3, and f_4) on the spikelet axis are initiated in turn. The differentiation and maturation of f_1 along the spikelet axis is acropetal (Plate I: J; Plate II: A, C, E, G), the rest floret meristem remains indifferent. When the spikelet axis elongates in *C. barbata*, the lemma primordium of f_1 arises (Plate I: I). Subsequently, the f_1 primordium initiates (Plate I: J). The lemma of f_2 initiates alternately (Plate II: A). Simultaneously, f_1 primordium differentiates. The palea primordium initiates first (Plate II: B). Three stamen primordia (E = 17.69 μm) arise after the formation of the palea (Plate II: C). Two of them are initiated on the lateral flanks of f_1 meristem and the other one, abaxially (Plate II: D). Following the initiation of the lemma of f_3 (Plate II: E), the gynoecial primordium (E = 16.08 μm) of the f_1 initiates from the remaining floret meristem, and develops a gynoecial ridge surrounding the ovule primordium (Plate II: F). The lemma of f_4 initiates from the remaining spikelet meristem (Plate II: G). After that, two lodicules of f_1 initiate in a whorl outside the stamen primordia (Plate II: H), at the same time, the stamen primordia of the f_1 expand to form anther (E = 57.20 μm). Later, the filaments of stamens gradually elongate and, the branches of the style and stigma develop. In *C. barbata*, the floral organs of f_1 differentiate accompanied with the lemma elongation of f_2, f_3, and f_4. The lemma of f_4 initiates from the remaining spikelet meristem and reduces to vestige without awn. Therefore, the lemmas of three florets stick their awns out glumes in the spikelet at the end of anthesis (Fig. 1B; Plate II: I). Finally, the 2° axis ends with a blind extension (Plate II: J).

The elongation of inflorescence peduncle occurred late in development, i.e. from the lodicule formation to the caryopsis maturity. The elongation extent varies between 1.50 ~ 2.02 cm in *C. barbata* (Fig. 1B).

3 Discussion

The transition of flowering in shoots of *Chloris barbata* involves the meristem elongation, which was also observed in other members of Poaceae[6,11]. The complexity of phyllotaxis in *C. barbata* is positively correlated with the diameter of the apical meristem and the number of orthostichies[3].

Our SEM observations reveal that several secondary axes circle the truncated main axis in the branch system. The 1° axis arrestation and 2° axis elongation in early development produce the distinct appearance of digitate inflorescences in *Chloris barbata*. This does not support the previous interpretation that one of the 2° axes in branch system is the main axis[8]. As *Chloris barbata* is wind-pollinated, its digitate inflorescence probably reflects alternate solutions to manipulate airstreams to enhance pollen export and import. Spikelets in diffuse inflorescence branch system of *C. barbata*, relatively independent oscillation, have the potential to sweep through a large volume of air. In addition, the flexible branches of digitate branches allow reconfiguration of inflorescence shape as wind speed increases, reducing the inflorescence's projected width and the associated drag substantially. These features introduce an alternate mean of effecting pollen removal and capture. However, these interpretations largely await verification.

Among the developmental features analyzed here the following ones cann't be discerned in mature inflorescence and could be potential sources of new morphological characteristics to be used in future cladistic analysis: (1) P of 1° axis primordium; (2) E of 1° axis primordium; (3) 100·P/E of 1° axis primordium; (4) shape of 1° axis primordium; (5) the 1° axis length at the moment of initiation of 2° axis primordia; (6) number of 2° axis primordia; (7) arrangement of 2° axis primordia on 1° axis; (8) angle between 1° axis and 2° axes; (9) the 2° axis length at the moment of initiation of 3° axis primordia; (10) end of 2° axis; (11) peduncle length; (12) P of proximal spikelet primordium; (13) P of distal spikelet primordium; (14) 100·P/E of spikelet primordia; (15) shape of spikelet primordia; (16) initiation succession of spikelets on 2° axis; (17) spikelet compression; (18) distal end of spikelet axis; (19) floret number per spikelet; (20) floret maturation number per spikelet; (21) E of stamen primordium; (22) E of gynoecial primordium; (23) E of anther.

Our study shows the precise developmental morphology in the branch system of *Chloris barbata*. This type of branching can be characteristic in certain tribes in Poaceae. The reports of this type of branching have been limited to monocotyledons and some highly specialized dicotyledonous group. It can be explained by the division of shoot apical meristem[12-13]. To clarify whether the branch primordia are derived from a part of the shoot apical meristem and/or axillary meristems, studies of the genetic control of grass inflorescence architecture involved in branching are imperative. A reevaluation of vegetative shoot organization among more examples of nonspecialized monocotyledons species with digitate inflorescence may lead to a new understanding of the branch system itself.

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Explanation of plates

1: 1° axis; 2: 2° axis; 3: 3° axis; A: Anther; f_1: First floret; f_2: Second floret; f_3: Third floret; f_4: Fourth floret; Gr: Gynoecial ridge; L_1: Lemma of f_1; L_2: Lemma of f_2; L_3: Lemma of f_3; L_4: Lemma of f_4; Lg: Lower glume; Lo: Lodicule; Lp: Leaf primordium; Ov: Ovule; P_1: Palea of f_1; Sa: Shoot apex; St: Stamen; Ug: Upper glume.

Plate I

A. Vegetative shoot apex;

B. Elongation of the 1° axis primordium and initiation of 2° axis primordia;

C. Elongation of 2° primordia;

D. Polar view of verticillate arrangement of 2° axes surrounding the arrested 1° axis;

E. Initiation of suboblate 3° axis primordia in basipetal succession;

F. Proximal spikelet primordia of the 2° axis;

G. Distal spikelet primordia of the 2° axis;

H. Differentiation of spikelet primordia in basipetal succession;

I. Initiation of glumes and the first lemma;

J. Initiation of the first floral meristem.

Scale bars = 10 μm in A, B, F, G, I, J and 100 μm in C ~ E, H.

Plate II

A. Initiation of the second lemma;

B. Initiation of palea in the first floret;

C. Elongation of lemmas and differentiation of floral organs in the first floret;

D. The first floret of left spikelet in Plate II: C, initiation of stamen;

E. Initiation of the third lemma and differentiation of gynoecium;

F. The first floret of left spikelet in Plate II: E, Initiation of gynoecial ridge;

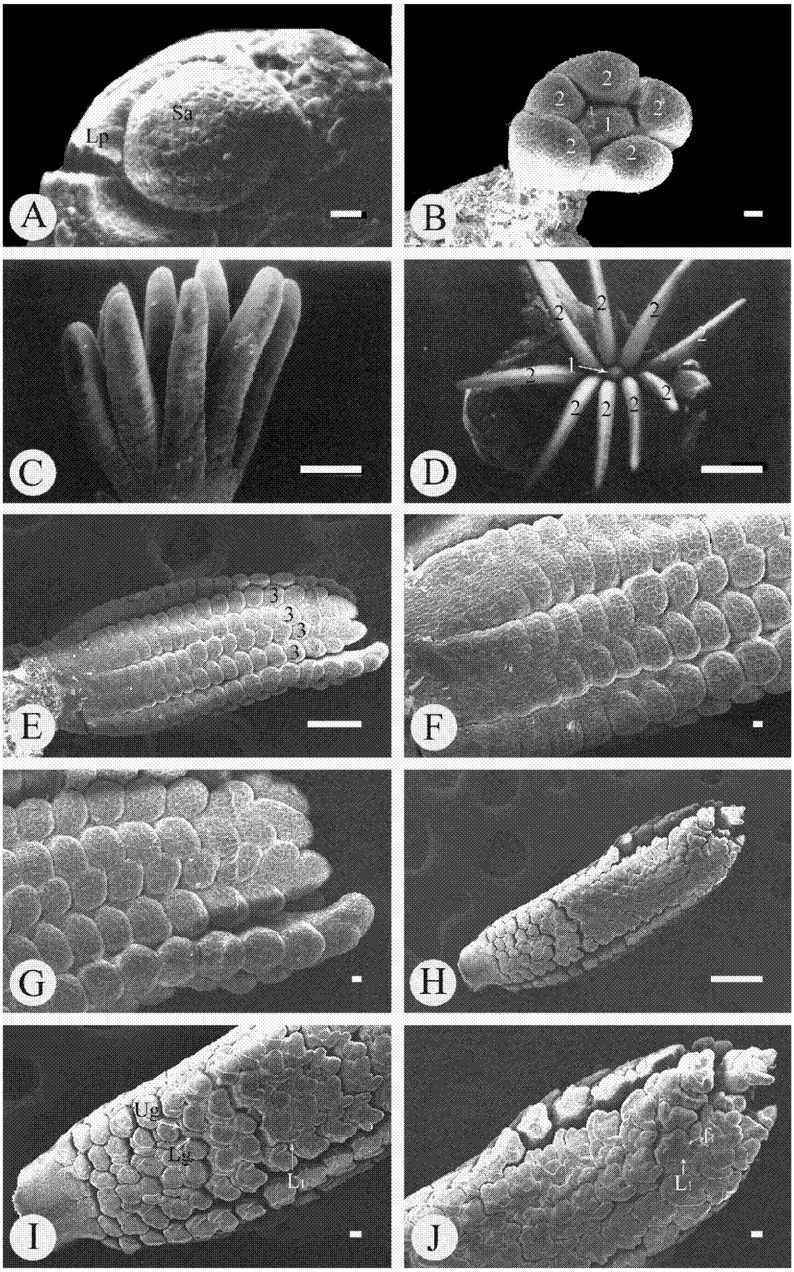
G. Initiation of the fourth lemma;

H. The first floret of left spikelet in Plate II: G, Initiation of lodicules and anther;

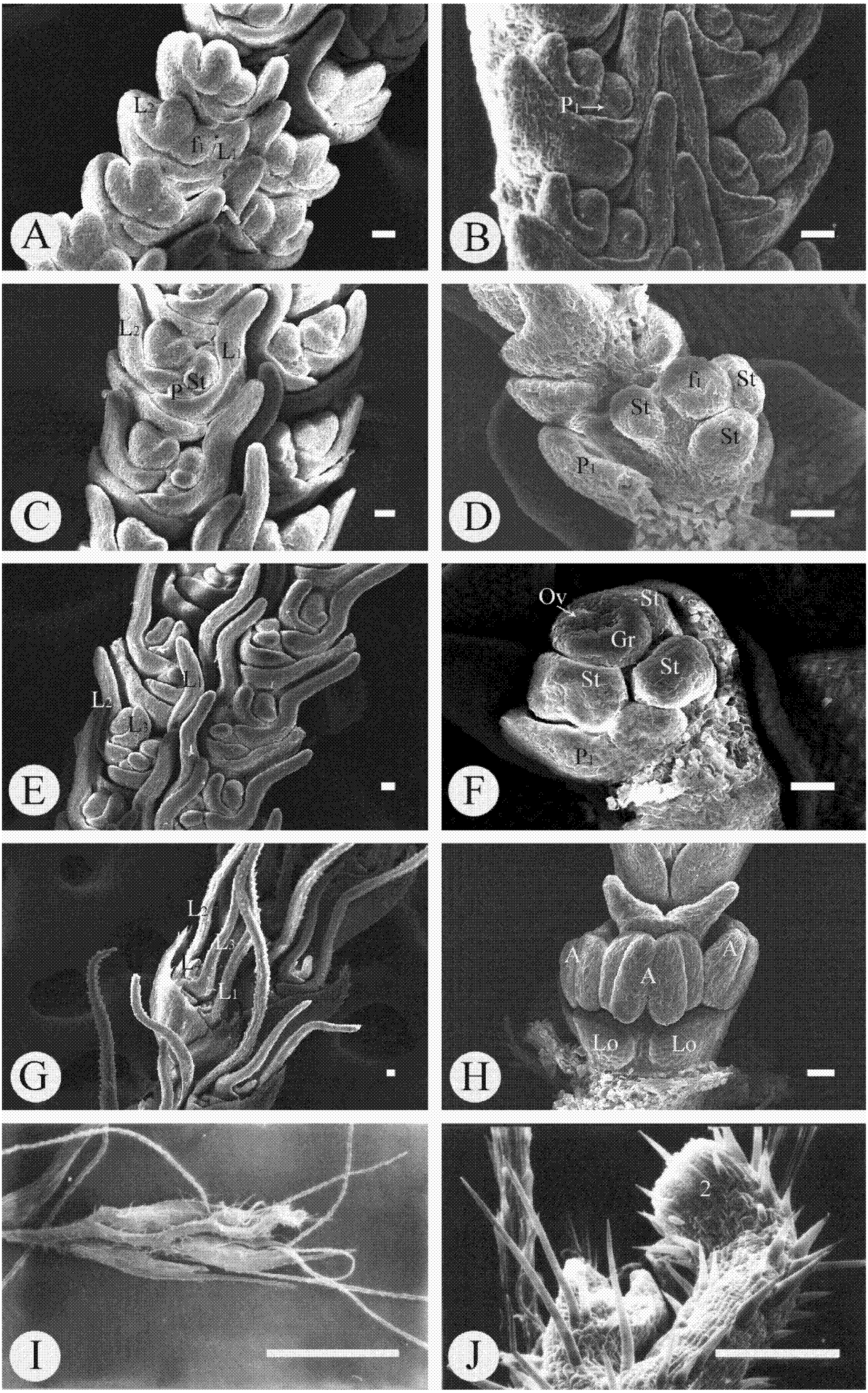
I. Three protruding awns of every spikelet in *C. virgata*;

J. A blind extension in 2° axis apex.

Scale bars = 10 μm in A ~ H and 100 μm in I ~ J.



LIU Qing: Plate I



LIU Qing: Plate II