

# 禾本科虎尾草亚科细胞学研究分析

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**摘要:**总结了虎尾草亚科 72 属 601 个分类单位的细胞学资料。虎尾草亚科的染色体基数是 10 和 9, 来源于原始染色体基数 6 经非整倍性减少为 5, 再经多倍化及非整倍性减少而来。细胞学性状对虎尾草亚科属上类群的分类具有相当重要的价值。推测染色体基数演化的趋势为:  $x=6 \rightarrow x=5 \rightarrow x=10 \rightarrow x=9$ 。据认为, 虎尾草亚科的原始染色体基数为 5 的二倍体类群在演化早期就灭绝了。

**关键词:**禾本科; 虎尾草亚科; 细胞学

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## Cytological Studies in the Chloridoideae (Poaceae): a Review

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**Abstract:** Recent researches on basic chromosome numbers of 601 taxa including 72 genera of the subfamily Chloridoideae are reviewed. Two main basic chromosome numbers occur in the majority of chloridoid genera, i.e. 9 and 10. Evidence indicates that  $x=9$  and 10 are paleopolyploid and aneuploid deviation basic chromosome numbers. Cytological characters have significant systematic value in recognizing supra-generic group in the Chloridoideae. An evolutionary trend of basic chromosome numbers is proposed:  $x=6 \rightarrow x=5 \rightarrow x=10 \rightarrow x=9$ . The primitive diploid group with  $2n=2x=10$  might have been extinct in the early evolution.

**Key words:** Chloridoideae; Cytology; Poaceae

禾本科比较系统的细胞学研究开始于 20 世纪 30 年代, Avdulov<sup>[1]</sup>首次报道了禾本科 232 种植物有三种染色体类型:  $x=9$  和 10 的小染色体;  $x=12$  的小染色体;  $x=7$  的大染色体。Stebbins<sup>[2]</sup>根据细胞学资料将禾本科分为四个亚科:  $x=9$  和 10 在热带分布的黍亚科和虎尾草亚科;  $x=7$  在温带分布的早熟禾亚科;  $x=12$  在热带雨林分布的竹亚科。McWilliam<sup>[3]</sup>认为不同的染色体基数对应 6 个亚科: 竹亚科 (Bambusoideae,  $x=12$ ); 酸膜芒亚科 (Centothecoideae,  $x=12$ ); 早熟禾亚科 (Pooideae,  $x=7$ ); 芦竹亚科 (Arundinoideae,  $x=6, 7, 13$ ); 虎尾草亚科 (Chloridoideae,  $x=9$ ,

10); 黍亚科 (Panicoideae,  $x=9, 10$ )。GPWG<sup>[4]</sup>基于分子系统学和形态学的数据, 将禾本科分为 12 个亚科, 印证了不同的染色体基数对应不同亚科的观点。然而不同亚科也有相同的染色体基数的情况, 因而单纯依靠染色体基数是不能证明单系类群的。

Hubbard<sup>[5]</sup>和 Stebbins<sup>[2]</sup>认为虎尾草亚科和黍亚科来源于共同的祖先。Takeoka<sup>[6]</sup>和 Clayton<sup>[7]</sup>认为这两个亚科的祖先是芦竹类群 (Arundinoid), 其染色体基数 6 经非整倍性减少成 5, 再多倍化成染色体基数 10, 有些再经非整倍性减少成 9。这个推论得到最近的分子数据的证明<sup>[8-11]</sup>。Roodt 和 Spies<sup>[12]</sup>提

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出虎尾草亚科的染色体基数是由  $x=5$  经古多倍化而来。目前,近一半的虎尾草亚科分类群的染色体资料已有报道,但缺乏系统的整理和分析。

本文对虎尾草亚科的细胞学资料进行了综述,整理该亚科的细胞学资料,分析染色体基数的演化趋势,为深入开展相关研究提供参考。

## 1 细胞学的资料来源

搜集整理主要的虎尾草亚科细胞学资料有: Avdulov<sup>[1]</sup>, Hunter<sup>[13]</sup>, Nielson<sup>[14]</sup>, Moffet<sup>[15]</sup>, Hurcombe<sup>[16,17]</sup>,

Moffet 和 Hurcombe<sup>[18]</sup>, Pienaar<sup>[19]</sup>, De Wet<sup>[20-23]</sup>, De Wet 和 Anderson<sup>[24]</sup>, Reeder 和 Singh<sup>[25]</sup>, Nordenstam<sup>[26]</sup>, Vorster 和 Liebenberg<sup>[27]</sup>, Jones 等<sup>[28]</sup>, Nordenstam<sup>[29]</sup>, Spies<sup>[30]</sup>, Davides 等<sup>[31]</sup>, Spies 和 Du Plessis<sup>[32-34]</sup>, Spies 和 Jonker<sup>[35]</sup>, Du Plessis 和 Spies<sup>[36]</sup>, Hoshino 和 Davidse<sup>[37]</sup>, Spies 和 Gibbs<sup>[38]</sup>, Spies 和 Voges<sup>[39]</sup>, Spies 等<sup>[40]</sup>, Strydom 和 Spies<sup>[41]</sup>, Roodt 和 Spies<sup>[12]</sup>。涉及到 72 属 547 种 9 亚种 41 变种 3 变型 1 杂交种共计 601 个分类单位 (表 1, 限于篇幅, 每个属仅列出一个分类单位的细胞学资料)。

表 1 虎尾草亚科属种的染色体基数  
Table 1 Chromosome numbers in Chloridoideae

Species (Tribe*)	x	n	References
<i>Acrachne racemosa</i> Ohwi (E)	9	18	Goldblatt and Johnson 1994
<i>Aegopogon cenchroides</i> Humb. & Bonpl. ex Willd. (E)	10	10, 20 (4), 30, 40	Ornduff 1968, 1969; Moore 1970, 1973, 1974
<i>Aeluropus lagopoides</i> Druce (E)	10	10 (2), 20, 25 (2)	Moore 1971, 1972; Goldblatt 1985; Goldblatt and Johnson 1994
<i>Allolepis texana</i> (Vasey) Soderstr. & H.F.Decker (E)	10	20 (2)	Ornduff 1968, 1969
<i>Astrebla lappacea</i> (Lindl.) Domin (C)	10	20 (3)	Federov 1969
<i>Blepharidachne benthamiana</i> Hitchc. (E)	7	7 (2)	Federov 1969; Goldblatt 1985
<i>Blepharoneuron tricholepis</i> (Torr.) Nash (E)	8	8 (4)	Moore 1973; Goldblatt 1981; Goldblatt and Johnson 1991, 1994
<i>Bouteloua alamosana</i> Vasey ex Rose (C)	10	30	Moore 1974
<i>Buchlomimus nervatus</i> (Swallen) Reeder (C)	10	20 (2)	Ornduff 1967, 1969
<i>Calamovilfa gigantea</i> Scribn. et Merr. (E)	10	20	Ornduff 1969
<i>Cathestecum annuum</i> Swallen (C)	10	10 (2)	Ornduff 1967, 1968
<i>Chaboissaea atacamensis</i> (Parodi) P.M.Peterson et Annable (C)	8	8	Goldblatt and Johnson 1996
<i>Chloris acuminata</i> Trin. (C)	10	20	Federov 1969
<i>Cottea pappophoroides</i> Kunth (P)	10	10 (4)	Federov 1969; Moore 1970
<i>Crypsis aculeata</i> Aiton (E)	8, 9	8 (2), 9 (4), 27	Moore 1977; Federov 1969; Goldblatt 1981; Goldblatt and Johnson 1996
<i>Ctenium canescens</i> Benth. (C)	9	9	Moore 1977
<i>Cynodon aethiopicus</i> Clayton et J.R.Harlan (C)	10, 9	9-18	Moore 1973
<i>Dactyloctenium aegyptium</i> (L.) Willd. (E)	10, 6	9 (3), 9+, 10 (6), 11, 11+, 23/2, 27/2, 17, 18 (3), 19 (3), 20 (11)	Ornduff 1967, 1968; Federov 1969; Moore 1971, 1972, 1973, 1974, 1977; Goldblatt 1980, 1981, 1985; Goldblatt and Johnson 1990, 1991, 1994, 1996
<i>Desmostachya bipinnata</i> Stapf (E)	10	10 (5), 20	Moore 1977; Goldblatt 1981, 1985; Goldblatt and Johnson 1990
<i>Dinebra arabica</i> Jacq. (E)	10	10	Federov 1969
<i>Diplachne bulgarica</i> Bornm. (E)	10	20 (2)	Moore 1977
<i>Distichilis palmeri</i> (Vasey) Fassett ex I.M.Johnst. (E)	10	20	Ornduff 1968
<i>Eleusine brevifolia</i> R.Br. (E)	9	18	Federov 1969
<i>Enneapogon borealis</i> (Griseb.) Honda (P)	10	10	Goldblatt and Johnson 1994
<i>Enteropogon gracilior</i> Rendle (C)	10	20	Federov 1969
<i>Eragrostiella bifaria</i> (Vahl) Bor (E)	10, 9	9, 20	Moore 1977; Goldblatt 1981
<i>Eragrostis acutiflora</i> Nees (E)	10	20 (2)	Moore 1972, 1977
<i>Erioneuron avenaceum</i> (Kunth) Tateoka (E)	8	8 (2), 16	Moore 1970; Goldblatt 1985
<i>Eustachys petraea</i> (Sw.) Desv. (C)	10	20 (3)	Ornduff 1968; Goldblatt 1981
<i>Gouinia gautemalensis</i> (Hack.) Swallen (E)	10	38	Moore 1974
<i>Griffithsochloa multifida</i> (Griffiths) G.J.Pierce (C)	10	10	Goldblatt 1981

续表 1 (Continued)

Species (Tribe*)	x	n	References
<i>Gymnopogon ambiguus</i> (Michx.) B.S.P. (C)	10	20	Moore 1970
<i>Harpachne schimperii</i> Hochst. (E)	10	20	Ornduff 1967
<i>Hilaria annua</i> Reeder et C.Reeder (C)	9	18	Goldblatt and Johnson 1991
<i>Jouvea pilosa</i> Scribn. (E)	10	10 (4)	Ornduff 1969; Moore 1973, 1974
<i>Kengia hackelii</i> (Honda) Packer (E)	10	20	Ornduff 1969
<i>Leptochloa coeruleascens</i> Steud. (E)	10	10 (3)	Moore 1977; Goldblatt 1981
<i>Leptochloopsis virgata</i> (Poir.) Yates (E)	10	20	Moore 1974
<i>Lepturus cylindricus</i> (Willd.) Trin. (L)	7	13, 26	Federov 1969
<i>Lycurus phleoides</i> Kunth (E)	10	14, 20 (6)	Ornduff 1967, 1969; Federov 1969; Moore 1973; Goldblatt 1981
<i>Microchloa kunthii</i> Desv. (C)	10, 6	12 (3), 20 (2), 22	Ornduff 1967, 1969; Moore 1974; Goldblatt 1981, 1985
<i>Monanthochloë littoralis</i> Engelm. (E)	10	20 (2)	Ornduff 1969; Goldblatt 1980
<i>Mosdenia phleoides</i> Stent (C)	10	20	Federov 1969
<i>Muhlenbergia agascalientensis</i> Y.Arrieta et Lacerda-Lemus (E)	10	10	Goldblatt and Johnson 1996
<i>Munroa mendocina</i> Phil. (E)	8	8	Federov 1969
<i>Neeragrostis reptans</i> (Michx.) Nicora (E)	10	30	Moore 1970
<i>Neostaphia colusana</i> Davy (O)	10	20 (2)	Ornduff 1967; Goldblatt 1985
<i>Neyraudia arundinacea</i> (L.) Henrard (E)	10	20	Goldblatt and Johnson 1990
<i>Oxychloris scariosa</i> (F.Muell.) Lazarides (C)	10	20 (3)	Ornduff 1968; Federov 1969
<i>Orcuttia californica</i> Vasey (O)	10, 6	12, 16	Federov 1969; Goldblatt 1985
<i>Oropetium capense</i> Stapf (E)	10	20	Moore 1974
<i>Pappophorum bicolor</i> E.Fourn. ex Hemsl. (P)	10	20, 30, 50 (3)	Ornduff 1968; Federov 1969; Moore 1970
<i>Pentarrhaphis polymorpha</i> Griffiths (C)	10	10	Federov 1969
<i>Pereilema brasilianum</i> Trin. (E)	10	20	Goldblatt 1981
<i>Perotis hilderbrandtii</i> Mez (C)	10	20	Ornduff 1968
<i>Pringleochloa stolonifera</i> Scribn. (C)	10	20 (2)	Ornduff 1968, 1969
<i>Redfeldia flexuosa</i> (Thurb.) Vasey (E)	10	25/2, 12II+II	Goldblatt 1981
<i>Reederochloa eludens</i> Soderstr. & H.F.Decker (E)	10	19 (2)	Ornduff 1969; Goldblatt 1981
<i>Schedonnardus paniculatus</i> Trel. (C)	10	10 (4), 15	Federov 1969; Ornduff 1969; Moore 1970; Goldblatt 1981, 1983
<i>Scleropogon brevifolius</i> Phil. (E)	10	14, 20 (4)	Ornduff 1969; Moore 1970, 1973; Goldblatt 1981
<i>Spartina alterniflora</i> Loisel. (C)	10, 7	20, 21, 28, 30, 31 (7), 35 (3)	Federov 1969; Moore 1970, 1972; Goldblatt 1981
<i>Sporobolus africanus</i> (Poir.) Robyns & Tournay (E)	6/9	18 (2)	Ornduff 1968; Federov 1969; Goldblatt and Johnson 1996
<i>Tetrapogon spathaceus</i> Hack. ex Dur. et Schinz (C)	9	9 (2)	Federov 1969
<i>Tragus berteronianus</i> Schult. (C)	10	10 (10)	Ornduff 1967, 1968, 1969; Federov 1969; Moore 1970, 1973, 1974; Goldblatt 1985; Goldblatt and Johnson 1994
<i>Trichloris crinita</i> (Lag.) Parodi (C)	10	20	Federov 1969
<i>Tridens albescens</i> Wooton et Standl. (E)	10	30 (3)	Moore 1970, 1973; Goldblatt 1981
<i>Triplasis purpurea</i> Chapm. (E)	10	20	Moore 1970
<i>Tripogon bromoides</i> Roth ex Roem. et Schult. (E)	10	10 (4)	Moore 1977; Goldblatt 1981, 1985
<i>Uniola latifolia</i> Michx. (E)	6	12, 24 (6)	Ornduff 1968; Federov 1969
<i>Vaseyochloa multinervosa</i> (Vasey) Hitchc. (E)	10	28?, 34	Federov 1969
<i>Willkommia texana</i> Hitchc. (C)	10	30	Federov 1969
<i>Zoysia japonica</i> Steud. (C)	10	20 (2)	Federov 1969

\* Abbreviations for tribes: P = Pappophoreae; O = Orcuttieae; E = Eragrostideae; C = Chlorideae; L = Leptureae (Classification according to Clayton and Renvoize<sup>(42)</sup>).

表中的数据来源于 Ornduff<sup>(61-63)</sup>, Federov<sup>(64)</sup>, Moore<sup>(65-70)</sup>, Goldblatt<sup>(71-73)</sup> and Goldblatt and Johnson<sup>(74-77)</sup>, 其中配子体染色体数目 n 括号中的数字是所检查的标本数目。Data in this table are cited from Ornduff<sup>(61-63)</sup>, Federov<sup>(64)</sup>, Moore<sup>(65-70)</sup>, Goldblatt<sup>(71-73)</sup> and Goldblatt and Johnson<sup>(74-77)</sup>, the number of specimens examined is indicated in brackets after each corresponding chromosome numbers.

## 2 统计分析

在虎尾草亚科的 601 个分类单位中,82.2%的分类群染色体基数是10,9.2%的种染色体基数是 9,其他的染色体基数还有 6,7,8,占所研究分类群总数的百分比分别是 3.3%,2.0%,3.3% (表 2)。x=6,7,8 仅在个别族的分类群中存在,如染色体基数 6 仅出现在 3 个族的 *Orcuttia greenei* Vasey, *Sporobolus trichodes* Hitchc., *Microchloa indica* (L. f.) P. Beauv. 等 20 个种中,染色体基数 7 仅出现在 3 个族的 *Blepharidachne kingii* Hack., *Spartina stricta* Roth, *Lepturus pannonicus* Kunth 等 10 个种中,染色体基数 8 仅出现在 2 个族的 *Chaboissaea atacamensis* (Parodi) P. M. Peterson et Annable, *Erioneuron awenaceum* (Kunth) Tateoka, *Munroa mendocina* Phil. 等 20 个种中。因此虎尾草亚科基本的染色体基数为 10 和 9。Roodt 和 Spies<sup>[12]</sup>新报道的属种资料如下: *Cladoraphis spinosa* (L. f.) S. M. Phillips (2n=4x=40); *Enneapogon pretoriensis* Stent (2n=2x=20); *Enteropogon macrostachyus* K. Schum. ex Engl. (2n=4x=40); *Eragrostis tenuifolia* (A. Rich.) Steud. (2n=2x=20); *Odyssea paucinervis* Stapf (2n=4x=36); *Sporobolus albicans* Nees (2n=6x=54); *Sporobolus virginus* (L.) Kunth (2n=2x=18); *Sibirius conrathii* Chiov. (2n=2x=20)。

从体细胞染色体数目来看,古多倍化染色体基数 (paleopolyploid basic chromosome number) 10 存在于 *Cladoraphis cyperoides* (Thunb.) S. M. Phillips.,

*C. spinosa* (L. f.) S. M. Phillips., *Enteropogon macrostachyus* K. Schum. ex Engl., *Eragrostis tenuifolia* Hochst. 等种中,古多倍化染色体基数 9 存在于 *Odyssea paucinervis* Stapf, *Sporobolus albicans* Nees 等种中,古多倍化染色体基数 10,9 存在于 *Schmidia pappophoroidea* Steud., *Sporobolus virginicus* Kunth 等种中。

大约 80%的种子植物是多倍体植物,多倍化是植物演化过程中最重要的细胞遗传学机制之一<sup>[2]</sup>,是成种事件 (speciation) 的促进因子。从表 2 可见,虎尾草亚科 38.8%的种是二倍体,61.2%的种是多倍体,其中 48.9%的种是四倍体,多倍体占有相当大的比例。由于 x=10 和 9 占总分类群的 91.4%,图 1 比较了染色体基数为 10 和 9 的多倍化水平。染色

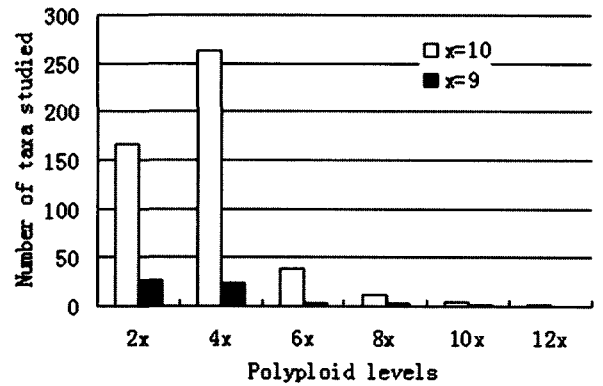


图 1 虎尾草亚科染色体基数为 9 和 10 的多倍化水平  
Fig. 1 Polyploid levels within subfamily Chloridoideae based on basic chromosome numbers x = 10 and 9

表 2 虎尾草亚科各族的染色体基数和多倍化水平

Table 2 Basic chromosome numbers and polyploid levels in tribes of Chloridoideae

Tribe	x					nx						Total
	6	7	8	9	10	2x	4x	6x	8x	10x	12x	
Chloridoideae	2	3	1	24	248	113	147	15	0	2	1	278
%	0.7	1.1	0.4	8.6	89.2	40.6	16.9	5.4	0	0.7	0.4	
Eragrostideae	16	3	19	29	231	109	137	24	23	5	0	298
%	5.4	1.0	6.4	9.7	77.5	36.6	46.0	8.0	7.7	1.7	0	
Leptureae	0	4	0	2	0	2	3	1	0	0	0	6
%	0	66.7	0	33.3	0	33.3	50.0	16.7	0	0	0	
Pappophoreae	0	0	0	0	9	8	1	0	0	0	0	9
%	0	0	0	0	100	88.9	11.1	0	0	0	0	
Orcuttieae	2	0	0	0	8	1	6	3	0	0	0	10
%	20.0	0	0	0	80.0	10.0	60.0	30.0	0	0	0	
Total	20	10	20	55	496	233	294	43	23	7	1	601
%	3.3	2.0	3.3	9.2	82.2	38.8	48.9	7.2	3.8	1.2	0.1	

Percentage of the total species in each tribe is indicated in the next line of each tribe.

体基数 10 的多倍体占 60.6%, 其中四倍体占明显的优势。

### 3 讨论

#### 3.1 染色体基数 $x=5,6,7$ 是禾本科原始的染色体基数

Raven<sup>[43]</sup>提出  $x=10,11,12$  是禾本科原始的染色体基数, 而 Stebbins<sup>[44]</sup>提出  $x=5,6,7$  是禾本科原始的染色体基数,  $x=10,11,12$  是其古多倍化的结果。目前虎尾草亚科的细胞学证据暗示 Stebbins<sup>[44]</sup>的推论可能是正确的。

首先从虎尾草亚科的祖先类群来看。De Wet<sup>[21]</sup>和 Stebbins<sup>[2]</sup>均支持芦竹亚科是虎尾草亚科的祖先的观点。Clayton<sup>[45]</sup>的观点: 芦竹亚科继续向两个方向演化, 其中一个为黍亚科, 另一个就是虎尾草亚科。许多学者的研究<sup>[1,642,46-48]</sup>也支持虎尾草亚科的祖先是芦竹亚科。从细胞学资料来看, 芦竹亚科的染色体基数是 6, 可能经过非整倍性减少为 5, 进一步多倍化成 10, 还有一些再经非整倍性减少为 9。并且染色体基数 10 和 9 在虎尾草亚科稳定下来。这一假设得到最近分子系统学证据的支持, Spangler 等<sup>[49]</sup>, Hilu 和 Esen<sup>[50]</sup> 的研究表明虎尾草亚科的外类群 *Danthonia* DC. 和基部类群 *Centropodia* Rchb. 的染色体基数均是 6。

其次从现存类群的染色体基数来看。虎尾草亚科和黍亚科发现有极个别的种  $x=5$ 。在虎尾草亚科, De Wet<sup>[51]</sup>报道产于北美的 *Muhlenbergia andina* Hitchc. 的染色体数目  $2n=2x=10$ , Pohl<sup>[52]</sup>报道产于津巴布韦的 *Dactyloctenium giganteum* Fisch. et Schweick 的染色体数目  $2n=2x=10$ , Roy<sup>[53]</sup>报道印度的 *Eragrostis diarrhena* Steud. 的染色体数目  $2n=4x=20$ 。而虎尾草亚科 91.4% 的种  $x=10, 9$ 。同样情况发生在黍亚科, Morakinyo 和 Olorode<sup>[54]</sup>报道黍亚科 *Sorghum* 属发现二倍体  $2n=2x=10$ 。Garber<sup>[55]</sup>和 Celarier<sup>[56]</sup>提出须芒草族 (*Andropogon*, *Panicoideae*) 的染色体基数为 5。Watson 和 Dallwitz<sup>[57]</sup>总结黍亚科其他几个属的染色体基数 5, 而黍亚科绝大多数种  $x=10$ 。

因此, 由芦竹亚科沿两条不同路线演化而来的虎尾草亚科和黍亚科,  $x=10$  和 9 在演化历史的早期就已经稳定下来, 而  $x=5$  的绝大部分类群在演化早期已经灭绝, 仅有个别“遗迹”存在于现生种。

#### 3.2 细胞学资料对虎尾草亚科属上类群的系统分类有相当重要的价值

Van den Borre 和 Watson<sup>[58]</sup>认为冠芒草族是虎尾草亚科的基部类群, 该族  $x=10$  和 9。这暗示祖先类群的多倍化和非整倍性减少均发生在演化史的早期。Uniolinae 亚族  $x=10$ , 同时 *Uniola latifolia* Michx. 的  $x=6$  则验证了非整倍性减少的事件。

*Sporobolus* 属染色体基数  $x=10$  和 9, 偶见  $x=6$  的种<sup>[20,22-24,31,33,35,39,40]</sup>。Brown<sup>[59]</sup>提出 *Sporobolus* 属的染色体基数 9 是由  $x=10$  非整倍性减少而来。Christopher 和 Samraj<sup>[60]</sup>报道 *Sporobolus maderaspatanus* Bor 的染色体数目  $2n=2x=12$ , 后来又在 *Sporobolus molleri* Hack 和 *Sporobolus tenuissimus* Kuntze 两种中发现  $2n=2x=12$ <sup>[28,31]</sup>, Hubbard<sup>[5]</sup>提出 *Sporobolus* 属与 *Eragrostis* 属有很近的亲缘关系, *Eragrostis* 属有古多倍化染色体基数 5<sup>[53]</sup>。因此, Christopher 和 Samraj<sup>[60]</sup>提出 *Sporobolus* 属的  $x=6$  是  $x=5$  经非整倍性增加而来。换句话说,  $x=6$  的类群代表虎尾草亚科相对原始的类群,  $x=9$  的类群是由  $x=10$  的类群经过非整倍性减少而来的, 所以,  $x=9$  的类群是相对进化的类群。

Hilu 和 Alice<sup>[11]</sup>的分子生物学研究显示  $x=9$  类群具有的形态性状是: 穗状花序, 而小穗中可育小花数目的减少, 外稃脉数的减少等, 大多出现在指状分支 clade  $C_1$  中, 暗示这一分支是虎尾草亚科相对特化的一支, 值得开展深入的研究。

#### 3.3 染色体基数的演化趋势

推测染色体基数的演化趋势是:  $x=6 \rightarrow x=5 \rightarrow x=10 \rightarrow x=9$ 。首先  $x=6$  仅出现在虎尾草亚科的祖先类群和基部类群, 而  $x=5$  出现在现生个别的种类; 其次 82.2% 的种  $x=10$ , 仅 8.2% 的种  $x=6, 7, 8$ , 说明经多倍化而来的  $x=10$  在演化史的早期就稳定下来; 再次  $x=9$  的“指状分支”类群具有相对进化的形态性状。因此, 推测染色体基数的演化趋势是:  $x=6 \rightarrow x=5 \rightarrow x=10 \rightarrow x=9$ 。

#### 3.4 $x=5$ 的大多数类群在虎尾草亚科的演化史早期就灭绝了

现存的虎尾草亚科植物中仅有个别的“遗迹”种  $n=x=5$  存在。另外, Stebbins<sup>[44]</sup>提出染色体的多倍化和非整倍性增减在成种事件的过程中扮演着关键的作用, 现存的虎尾草亚科植物 61.2% 是多倍体,

暗示这一类群是“成种事件”活跃的一支, 高频率的多倍体和“成种事件”造成的早期的  $n=x=5$  的类群灭绝, 进一步证明 Stebbins 的推论, 即虎尾草亚科早期分化产生的二倍体类群  $2n=2x=10$  已经灭绝。

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