

高原生物学集刊

ACTA BIOLOGICA PLATEAU SINICA

第十四集 No.14

中国科学院西北高原生物研究所 编辑

1998—1999



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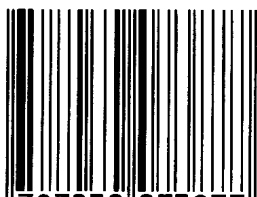
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从叶片表皮结构试论狷草属与披碱草属间的分合与演化

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摘 要

狷草属在小麦族中究竟应合入披碱草属, 还是继续独立成属, 历来为禾本科分类学者所争议。为此, 本文特以叶表皮解剖特征为依据、以国产类群为对象, 结合外部形态对两属植物的分合与演化进行了讨论。认为狷草属植物的叶片表皮结构与披碱草属的老芒麦组基本相似, 应归合于披碱草属。尤其在一些特征上与老芒麦组中的老芒麦完全一致, 显示了狷草类植物与老芒麦植物关系最为密切, 而不同的一些差异特征又显示了狷草类植物在系统位置上高于老芒麦, 可能由原始的老芒麦衍生而来。

关键词: 狷草属; 披碱草属; 叶表皮; 系统处理; 演化

狷草属原来的拉丁名称是 *Asperella* Humb., 但由于该名称之前还有一个属名 *Asprella* Schreb. 与之近似, 故这一缀法错误导致了后来 Moench (1794) 的新属名 *Hystrix* Moench 得以成立。Moench 当时命名的新属是以新种 *Hystrix patula* Moench 作为模式, 而此模式恰与 1753 年 Linnaeus 命名的披碱草属种 *Elymus hystrix* L. 实为同种, 可见狷草属与披碱草属间的联系, 早在分类学泰斗的眼里就已形成。而且近年来, 美国分类学家 Löve (1984) 干脆将该属直接归入到披碱草属中, 作为披碱草属下的一个新组, 所以 Löve 的作法是否合理? 狷草属能否继续独立为属是个值得探讨的问题。为此本文特以叶表皮解剖特征为依据、以国产类群为对象、结合外部形态讨论两属植物的分合及系统发育的演化关系。

材料和方法

提供实验的材料全为腊叶标本, 均取自旗叶下第一叶片的中间部段, 按常规的叶表皮解剖法操作。即先将叶片水煮 5~10 分钟, 待材料软化后放于塑料板上用单面刀片轻

* 中国科学院西北高原生物研究所资助课题。
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轻刮削,使其保留叶片上表皮或下表皮薄膜层;然后清水洗净薄膜,用1%的番红染液染色1分钟,每置于光镜下观察;观察的同时进行描述、绘图、拍照等工作;最后以常规的永久制片法脱水封固保存。整个实验共取材38份,其中猓草属2个种5份,披碱草属10个种33份,其各个种的代表标本名录如下:

猓草 *H. duthiei* (Stapf) Bor 西藏:青藏补点组 750642

东北猓草 *H. komarovii* (Roshev.) Ohwi 陕西:魏志平 1249

老芒麦 *E. sibiricus* L. 青海:郭本兆、谢文忠 0024

垂穗披碱草 *E. nutans* Griseb. 青海:梅丽娟 166

短芒披碱草 *E. brachyaristatus* Löve 青海:王为义等 26657

无芒披碱草 *E. submuticus* (Keng) Keng f. 四川(引种青海):雷更新 660001

披碱草 *E. dahuricus* Turcz. ex Griseb. 新疆:新疆队 672

肥披碱草 *E. excelsus* Turcz. ex Griseb. 黑龙江:付沛云 3315

麦荻草 *E. tangutorus* (Nevski) Hand.-Mazz. 青海:苟新京等 446

硕穗披碱草 *E. barystachyus* L. B. Cai 西藏:青藏补点队 750598

圆柱披碱草 *E. cylindricus* (Franch.) Honda 青海:何廷农 808

毛披碱草 *E. villifer* C. P. Wang et H. L. Yang 山西:中阳甲队 254

观察结果

在光镜下,国产猓草属和披碱草属的叶片表皮结构是比较规范的,这种规范主要体现在组成表皮的细胞类型和各类型细胞形态、分布上。通常,在类型上两属植物的叶面普遍存在的是长细胞,其次是气孔器细胞和刺毛,而短细胞和大毛仅在少数或一定数量的类群中出现。在形态、分布上,长细胞普遍延长呈长条形,一般纵向相接成行,各行平行排列于脉上和脉间,其中泡状细胞集中分布于上表面脉间中部;气孔器体积较大,着重分布于叶片上表皮脉间,而下表皮脉间分布少或根本不分布,常靠近两侧脉带着生,并与长细胞相间排列成行形成气孔带,副卫细胞近于平顶形;刺毛量多,主生于叶表皮脉上,脉间数量稀少或不着生,并且脉上多生刺,脉间多生钩;短细胞在类群间的数量悬殊极大,通常分布稀少的短细胞单生呈马鞍形,分布密集的短细胞孪生呈新月形和圆球形;大毛不仅在少数类群中出现,而且出现的类群数量也较为稀少,一般为刺基大毛,多见于表皮脉上,且上表面大毛常比下表面大毛显细长。

再者,从两属植物整个叶表皮结构的大致差异来看,可以划分为两大结构类型,这两大结构类型正与外部形态上颖的大小、花序是否下垂而展示的两类是基本吻合的,故命名为小颖垂穗型和大颖直穗型。小颖垂穗型和大颖直穗型在叶面上又主要通过下表皮脉间细胞的形态变异及数量分布来显现的,尤其长细胞壁是否弯曲、脉间有无刺毛、短细胞是否普通分布等性状是识别两大类型的可靠依据。现特将下表皮脉间类型差异的主要特征及所附类群简述如下:

小颖垂穗型:长细胞壁薄、平直无波纹;具刺毛;无短细胞或短细胞稀少、单生呈马鞍形。为猓草 *H. duthiei* (Stapf) Bor、东北猓草 *H. komarovii* (Roshev.) Ohwi、老芒麦 *E. sibiricus* L.、垂穗披碱草 *E. nutans* Griseb.、短芒披碱草 *E. brachyaristatus* Löve

和无芒披碱草 *E. submuticus* (Keng) Keng f. 等类群所拥有。

大颖直穗型：长细胞壁厚、波状弯曲；无刺毛；短细胞普遍分布，常以新月状和圆球状结伴孪生。为披碱草 *E. dahuricus* Turcz. ex Griseb.、肥披碱草 *E. excelsus* Turcz. ex Griseb.、麦莢草 *E. tangutorus* (Nevski) Hand.-Mazz.、硕穗披碱草 *E. barystachyus* L. B. Cai、圆柱披碱草 *E. cylindricus* (Franch.) Honda 以及毛披碱草 *E. villifer* C. P. Wang et H. L. Yang 等类群所具有。

讨 论

(1) 从国产狷草属和披碱草属的叶片表皮结构特征来看，这两属植物的叶面都同具长细胞、气孔器细胞、短细胞、刺毛和大毛，而这些细胞在禾本科中恰恰符合早熟禾亚科 Pooideae 叶表皮 5 类结构细胞的通性(陈守良等, 1993; 蔡联炳等, 1995, 1996; Clifford et Watson, 1977; Metcalfe, 1960)，因而与外部形态上它们同为草本、具延伸小穗轴、小穗小花向心发育、外稃 5 脉而归于早熟禾亚科的性状是陪衬的，在分类类别上属于该亚科无疑。但它们的叶表皮上刺毛较多，脉上多数类群具钩，无垫的刺基大毛主生于脉上，短细胞如有则为马鞍形、新月形或圆球形，气孔器体积较大，副卫细胞平顶形以及长细胞普遍延长的特征又是只有在早熟禾亚科的小麦族 Triticeae、甚至大麦亚族 Hordeinae 中才能明显表现出来的性状，这些性状同外部形态上两属植物同具穗状花序、穗轴每节通常 2~3 枚无柄小穗的特征是相对映的，从而从微形态上揭示了它们是禾本科、早熟禾亚科、小麦族、大麦亚族下的一个自然类群的真实面目。

(2) 根据实验结果可知，国产狷草属和披碱草属的叶片表皮总体可以划分为两大结构类型，其中狷草属仅占据一个类型，披碱草属占据两个类型，而披碱草属占据的两个类型正好是披碱草属外部形态划分上的两个组，这说明狷草属与披碱草属间的差异还不如披碱草属内部的组间差异大，即狷草属不能继续独立为属而应归并到披碱草属中。这同外部形态上狷草属基本没有一个大的间断特征与披碱草属相区别是吻合的，从而也支持了先前学者以及 Löve (1984) 作出的两属植物相并合的科学结论。对此，特将先前学者组合的国产狷草属植物新拟中文名称如下：

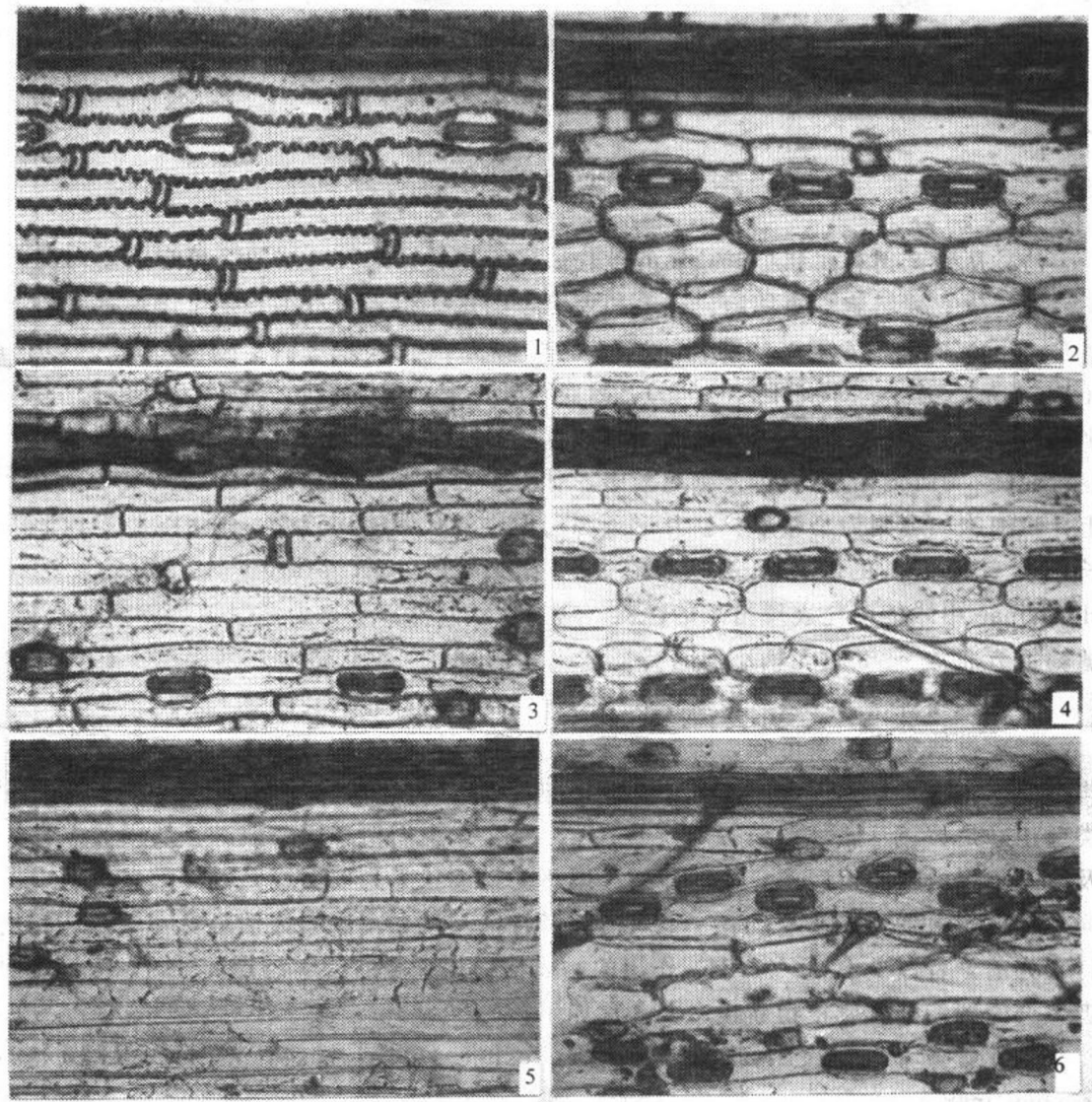
东北披碱草(新拟) *Elymus komarovii* (Roshev.) Ohwi (based on *Asperella komarovii* Roshev. in Bot. Mat. 5: 152. 1924)

单花披碱草(新拟) *Elymus duthiei* (Stapf) Bor (based on *Asperella duthiei* Stapf in Hook. f., Fl. Brit. India 7: 375. 1896)

并且，从表皮结构上原狷草类植物所具的表皮类型正与披碱草属中老芒麦组 Sect. *Elymus* 所具的表皮类型完全一致，而它们在外形上又同属于花序下垂、颖细小或无、并与稃体相疏离的类群，故原狷草属合于披碱草属中，是同披碱草属的老芒麦组有着密切的亲缘关系。

(3) 既然原狷草类植物与披碱草属中的老芒麦组有亲缘关系，那么又同该组何种类群关系最近呢？实验观察还表明，原狷草类植物与老芒麦组中的老芒麦 *E. sibiricus* L. 关系最近。因为从叶面上可以看出，两类植物的普通长细胞均明显延长、下表皮无气孔器或气孔器间断分布、短细胞缺如或稀少、刺分布于脉上和脉间、下表皮或上表皮脉上常

具或偶具大毛（图版1），而这些相似的特征可以说在老芒麦组其他种中至少是不完全具备的，反映在外部形态上则与两类植物疏松、柔弱、细长的穗状花序，穗轴节稀而每节通常着生2枚具芒小穗的特征相印证的。



图版 I 猓草属与披碱草属的叶片表皮结构

Plate I The structure of leaf epidermis of the genera *Hystrix* and *Elymus*

叶片表皮结构（1、3、5. 下表皮，2、4、6. 上表皮，各图均为×100）

1~2. 披碱草；3~4. 老芒麦；5~6. 单花披碱草。

The structure of leaf epidermis (1. 3. 5. abaxial epidermises, 2. 4. 6. adaxial epidermises; all×100)

1~2. *Elymus dahuricus* Turcz. ex Griseb. ; 3~4. *Elymus sibiricus* L. ; 5~6. *Elymus duthiei* (Stapf) Bor.

（4）原猓草类植物虽然与披碱草属植物在叶表皮结构和外部形态上具有相似的特征而被归划到披碱草属中，但它们之间毕竟还是有差异的。这种差异不单表现在与披碱草属的披碱草组 Sect. Turczaninovia (Nevski) Tzvel. 上，而且就是老芒麦组中的老芒麦种也较为明显。其中一些特别有价值的性状差异，如原猓草类植物的普通长细胞和泡状细

胞较之老芒麦的更长，下表皮脉间长细胞的列数也较老芒麦的多，气孔器基本全部转入到了叶片的上表面、且带数明显增多，完全消净了短细胞，上表面脉间出现了钩，大毛在老芒麦中存在稀少、在原刍草属中出现普遍等不仅可以作为属下类群区分的依据，而更重要的还可作为推知属下类群演化的旁证。我们知道，原始的禾本科植物植株低矮，叶子瘦小 (Stebbins, 1972)，但随着植株的高大演化，叶子也逐渐变得宽长起来。然而叶子的宽长体现在表皮结构上则主要是长细胞的延长、列数的增多，气孔器的向光集生，短细胞的伸延消失，刺毛体积的收缩、钩的出现以及抗寒大毛的普遍着生等。因此，这就不难看出原刍草属植物叶片表皮表现的特征较之披碱草属的老芒麦来要高级一些，原始的老芒麦类植物在一定程度上可能衍生了原刍草类植物。

此外，这种类群间的演化关系投影在外部形态上也是非常明显的。因为从禾本科的圆锥花序进化到穗状花序，一般小穗、小花数的减少、颖体的短缩变细总是与类群的演化趋势相顺应的。所以从老芒麦植物的花序有时穗轴 1 节具 3 枚小穗、每小穗含 3~5 小花，原刍草类植物的花序至多 1 节具 2 枚小穗、每小穗含 2~3 花或单花来也显得原刍草类植物高级，而颖体在原刍草类植物中已退化为芒状或以至消失，乃是原始老芒麦植物颖体继续短缩的最终结果。整个进化路线可简示为：老芒麦 *E. sibiricus* L. → 东北披碱草 *E. komarovii* (Roshev.) Ohwi → 单花披碱草 *E. duthiei* (Stapf) Bor.

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ON THE SYSTEMATIC TREATMENT AND EVOLUTION OF THE GENERA *HYSTRIX* AND *ELYMUS* BASED ON THE STRUCTURE OF LEAF EPIDERMIS

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Abstract

Whether the genus *Hystrix* should be incorporated into the genus *Elymus* in the tribe Triticeae or

isolated continuously as one genus is a problem which is disputed always by herbalists. For this reason, according to the characters of leaf epidermis, the authors discuss the division or combination and evolution of the genera *Hystrix* and *Elymus* with the viewpoint of combining external morphology in the present paper. The results show that the genus *Hystrix* is similar to the Sect. *Elymus* of the genus *Elymus* by the straightness or sinuosity of walls of long-cells, the distribution of prickly-hairs and the shapes or quantity of short-cells, the genus should be combined into the genus *Elymus* in taxonomic category; especially some characters of *Hystrix*, such as the elongation of long-cells, the distribution of stomatal apparatus, the absence of short-cells, the presence of prickles over and between the veins and the appearance of macro-hairs, etc., agree with those of the *Elymus sibiricus* L. of the section, so the genus and the *E. sibiricus* L. are closely related taxa. Moreover, the genus *Hystrix* has no stomatal apparatus and short-cell between the veins on the lower epidermis, the rows or length of its long-cells are more or longer than those of the genus *Elymus*; while on the upper epidermis the bulliform cells of this genus are obviously elongated, its macro-hairs are abundant, and stomatal apparatus gather nearby the bulliform cell zone, therefore, generally speaking this genus in systematic position is more advanced than the genus *Elymus*, it may be derived from primitive Siberian Wildryegrass.

Key words: *Hystrix*; *Elymus*; Leaf epidermis; Systematic treatment; Evolution

NEW TAXA OF THE GENUS *ELYMUS* FROM THE QING-ZANG PLATEAU

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Abstract

Two new species and one new variety of the genus *Elymus* L. from the Qing-Zang Plateau are reported. They are *E. molliusculus* L. B. Cai, *E. alpinus* L. B. Cai and *E. sibiricus* L. var. *erectiuculus* L. B. Cai.

Key words: *Elymus*; New taxa; The Qing-Zang (Tibet) Plateau

***Elymus molliusculus* L. B. Cai, sp. nov.** Fig. 1: 1~9

Species nova *E. tangutoro* (Nevski) Hand. -Mazz. Similis, sed spicis mollibus, viridulis; spiculis 2~5 vulgo natis e nodo; glumis 3~4-nervibus, margine membranaceis; aristis lemmatum gracilibus, 3~5 mm longis; vaginis foliorum superioribus internodiis evidenter longioribus differt.

Herba perennis, fibris crassiusculis longiusculis. Culmi solitarii vel laxe caespitosi, basi leviter geniculati, glabri, 55~110 cm alti, 3~5 mm diam., saepe 5-nodes. Vaginae foliorum glabrae, superiores internodiis evidenter longiores; ligulae papyraceae, apice truncatae vel rotundatae, 0.4~1mm longae; laminae complanatae, 9~25 cm longae, 5~12 mm latae, utrinque glabrae. Spica erecta, conferta, mollis, viridula, 8~13 cm longa, 8~12 mm lata; rhachis dorso glabra vel scaberula, secus acies breviter ciliata, internodiis generatim 4~8 mm longis; spiculae 2~5 vulgo natae e nodo, 9~15 mm longae (aristis exclusis), 3~5 -florae, rhachillis dense puberulis; glumae lineari-lanceolatae, 3~4 -nerves, secus nervos scabrae, margine membranaceae, duae subaequales, 8~9 mm longae, apice acuminatae vel mucronibus 1~2 mm longis praeditae; lemma lanceolata, dorso glabra vel sparse spinulosa, superne distincte 5~nervia, id primum 8~9 mm longum, apice aristatum, arista gracili 3~5mm longa; paleae lemmata aequantes, vel eis leviter longiores, apice retusae, superne ad carinas sparse breviter spinosae, inter carinas saepe glabrae; antherae flavae, 2~2.6mm longae; ovaria apice pubentia.

Xizang: Changdu, in pratis clivorum, alt, 3950 m, Jul. 16, 1997, P. C. Kuo et W. Y. Wang 21559 (holotypus, HNWP); **Qinghai:** Yushu, alt. 3700 m, Jul. 12, 1964, Y. C. Yang 0359.

This species resembles *E. tangutorus* (Nevski) Hand. -Mazz., but differs by the viridescent, gentle and agreeable spikes, the spikelets usually in twos to fives at each node of the spike-axis, the 3- to 4-nerved glumes, with membranous margins, the lemma awns thin, delicate, 3~5mm long, and the leaf sheaths at upper part of culm being obviously longer than the internodes.

Perennial grasses, fibrous roots comparatively thick, long. Culms solitary or loosely caespitose, slightly geniculate at lower part, glabrous, 55~110 cm tall, 3~5mm in diameter, usually with 5 nodes. Leaf sheaths glabrous, the upper ones obviously longer than the internodes; ligules papyraceous, truncate or rotundate at the top, 0.4~1mm long; leaf blades flat, 9~25 cm long, 5~12mm broad, both surfaces glabrous. Spike erect, dense, viridescent, gentle and agreeable, 8~13 cm long, 8~12mm broad; back of rachis glabrous or slightly scabrous, margin breviciliate, internodes generally 4~8mm long; spikelets usually in twos to fives at each node of the rachis, 9~15mm long (excluding awn), 3- to 5-flowered, rachilla densely puberulent; glumes linear-lanceolate, 3- to 4-nerved, with scabrous nerves, with membranous margins, nearly equal, 8~9mm long, with acuminate tip or apex ending in a 1~2mm long mucronation; lemmas lanceolate, glabrous or sparsely spinulate on the back, obviously with 5 veins at upper part, first lemma 8~9mm long and with a thin delicate 3~5mm long awn at the apex; palea equal to or slightly longer than lemma, with slightly emarginate apex, with sparsely spinuliferous keels at upper part, usually glabrous between keels; anthers yellow, 2~2.6mm long; ovary with a puberulous tip.

Elymus alpinus L. B. Cai, sp. nov. Fig. 1: 10~18

Species nova *E. nutanti* Griseb. Affinis, sed spicis erectis vel leviter flexis, viridulis; glumis anguste lanceolatis, 1~3-nervibus, 3~4mm longis; aristis lemmatum gracilibus, 3~7mm longis; paleis lemmatibus leviter longioribus, apice emarginatis; culmis saepe 5-nodibus; vaginis foliorum internodiis longioribus different.

Herba perennis, radicibus fibrosis. Culmi erecti, solitarii vel laxe caespitosi, 25~35 cm alti, saepe 5-nodes. Vaginae foliorum glabrae, internodiis longiores; ligulae breves, circ. 0.3mm longae, apice truncatae; laminae complanatae vel leviter involutae, 6~10 cm longae, 3~5mm latae, superne et inferne glabrae, sed margine ciliatae. Spica conferta, erecta vel leviter flexa, viridula, 4~6cm longa, circ. 9mm lata; rhachis dorso glabra, secus acies breviter ciliata, internodiis vulgo 2~3mm longis; spiculae binae vel superiores solitariae, pedicellis brevissimis, 10~12mm longae (aristis exclusis), 3~4-florae, rhachillis dense puberulis; glumae anguste lanceolatae, 1~3-nerves, nervo medio scabro, duae subaequales, 3~4mm longae, apice acuminatae; lemmata lanceolata, dorso pubescentia, su-



Fig. 1 1~9. *Elymus molliusculus* L. B. Cai; 10~18. *Elymus alpinus* L. B. Cai. 1, 10. Lower portion of the plant; 2, 11. Spike; 3, 12. Spikelet; 4, 13. First glume; 5, 14. Second glume; 6, 15. Dorsal view of the first floret; 7, 16. Ventral view of the first floret; 8, 17. Pistil; 9, 18. Anthers. (drawn by Y. Wang)

perne distincte 5-nervia, id primum 7~8mm longum, apice aristatum, arista gracili, 3~7mm longa; paleae lemmatibus leviter longiores, apice emarginatae, superne ad carinas

breviter ciliatae, inter carinas puberulae; antherae denigratae, circ. 1.5 mm longae; ovaria apice pubentia.

Qinghai: Gonghe, in pratis, alt. 3200 m, Jul. 5, 1963, Y. C. Yang 188 (holotypus, HNWP); Ulan, alt. 2950 m, Jul. 2, 1963, Coll. Ignotus 017.

This species resembles *E. nutans* Griseb., but differs by the viridescent erect or slightly curved spikes, the glumes narrowly lanceolate 3~4 mm long with 1~3 veins, the thin delicate 3~7 mm long lemma awns, the palea slightly longer than lemma with slightly emarginate apex, the culms usually with 5 nodes and the leaf sheaths longer than the internodes.

Perennial herbs with fibrous roots. Culms erect, solitary or loosely caespitose, 25~35 cm tall, usually with 5 nodes. Leaf sheaths glabrous, longer than the internodes; ligules short, circa 0.3 mm long, with a truncate apex; leaf blades flat or slightly involute, 6~10 cm long, 3~5 mm broad, upper and lower surfaces glabrous, but with ciliate margins. Spike dense, viridescent, erect or slightly curved, 4~6 cm long, circa 9 mm broad; back of rachis glabrous, margin breviciliate, internodes generally 2~3 mm long; spikelets in pairs at each node of rachis or solitary near the apex, with most short pedicels, 10~12 mm long (excluding awn), 3- to 4-flowered, rachilla densely puberulent; glumes narrowly lanceolate, 1- to 3-nerved, medial vein scabrous, nearly equal, 3~4 mm long, with acuminate tip; lemmas lanceolate, shortly puberulous on the back, distinctly 5-nerved at upper part, first lemma 7~8 mm long and with a thin delicate 3~7 mm long awn at the apex; palea slightly longer than lemma, with slightly emarginate apex, with breviciliate keels at upper part, puberulous between keels; anthers blackish, circa 1.5 mm long; ovary with a puberulous tip.

Elymus sibiricus L. var. *erectiusculus* L. B. Cai, var. nov.

A varietate typica differt spicis erectis, leviter confertis; glumis lanceolatis, 6~7 mm longis (aristis exclusis).

Qinghai: Huzhu, in sylvis, alt. 2300 m, Jul. 10, 1986, Y. H. Wu et al. 2781 (holotypus, HNWP); Jainca, alt. 2140 m, Aug. 5, 1992, Z. D. Wei 443; Yushu, alt. 3750 m, Aug. 24, 1980, W22104; Monyuan, alt. 3100 m, Jul. 24, 1958, P. C. Tsoong 8507.

Elymus sibiricus L. var. *erectiusculus* L. B. Cai differs from the other varieties by the erect slightly dense spike, the lanceolate 6~7 mm long (excluding awn) glume.