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Biosystematic relationships among *Psathrostachys*, *Critesion* and *Hordelymus* in Hordeinae (Poaceae) based on the anatomical characteristics of leaf blades

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The anatomical characteristics of leaf blades of the major species of *Psathyrostachys*, *Critesion* and *Hordelymus* in Hordeinae were examined, their similarities and differences on the leaf blades were summarized, and the taxonomic significance of leaf anatomical features among them also were discussed. Furthermore, according to the evolutionary trends of anatomical characteristics of three genera, their evolutionary positions and relationships were inferred. The results showed that *Psathyrostachys* was the most primitive one among three genera, *Critesion* was slightly more advanced than the former, and *Hordelymus* was the most advanced of them; *Psathyrostachys* might produce immediately *Critesion*, whereas *Hordelymus* might derive immediately form *Critesion*. The biosystematic relationships of these three genera were corroborated by the evolutionary trend of trispikelet in the external morphology.

Key words: *Critesion*, *Hordelymus*, *Psathyrostachys*, biosystematic relationship, leaf anatomical characteristics.

INTRODUCTION

Psathyrostachys, *Critesion* and *Hordelymus* are three genera belonging to Hordeinae of Triticeae in Poaceae (Löve, 1984). Thereinto, *Critesion* was established by Rafinesque in 1819 according to *Critesion jubatum* (L.) Nevski (Rafinesque, 1819). It is the earliest among them and now contains 28 species. 5 species are originally found in China. *Hordelymus* was established by Harz in 1885 based on *Hordelymus europaeus* (L.) Harz described (Harz, 1885); now it only contains a type species, and was introduced by China; it is later than the former. However, *Psathyrostachys* was established as the latest. It was established by Nevski in 1934 according to *Psathyrostachys lanuginosa* (Trin.) Nevski (Nevski, 1934). At present, it contains about 10 species, 5 species originally produce in China. In the external morphology, three genera′ plants all have the structural characteristics with triple-spikelet similar to *Hordeum* with narrowed meaning. Hence, many scholars placed some/whole species of them to the earlier *Hordeum* before three genera were established. Especially *Critesion*, some scholars still merged it into narrow *Hordeum* in order to form generalized *Hordeum* with covering more than 30 species (Chen et al., 2006). However, according to new studies from some scholars (Cai et al., 2003; Su and Cai, 2009; Su, 2009), we completely agreed with the case of independence on *Critesion* to distinguish with narrow *Hordem* of significantly different characteristics.

Certainly, it opens out the intimate relationships of three

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Table 1. Names and sources of materials for anatomical experiments.

Genus	Species	Voucher[1)]	Locality	Experimental uses[2)]
Psathyrostachys	*Psathyrostachys juncea* (Fisch) Nevski	G. L. Fu & R. S. Zhang 4418 HNWP	Kuitun, Xinjiang	LE, TS
	P. huashanica Keng ex P. C. Kuo	Y. Shi, et al. 005 HNWP	Huayin, Shanxi	LE, TS
	P. kronenburgii (Hack) Nevski	Y. H. Wu, et al. 2330 HNWP	Gonghe, Qinghai	LE, TS
	P. lanuginosa (Trin) Nevski	Xinjiang Exp. 370 HNWP	Sailimu Lake, Xinjiang	LE
Critesion	*Critesion bogdanii* (Wilens) Á Löve	P. C. Kuo & W. Y. Wang 045 HNWP	Dulan, Qinghai	LE, TS
	C. bulbosum (L.) Á. Love	S. D. Yang 1 HNWP	Xining, Qinghai	TS, TS
	C. procerum (Nevski) Á Löve	L. B. Cai 04 HNWP	Xining, Qinghai (Introduction)	LE, TS
	C. jubatum (L.) Nevski	J. H. Li 06 HNWP	Xining, Qinghai (Introduction)	LE
	C. roshevitzii (Bowden) L. B. Cai	B. W. Li & H. Z. Zhang 021 HNWP	Guinan, Qinghai	LE
	C. brevisubulatum (Trin) Á Löve	R. F. Huang 274 HNWP	Dulan, Qinghai	LE
	C. marinum (Hudson) Á. Löve	Y. H. Sun 25 HNWP	Xining, Qinghai (Introduction)	LE
	C. murinum (L.) Á. Löve	Y. H. Sun 12 HNWP	Xining, Qinghai (Introduction)	LE
	C. chilense (Roem. & Schult.) Á. Löve	L. B. Cai 011 HNWP	Xining, Qinghai (Introduction)	LE
	C. brachyantherum (Philippi) Á. Löve	L. B. Cai 07 HNWP	Xining, Qinghai (Introduction)	LE
	C. muticum (K. Presl) Á. Löve	L. B. Cai 03 HNWP	Xining, Qinghai (Introduction)	LE
Hordelymus	*Hordelymus europaeus* (L.) Harz	Y. H. Zhou PI 531564 SAUT	Dujiangyan, Sichuan (Introduction)	LE, TS
Bromus	*Bromus inermis* Layss	Z. H. Zhang, et al. 2908 HNWP	Xining, Qinghai	LE, TS

1) Vouchers are conserved in HNWP and SAUT. 2) LE, used for leaf epidermal observation; Ts, used in the transverse sections of leaf blades.

genera in a certain extent because they have the common characteristics of triple-spikelets. But these intimate relationships have only been expatiated on by Su and Cai (2009) based on the micromorphological characteristics of leaf epidermise and reports on them are never seen from other aspects. Thus, based on the micromorphological characteristics of epidermises and transverse sections of leaf blades, the objects of widespread species and the external morphological characteristics, we have it competitively analyzed and discussed the biosystematic relationships about three genera′ plants. Its aim is to provide a useful circumstantial evidence of anatomy for the research of systematics and evolution of Triticeae.

MATERIALS AND METHODS

The vast majority of tested materials were taken from accessory herbarium specimens and a few of them were fresh plants collected in the fields. The typical vouchers of each species were shown in Table 1. The total taken materials of leaf epidermal and transverse section anatomy included 76 pieces including outgroup-*Bromus inermis* Layss. 5 pieces of specimens were all selected in other species except that 2 or 3 pieces of them of individual species participate in experiments. We selected 2 to 3 pieces of materials of different latitudes and altitudes in order to make repetitive experiments. Our final aim was to obtain the comprehensive understanding on variation extent of genera characteristics.

Referring to Journal of Evolutionary Biology Research Vol. 5(1): 6-20 (Su et al., 2013); terms and concepts of leaf anatomy were based on Metcalfe (Metcalfe, 1960).

RESULTS

The micro-structural characteristics of leaf blades in Hordeinae

The leaf anatomy of 16 representative species of *Psathrostachys*, *Critesion* and *Hordelymus* in Hordeinae were observed on the light microscope.

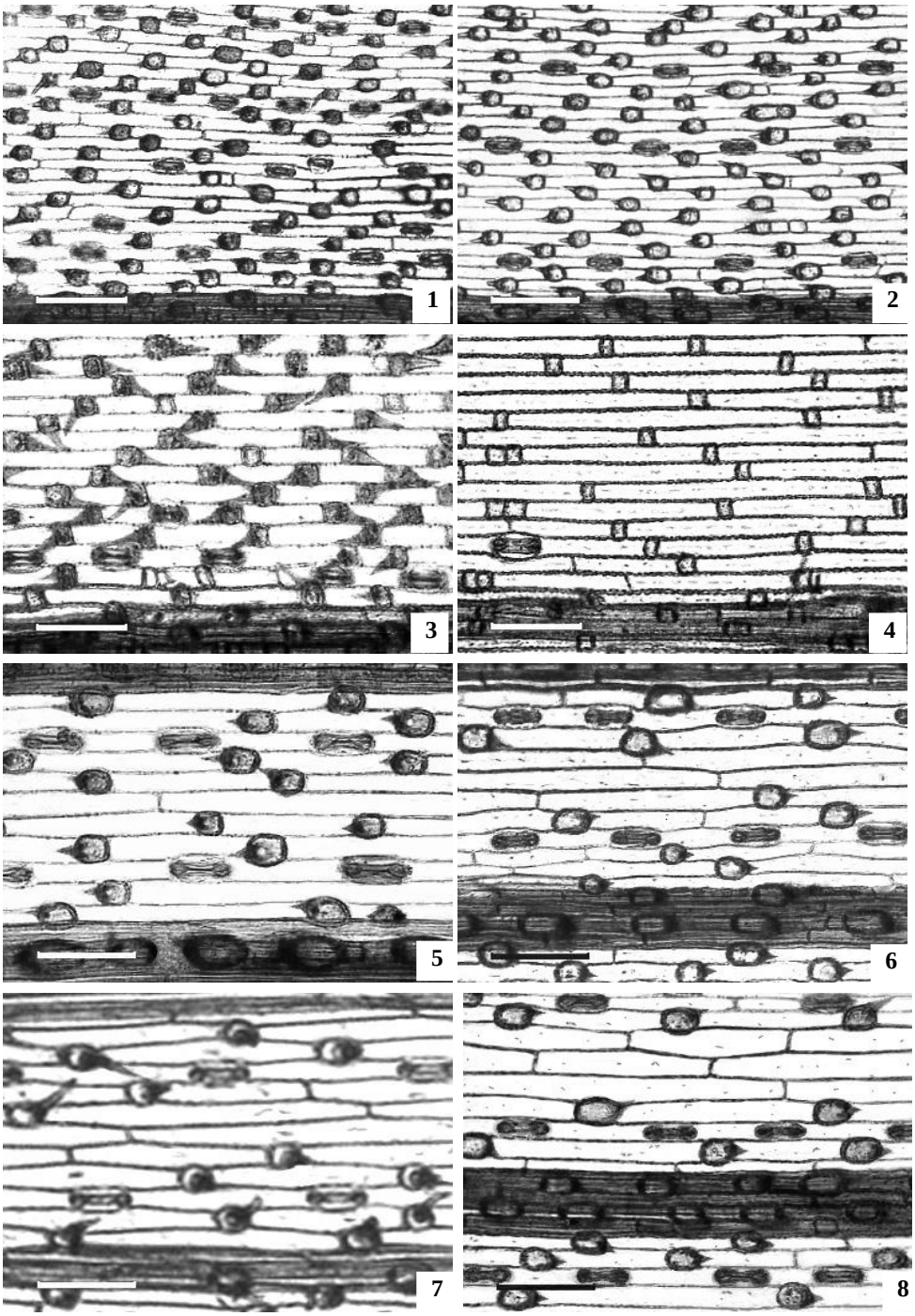

Figure 1. Light microscopic micrographs of the lower epidermises of leaf blades in 8 species of Hordeinae 1. *Psathyrostachys lanuginosa*; 2. *P. juncea*; 3. *P. kronenburgii*; 4. *P. huashanica*; 5. *Critesion jubatum*; 6. *C. brevisubulatum*; 7. *C. bogdanii*; 8. *C. roshevitzii* (scale bars in all figures indicate 100 μm).

The results showed that leaf epidermises (Figures 1 and 2) of three genera' plants were all consisted of long-cells, stomatal apparatus, short-cells and prickle-hairs and macro-hairs have also been found in specific taxa, while the transverse sections (Figure 3) of leaf blades were made up of epidermis, mesophyll and vascular bundle. Obviously, if according to the classification standard of grass leaf anatomy from Avdulov (1931) or Prat (1936), there is no doubt that this kind of structure style of leaf transverse sections belongs to the Festucoid type. In leaf

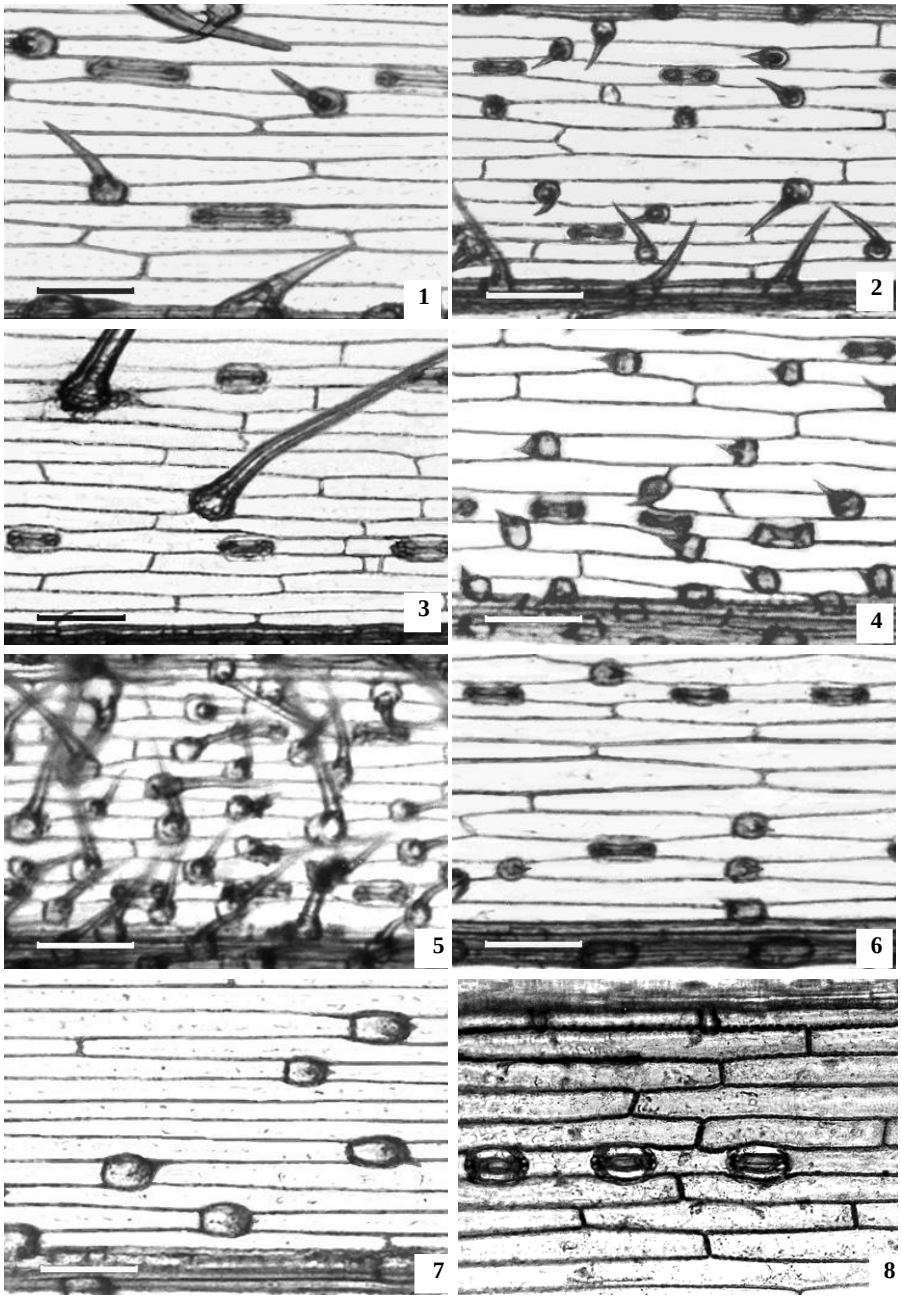

Figure 2. Light microscopic micrographs of the lower epidermises of leaf blades in 8 species of *Bromus* and Hordeinae. 1. *C. procerum*; 2. *C. marinum*; 3. *C. murinum*; 4. *C. chilense*; 5. *C. brachyantherum*; 6. *C. muticum*; 7. *Hordelymus europaeus*; 8. *Bromus inermis* (scale bars in all figures indicate 100 μm).

epidermal characteristics, long-cells are rectangle and cell-walls are thin and straight. Stomatal apparatus are slightly oblong/ellipse. Subsidiary cells are approximately parallel-sided or low dome-shaped. Short-cells are single and sparsely paired including prickle, hook and hook-hair. In exceptional taxa, there are macro-hairs. In transverse sections of leaf blades, the cells are smaller and epidermises are thinner around relative area of vascular bundles, while they are larger and skins are thicker. Mesophyll cell shape, magnitude and arrangement level are not very clear. It is not distinguished into palisade tissue and spongy tissue.

Vascular bundles are round or elliptic and shape of them is uneven. They have obvious double layer bundle sheath with the small inner sheath cell thickening on tangential wall and radial wall, and large outer one with

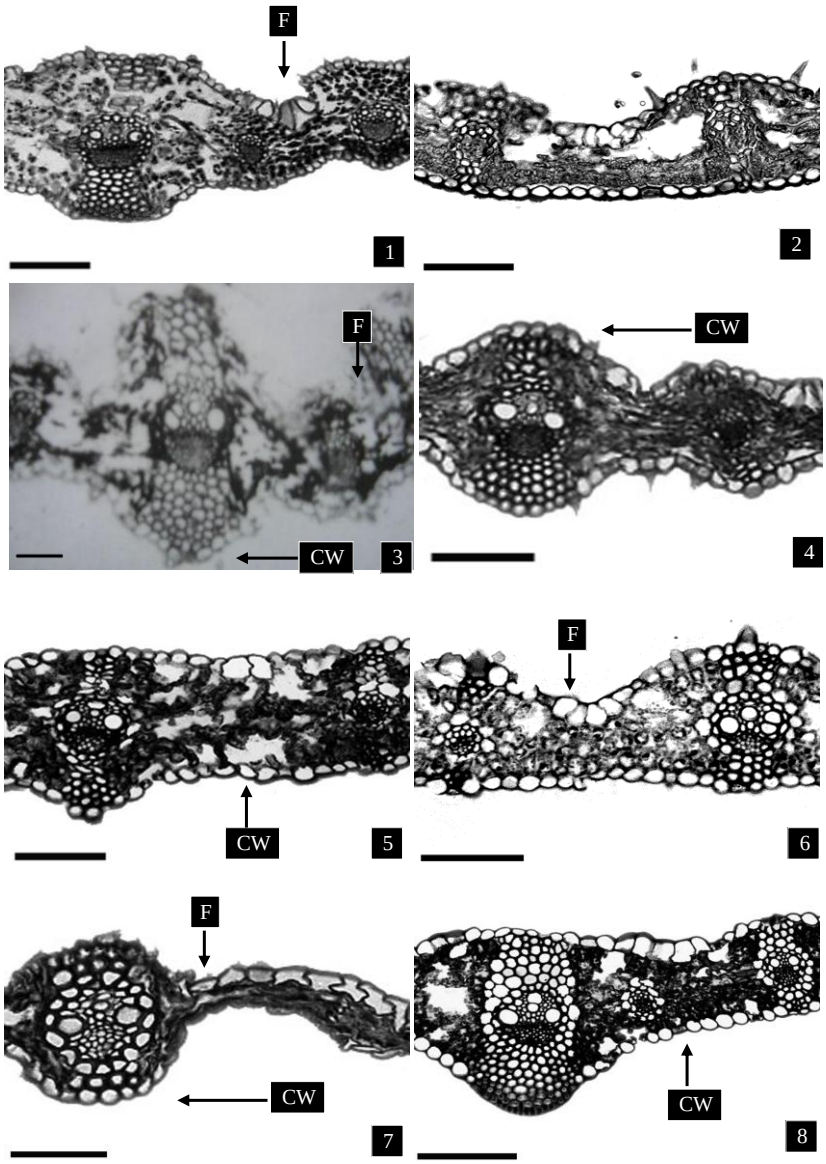

Figure 3. Light microscopic micrographs on the transverse sections of leaf blades in 8 species of *Bromus* and Hordeinae. 1. *Psathyrostachys juncea*; 2. *P. huashanica*; 3. *P. kronenburgii*; 4. *Critesion bogdanii*; 5. *C. bulbosum*; 6. *C. procerum*; 7. *Hordelymus europaeus*; 8. *Bromus inermis* (scale bars in all figures indicate 100 μm) CW, cell wall; F, furrow.

thin wall and sometimes having a clear chloroplast. Otherwise, the transverse sections of *Bromus inermis* are similar to those of Hordeinae, shape of epidermis is extremely regular and arrangement of lower epidermis is very close.

The differences on micro-structure of leaf blades of three genera′ plants in Hordeinae

From Tables 2 and 3, anatomical characteristics of leaf blades are listed. The tested species have the differences with respective characters in leaf blades anatomy. They are the important foundations analyzing the relationships among species and sects in the article. As far as leaf epidermises are concerned, the differences are completely performed in several structural cells (Table 2). For example, in *Psathyrostachys* plants, long-cells are shorter and narrower, short-cells are sparse or universal distributing, stomata are smaller and densely distribute, subsidiary cells are low dome-shaped; while in *Critesion* ones, long-cells are much longer and wider, short-cells are occasionally seen, stomata are larger and sparsely distributes and subsidiary cells are often parallel-sided.

Table 2. Comparisons of the main characteristics of lower epidermises of leaf blades in 16 species of *Psathyrostachys*, *Critesion* and *Hordelymus* in Hordeinae.

Species	Long-cell*	Short-cell	Stoma	Prickle-hairs	Macro-hairs
P. lanuginosa	30-105 μm long, 8-13 μm wide	Infrequent, solitary	23-32 μm long, ca. 12 μm wide, dense, commonly with low dome-shaped subsidiary cells	Small, abundant, hooked	Absent
P. juncea	32-130 μm long, 8-14 μm wide	Infrequent, solitary, occasionally paried	28-34 μm long, ca. 14 μm wide, dense commonly with low dome-shaped subsidiary cells	Small, abundant, mostly hooked, infrequently prickly	Absent
P. kronenburgii	37-113 μm long, 13-20 μm wide	Infrequent, solitary, occasionally paried	34-41 μm long, ca. 20 μm wide, dense, with low dome-shaped subsidiary cells	Small, abundant, hooked	Absent
P. huashanica	83-250 μm long, 14-21 μm wide	Common, mostly solitary, infrequently paried	38-45 μm long, ca. 23 μm wide, sparse, with low dome-shaped subsidiary cells	Small, infrequent, only hooked	Absent
C. jubatum	90-313 μm long, 16-24 μm wide	Absent or occasional, solitary	48-56 μm long, ca. 24 μm wide, relatively sparse, with parallel-sided subsidiary cells	Relatively large, relatively abundant, prickly and hooked	Absent
C. brevisubulatum	84-278 μm long, 15-22 μm wide	Occasional, solitary	38-46 μm long, ca. 21 μm wide, relatively sparse, with parallel-sided subsidiary cells	Relatively large, relatively abundant, prickly and hooked	Absent
C. bogdanii	98-310 μm long, 17-25 μm wide	Absent or occasional, solitary	45-51 μm long, ca. 21 μm wide, relatively sparse, with parallel-sided subsidiary cells	Relatively large, relatively abundant, hooked or barbed	Absent
C. roshevitzii	95-318 μm long, 15-24 μm wide	Occasional, solitary	40-47 μm long, ca. 20 μm wide, relatively sparse, with parallel-sided subsidiary cells	Relatively large, relatively abundant, prickly, occasionally hooked	Absent
C. procerum	195-347 μm long, 18-28 μm wide	Absent	75-87 μm long, ca. 26 μm wide, relatively sparse, with parallel-sided subsidiary cells	Relatively large, infrequent, prickly, hooked and barbed	Absent
C. marinum	132-349 μm long, 18-26 μm wide	Absent	42-51 μm long, ca. 18 μm wide, relatively sparse, with parallel-sided subsidiary cells	Relatively large, relatively abundant, hooked and barbed	Absent
C. murinum	142-358 μm long, 18-27 μm wide	Absent or occasional, solitary	45-59 μm long, ca. 29 μm wide, relatively sparse, with slightly parallel-sided subsidiary cells	Relatively large, infrequent, prickly	Present

Table 2. Contd.

C. chilense	85-308 µm long, 18-28 µm wide	Absent or occasional, solitary	43-52 µm long, ca. 22 µm wide, relatively sparse, with parallel-sided subsidiary cells	Relatively large, relatively abundant, mostly hooked, infrequently prickly	Absent
C. brachyantherum	47-173 µm long, 14-21 µm wide	Absent	40-47 µm long, ca. 21 µm wide, relatively dense, with parallel-sided subsidiary cells	Relatively large, relatively abundant, hooked or barbed	Absent
C. muticum	119-321 µm long, 17-28 µm wide	Absent	49-56 µm long, ca. 22 µm wide, sparse, with parallel-sided subsidiary cells	Relatively large, infrequent, prickly	Absent
H. europaeus	275-556 µm long, 18-29 µm wide	Absent	Absent	Large, infrequent, only prickly	Absent
B. inermis	28-89 µm long, 9-14 µm wide	Sporadic, solitary	20-34 µm long, ca. 13 µm wide, dense, commonly with low dome-shaped subsidiary cells	Small, abundant, prickly	Absent

* Data is expressed by the mean.

Table 3. Comparisons of the main characteristics of transverse sections of leaf blades in 8 species of *Psathyrostachys*, *Critesion*, *Hordelymus* and *Bromus* in Hordeinae.

Species	Thickness at midrib of leaf blade (µm)*	Upper epidermis		Lower epidermis		
		Furrow	Rib	Furrow and rib	Cell arrangement	Thickness of cell wall
P. juncea	284	Deep	Obtuse	Conspicuous	Close	Thin
P. huashanica	238	Relatively deep	Obtuse	Conspicuous	Close	Thin
P. kronenburgii	246	Deep	Obtuse	Relatively conspicuous	Close	Thin
P. lanuginosa	231	Deep	Obtuse	Relatively conspicuous	Relatively close	thin
C. bogdanii	225	Shallow	Obtuse	Relatively conspicuous	Relatively close	Relatively thin
C. bulbosum	197	Relatively deep	Inconspicuous	Inconspicuous	Relatively close	Relatively thin
C. procerum	264	Relatively deep	Inconspicuous	Relatively conspicuous	Relatively close	Relatively thin
C. jubatum	200	Relatively deep	Inconspicuous	Relatively conspicuous	Relatively close	Relatively thin
C. roshevitzii	198	Relatively deep	Inconspicuous	Relatively conspicuous	Relatively close	Relatively thin
C. brevisubulatum	246	Relatively deep	Inconspicuous	Relatively conspicuous	Relatively close	Relatively thin
H. europaeus	232	Shallow	Inconspicuous	Relatively conspicuous	Relax	Thick
B. inermis	327	Relatively deep	Obtuse	Relatively conspicuous	Close	Thin

*Data is expressed by the mean.

Table 3. Contd.

Mesophyll	Vascular bundle			Plates
Thickness between the strand in middle part (μm)	Number	Midrib diameter in horizontal (μm)	No. of the large vessel	
123	17-23	98	8-11	Figure 3, 1
90	18-23	100	9-12	Figure 3, 2
135	17-22	98	8-11	Figure 3, 3
91	17-24	112	8-14	Unlisted
89	17-29	92	7-9	Figure 3, 4
135	18-26	80	7-9	Figure 3, 5
123	17-28	85	7-10	Figure 3, 6
118	19-24	91	6-9	Unlisted
132	20-23	87	8-9	Unlisted
121	18-25	89	7-9	Unlisted
154	15-20	78	5-7	Figure 3, 7
112	20-31	154	9-13	Figure 3, 8

*Data is expressed by the mean.

Meanwhile, in point of transverse sections of leaf blades, those are performed in epidermis, mesophyll tissue and vascular bundle (Table 3).

In *Psathrostachys* plants, cell is regular, arrangement of cells is dense, the mean value of midrib diameter in horizontal is large; in *Critesion* ones, cell is more regular, arrangement of cells is denser, the mean value of midrib diameter in horizontal is small; while in *Hordelymus* ones, cell is the most regular, arrangement of cells is loose, the mean value of midrib diameter in horizontal is small. So they should belong to the obviously discontinuous and different species in anatomical characteristics.

DISCUSSION

According to the leaf anatomical characteristics of representative species from three genera' plants in Hordeinae, it is known that two kinds of anatomical structural modality should belong to the Festucoid type by comparing with the leaf blades of the main plants anatomized in Poaceae in the past (Prat, 1932, 1936; Metcalfe, 1960; Clifford et al., 1977; Cai and Guo, 1995, 1996; Su et al., 2013). By further comparing with the previous research results, we found that they should also belong to the leaf anatomy of Triticeae below Pooideae again (Cai and Zhang, 2006; Su and Cai, 2009; Su et al., 2013). Such as observation results mentioned, there are obvious differences in anatomical structure of leaf blades in three section plants.

Systematic relationships among genera and evolutionary trends of leaf blades

If you deduce the relationships among genera with aforementioned differences, you need to make it clearer the evolutionary trend on different characteristics of each taxon. In leaf epidermal characters, the basic developmental trend and systematic relationships are in accordant with our previous result (Su and Cai, 2009). That is to say, *Hordelymus* can directly derive from *Critesion* and *Psathrostachys* producing *Critesion*. Similarly, in transverse sections of leaf blades, the characters from epidermises with obvious state grades include malformed or regular or more irregular of cell shape, thick or thin or thinner of cell-walls, lax or dense or more laxer of cell arrangement. However, the characters with regular cell-shape always exist together with those of thin cell-walls and dense cell-arrangement; those with malformed ones depend on those of thick cell-walls and relax cell-arrangement. The former is very similar to those of outgroup; while the latter is greatly different with those of outgroup. Hereby,

we speculate that the epidermal evolutional trend should be: cell-shape is from regular to malformed, cell-wall is from thin to thick and cell-arrangement is from dense to lax. Through further research, we can also find that the aforementioned evolutionary trend is not independent. Generally, the characters with nonuniform performance and relax arrangement of epidermis are always concomitant deposit with those of small concave curvature, few numbers of the large vessels and small midrib diameter in horizontal; therefore, we think that the character having ascensivly and extrusively evolutionary trends in transverse sections of leaf blades should be that: uneven magnitude and dense arrangement and thin cell-wall of upper epidermal cells→even magnitude and lax arrangement and thick cell-wall, big concave curvature of upper epidermises→smaller concave curvature→small concave curvature, small mean value of thickness between the strand in middle part→large one, many numbers of large vessels in vascular bundles→fewer ones→few ones, large midrib diameter in horizontal→small one. Hereby, seeing the main difference of each genus, *Psathrostachys* should be the most primordial taxon, *Critesion* should be the more evolutional one than the former, while *Hordelymus* should be the most evolutional one among three genera.

Meantime, the taxa with closer relationship in Hordeinae should include *Psathrostachys* and *Critesion*, *Critesion* and *Hordelymus*. It is because that the former has much similarity including density of cell-arrangement, thickness of cell-wall; while the latter has similar of those concave curvature of lower eipidermis and thickening style of inner sheath cells. If seeing deriving origin among them, *Psathrostachys* with thin mesophyll tissue can directly produce *Critesion* with thick one, *Hordelymus* with thick cell-wall can also derive *Critesion* with thin one.

Systematic relationships among genera and evolutionary trends of external morphological characters

If the relationship of three genera' plants confirms to the external modality, the relationships among three genera is also very clear. If we take account of the primary characters of *Psathrostachys* with perennial grass and having dense and long rhizomatosae, and the secondary those of *Critesion* and *Hordelymus* with annual grass and often having sparse and no rhizomatosae, only considering the common trait of triple-spikelets, we also see their evolutional grade. The triple-spikelets of *Psathrostachys* all have no handle and procreate generation and there are 2 to 3 florets per spikelet; the middle spikelet of triple-spikelets of *Critesion* can procreate generation but it has no handle, and there is 1 to 2 floret per spikelet; while the triple-spikelets all have short handle and procreate generation or the middle spikelet is male, and there is one floret and one further reduced floret in per spikelet. According to the theory of spica in Triticeae being able to evolve from complexity to simplicity (Kuo and Wang, 1981), it is not difficult that the inflorescences of *Psathrostachys*, *Critesion* and *Hordelymus* must be secondary adequate variation after the location of spikelets regularly arranges. Thus, they make each spikelet of triple-spikelets owning larger placing and developmental space.

As a result, the evolutional pattern, which *Psathrostachys* is the most primordial taxon and *Critesion* does the more evolutional and *Hordelymus* is the most one that has formed. What is more, during the aforementioned course, *Psathrostachys* with no handle of triple-spikelets and having 2 to 3 florets per spikelet naturally has the close relationship with *Critesion* of triple-spikelet partly having handle and having 1 to 2 floret per spikelet. They have directly original relationship; while it should have far relationship with *Hordelymus* with having handles and only one floret in triple-spikelet, they can have indirectly deriving relationship. Meantime, *Critesion* lies in the middle state of characteristic evolution and serves as the transition bridge of two genera' evolution.

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