

Studies on

Old World Bluestems III

by

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W. L. Richardson, and H. R. Chheda

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Introduction

This bulletin summarizes the highlights of work conducted on Old World bluestems since the last bulletin in this series was issued in October 1958.

Included are chromosome numbers of 306 accessions not reported in the previous bulletins (Celarier and Harlan 1955; Harlan, Celarier, Richardson, Brooks, and Mehra 1958).

Artificial hybrids produced in the crossing program are listed and include 278 hybrids between 56 parents representing 20 different species belonging to three genera. Fifteen backcrosses are also listed.

F₂ populations of 267 hybrid plants were grown and the segregating populations indicated.

The morphological characters associated consistently with presumptive genomes are given and used to indicate phylogenetic relationships of some of the species.

The nature and extent of some of the genetic barriers between taxa are discussed and the parameters of intercrossability within the group partially defined.

Some indications of agronomic potential are presented and discussed.

¹Cooperative investigations between the Crops Research Division, ARS, USDA and the Okla. Agric. Expt. Station.

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Cytological Studies

The cytological studies listed here represent considerable expansion over those reported in previous bulletins. The key and classification previously used is generally valid but inadequate to cover all the materials now studied. Publication of a more complete treatment will be made by de Wet and Harlan at a later date. Although experimental results clearly indicate some change in taxonomy is desirable, this will be deferred until evidence is more complete. The species used here are widely accepted by taxonomists familiar with the group and nomenclature will be changed only after sufficient experimental evidence is available to improve the classification.

Accessions studied since the 1958 bulletin was issued are as follows:
Bothriochloa alta (Hitchc.) Henrard

Duodecaploids ($2n = 120$) VENEZUELA: 4253; TEXAS: 3063; 6094.

B. ambigua S. T. Blake

Hexaploid ($2n = 60$) AUSTRALIA: 5643 Canberra.
B. barbinodis (Lag.) Herter

Hexaploid ($2n = 60$) TEXAS: 6095; 6097 Marfa.

Duodecaploid ($2n = 120$) ARGENTINA: 4606 Buenos Aires.
B. caucasica (Trin.) C. E. Hubb.

Tetraploid ($2n = 40$) Accessions previously reported from USSR.
B. decipiens (Hack.) C. E. Hubb.

Tetraploids ($2n = 40$) AUSTRALIA: 3727, 5421 New South Wales; 4598. 4611 Queensland.

B. decipiens (Hack.) C. E. Hubb. var. *cloncurrrens* (Domin) C. E. Hubbard

Tetraploids ($2n = 40$) AUSTRALIA: 6510, Queensland; and 4789, 7501, 7545 7548; NEW GUINEA: 7558.

B. edwardsiana (Gould) Parodi

Hexaploid ($2n = 60$) TEXAS: 3682.
B. erianthoides (F. Muell.) C. E. Hubb.

Hexaploid ($2n = 60$) AUSTRALIA: 4786.

B. ewartiana (Domin) C. E. Hubb.

Pentaploids ($2n = 50$) AUSTRALIA: 5803 Queensland; UNITED STATES (INTRODUCED): 503.

Hexaploids ($2n = 60$) AUSTRALIA: 6137, 6138 Queensland; KANSAS (INTRODUCED): 6136.

B. exaristata (Nash) Henrard.

Hexaploids ($2n = 60$) BRAZIL: 6591; ARGENTINA: 6326.

B. glabra (Roxb.) A. Camus

Diploids ($2n = 20$) INDIA: 8298, 8300 Poona; 8301 Sangamner.

Tetraploids ($2n = 40$) INDIA: 8294 Sangamner; 8295 Malavali; 8296 Dehra Dun; 8297 Nagpur.

B. insculpta (Hochst.) A. Camus

Pentaploids ($2n = 50$) SOUTH AFRICA: 4090, 4091, 4905, 6902; KENYA 3239 Nairobi.

Hexaploids ($2n = 60$) SOUTHERN RHODESIA: 4624, 4626, 4627, 4628; SOUTH AFRICA: 5168, 5190, 5192, 5194; AFRICA: 4906, 4907, 5152; TRINIDAD (INTRODUCED): 4293.

B. intermedia (R. Br.) A. Camus

Tetraploids ($2n = 40$) INDIA: 4394, 5312 Dehra Dun; 5297, 5401 Lonavla; 5324 Indore; 5408 Coimbatore; 5409 Bareilly; 5410 Punjab; 6152, 6176 West Bengal; 6864, 7154 New Delhi; 7010 Palampur; 7232 Poona; IRAN: 7529; MALAYA: 5752 Kedah; PHILIPPINES: 4633 Quezon; 6482 Laguna; 7176 Mindanao; NEW GUINEA: 7765 Sorong; 7555; 7556; 7557; FIJI: 5593; 5594; SOUTH AFRICA: 7030, 7544 Pretoria; and 4090, 7700; EAST AFRICA: 7699; KENYA: 5470; AUSTRALIA: 5803b Queensland; 6511, 6551 Northern Territory; and 7547, 7548, 7549, 7550, 7551; AMERICA (INTRODUCED): 4088, 6363 Texas; 7454, 7457, 7460 Alabama; 7462 Georgia.

Pentaploids ($2n = 50$) INDIA: 6841 New Delhi; AUSTRALIA: 7554b; SOUTH AFRICA: 5168; AMERICA (INTRODUCED): 6265 Puerto Rico; 50, 52 Kansas; 4896 Unknown.

Hexaploids ($2n = 60$) INDIA: 4820 Delhi; 7201 Poona; AUSTRALIA: 7554; SOUTH AFRICA: 5168b; AMERICA (INTRODUCED): 4293 Trinidad; 5800 Puerto Rico.

Octoploid ($2n = 80$) AUSTRALIA: 4607 Lawes.

B. intermedia gangetica type

Tetraploids ($2n = 40$) INDIA: 4028 Mt. Abu; 4394b Dehra Dun; 5400 Poona; 5405, 6149 New Delhi; 4806 Hyderabad; 6580 Southeast India. AMERICA (INTRODUCED): 4393b Trinidad.

B. intermedia indica type

Tetraploids ($2n = 40$) PAKISTAN: 4634, 4636 Sargodha, and 6587b; AFGHANISTAN: 6573b Kandahar.

B. ischaemum (L.) Keng

Common type (*B. ischaemum* var. *ischaemum*)

Tetraploids ($2n = 40$) INDIA: 3057 Punjab; HUNGARY: 4798 Budapest; 5422 Szentes; and 7041, 7043, 7044, 7045, 7059; GERMANY: 3075; BELGIUM: 3240 Brussels; and 6582; YUGOSLAVIA: 4800 Belgrade; GREECE: 6585; ROMANIA: 7057; TURKEY: 3457 Tunceli and 7496; SOVIET UNION: 7056 Ashkhabad, 7240 Ukraine, IRAN: 6586, 6985; AFGHANISTAN: 6584; KENYA (INTRODUCED): 6982; AMERICA (INTRODUCED): 1356 Brazil; 4092, 5110 Arizona; 5193 Texas.

Hexaploid ($2n = 60$) GREECE: 4771.

Oriental type (*B. ischaemum* var. *songarica* (Rupr.) Celar. & Harl.)

Pentaploids ($2n = 50$) ITALY: 3958 Sicily; HONG KONG: 6459; JAPAN (via Taiwan): 7055.

Hexaploids ($2n = 60$) TAIWAN: 2582; CHINA: 5638 Hunan Province; 3344 Triangle City.

B. kuntzeana (Hack.) Henrard

Tetraploid ($2n = 40$) INDIA: 8299 Khandala.

B. pertusa (L.) A. Camus

Tetraploids ($2n = 40$) INDIA: 3713 Allahabad; 4564 Nadia; 4806 Hyderabad; 5405 Delhi; 5408 Bareilly; 5452 Poona; and 5403; PAKISTAN: 6587; CHINA: 6154; CEYLON: 7500; AMERICA (INTRODUCED): 6267, 6268 Puerto Rico; 6903 Georgia.

B. radicans (Lehm.) A. Camus

Tetraploids ($2n = 40$) KENYA: 3055, 5469; ETHIOPIA: 4518.

B. saccharoides (Sw.) Rydb. var. *longipaniculata* (Gould) Gould

Duodecaploids ($2n = 120$) ARGENTINA: 3133; TEXAS 3693.

B. saccharoides (Sw.) Rydb. var. *torreyana* (Steud.) Gould

Hexaploids ($2n = 60$) ARGENTINA: 4396; URUGUAY: 6235; OKLAHOMA: 2579, 2580, 7302; TEXAS 6096.

Octoploid ($2n = 80$) HAWAII: 4085.

Capillipedium hugelii (Hack.) A. Camus

Diploids ($2n = 20$) INDIA: 5794 Bombay; HONG KONG: 6460b.

C. parviflorum (R. Br.) Stapf

Diploid ($2n = 20$) INDIA: 6856 New Delhi.

Tetraploids ($2n = 40$) KENYA: 3054; JAPAN: 6156, 7128; INDIA: 7158 New Delhi; HONG KONG 6458.

C. spicigerum (Benth.) S. T. Blake

Tetraploids ($2n = 40$) AUSTRALIA: 4599, 4608 Queensland; and 4101; IRAQ: 5113 Baghdad.

Pentaploid ($2n = 50$) AUSTRALIA: 4788.

Dichanthium annulatum (Forsk.) Stapf

Tropical type

Diploids ($2n = 20$) INDIA: 6180 Calcutta; 6224, 6577 New Delhi; BURMA: 6192.

Tetraploids ($2n = 40$) INDIA: 3227 Allahabad; 4019, 6090 Hyderabad; 4593 Himayet Sagar; 5405, 6837, 6838, 6863, 7158b, New Delhi; 5438, 7026 Poona; 6175b Khandala; 6866 Amritsar; 7018b Palampur; 7133 Benares; 7183 Thana; 8293 Sangamner; PAKISTAN: 6574; AFGHANISTAN: 6225, 6573 Kandahar; FIJI ISL.: 5602 Suva; NEW GUINEA: 7571; AMERICA (INTRODUCED): 5584, 6373, 6375 Texas; 6263 Puerto Rico.

Mediterranean type.

Tetraploids ($2n = 40$) IRAQ: 3903 Abu Ghraib; 5113, 5114, 5115, 5116, 5119, 5120, 5125, 5126, 5128, 5134, 5136, 5137, 5139, 5143, 5145, 5146 Baghdad; and 6576; MOROCCO: 7419 Ait Hamadi.

Senegalese type

Tetraploid ($2n = 40$) SENEGAL: 5429, 5430 Bambey.

Unclassified types

Tetraploids ($2n = 40$) TANGANYIKA: 4804; GOLD COAST: 6877 Achinoto.

Hexaploid ($2n = 60$) AUSTRALIA: 4788b Rodd's Bay.

D. aristatum (Poir.) C. E. Hubb.

Tetraploids ($2n = 40$) SOUTH AFRICA: 2611 Pretoria; and 5111; AMERICA (INTRODUCED): 4290 Trinidad.

D. aristatum mollicomus type

Diploid ($2n = 20$) INDIA: 7199 Sangli.

Tetraploids ($2n = 40$) INDIA: 6149 Delhi; EAST AFRICA: 7499; HUNGARY (INTRODUCED): 7047.

Hexaploid ($2n = 60$) PHILIPPINES: 6406.

D. caricosum (L.) A. Camus

Tetraploids ($2n = 40$) INDIA: 5287 Sangar; 5399 Rohtak; 5440 Poona; 6179 South India; 8280 Lonavla; AMERICA (INTRODUCED): 5584 Texas; 5799 Puerto Rico.

D. fecundum S. T. Blake

Tetraploid ($2n = 40$) AUSTRALIA: 6525 Queensland.

D. humilius J. M. Black

Diploid ($2n = 20$) AUSTRALIA: 3723 Sydney; and 7256; NEW GUINEA: 7566.

D. pallidum (Hook. f.) Stapf ex Fischer

Tetraploids ($2n = 40$) INDIA: 5452 Poona; 6172 Dharwar; 6177, 6178 Bihar

D. panchganiense Blatter & McCann

Diploid ($2n = 20$) INDIA: 8278 Panchgani

D. papillosum (Hochst.) Stapf

Hexaploids ($2n = 60$) SOUTH AFRICA: 4105, 5112; SENEGAL: 5429 Bambey

D. sericeum (R. Br.) A. Camus

Diploids ($2n = 20$) AUSTRALIA: 2572, 2573 Brisbane, 2574, 4610, 4612, 5640, 6139 Queensland; and 1349, 4102, 6261, 6826, 6836, 7568.

D. sericeum (R. Br.) A. Camus var. *mollis* (F. M. Bailey) de Wet, comb. nov. *Andropogon sericeus* var. *mollis* F. M. Bailey, Queensland Agr. Journ. 30:316. 1913.

Diploids ($2n = 20$) AUSTRALIA: 4594, 6140 Queensland; and 4101, 4103, 7570.

D. setosum S. T. Blake

Diploids ($2n = 20$) AUSTRALIA: 4100, 7784, 7865.

D. superciliatum (Hack.) A. Camus

Diploids ($2n = 20$) AUSTRALIA: 5626, 5628.

D. tenue (R. Br.) A. Camus

Tetraploids ($2n = 40$) MALAYA: 2583 Kuala Lumpur; INDIA: 5326 Indore; FIJI ISL: 5599; AMERICA (INTRODUCED): 4291 Trinidad; UNKNOWN: 4029.

Eremopogon foveolatus (Del.) Stapf

Tetraploids ($2n = 40$) INDIA: 2662 Coimbatore; 4072 Ajmer; 8305 Poona.

Pseudosorghum fasciculare (Roxb.) A. Camus

Diploid ($2n = 20$) INDIA: 6168 Bihar.

Crossing Studies

The hybrids reported in this section were nearly all produced by W. L. Richardson using the method described by him (1958). In the case of hybrids using X750 as the female, emasculation was usually not practiced. This particular plant is quite sexual and highly self-sterile although it will produce up to two or three selfed seeds per inflorescence. It was derived from a cross between two facultatively apomictic *Bothriochloa intermedia* gangetica type plants. Another sexual synthetic, *Dichanthium annulatum* X98 has been used less extensively. This plant is quite sexual and very highly self-sterile, but its own pollen seems to interfere with foreign pollen and tends to block hybridization when emasculation is not practiced. Hybrids with this parent have, therefore, been limited.

The hybrids listed do not by any means represent all the hybrids actually produced in the program. In some combinations a large number of F_1 's were obtained, but only a few selected for cytological study. Only those which have been studied are reported. In all, 56 parents are involved representing 44 combinations of some 25 types of 20 different species belonging to three genera. Of particular interest from an evolutionary point of view are the several hybrids between New World and Australian species.

Table 1.—Hybrids Produced Experimentally in the Bothriochloineae.

Female Parent	Male Parent	No. F ₁ 's	Chromosome No. F ₁ 's
<i>Bothriochloa intermedia</i> , gangetica type (4n) × <i>B. intermedia</i> , gangetica type (4n)			
X750 (Synthetic)	5450 (India)	3	40
" "	5168b (So. Africa)	3	40
5400 (India)	5450 (India)	1	40
" "	2655 (Br. Guiana)	2	40
" "	5168b (So. Africa)	1	40
5450 (India)	5592 (Fiji Isl.)	2	40
" "	2655 (Br. Guiana)	3	40
5592 (Fiji Isl.)	5450 (India)	1	40
2655 (Br. Guiana)	5592 (Fiji Isl.)	3	40
<i>B. intermedia</i> , gangetica type (4n) × <i>B. intermedia</i> (4n)			
5168b (So. Africa)	5297 (India)	4	40
		1	60
2655 (Br. Guiana)	7010 (India)	1	40
" "	5297 (India)	4	40
		1	60
5450 (India)	" "	2	40
" "	7010 (India)	1	40
X750 (Synthetic)	5410b (India)	1	39
		6	40
5450 (India)	5410b (India)	6	40
		3	60
2655 (Br. Guiana)	5410b (India)	1	40
		1	60
5168b (So. Africa)	" "	5	40
		2	60
5400 (India)	" "	2	40
		1	60
5450 (India)	6511 (Australia)	3	40
" "		2	60
" "	6580 (India)	5	40
		2	60
<i>B. intermedia</i> (4n) × <i>B. intermedia</i> gangetica type (4n)			
5297 (India)	2655 (Br. Guiana)	1	40
" "		2	60
" "	5450 (India)	2	40
		2	60
5410b (India)	5400 (India)	1	60
" "	2655 (Br. Guiana)	2	40
		3	60
<i>B. intermedia</i> , gangetica type (4n) × <i>B. caucasica</i> (4n)			
X750 (Synthetic)	4066 (Kew-Intro.)	2	39
		4	40
<i>B. intermedia</i> , gangetica type (4n) × <i>B. ewartiana</i> (6n)			
2655 (Br. Guiana)	6138 (Australia)	1	70
<i>B. intermedia</i> , gangetica type (4n) × <i>B. ischaemum</i> var. <i>ischaemum</i> (4n)			
5450 (India)	7162 (USSR)	1	40
" "	7498 (Turkey)	2	40
" "	5704 (China)	3	40
2655 (Br. Guiana)	7162 (USSR)	3	40
		2	60
5168b (So. Africa)	5704 (China)	1	40

(Table continued on next page.)

Table 1.—(Continued) Hybrids Produced Experimentally in the Bothriochloinaeae.

Female Parent	Male Parent	No. F ₁ 's	Chromosome No. F ₁ 's
5168b (So. Africa)	7162 (USSR)	$\left. \begin{array}{l} 1 \\ 1 \\ 1 \\ 2 \end{array} \right\}$	40
			42
			43
			60
4028 (India)	" "	1	40
X750 (Synthetic)	7498 (Turkey)	5	40
<i>B. intermedia</i> , gangetica type (4n) × <i>B. ischaemum</i> var. <i>songarica</i> (5n)			
X750 (Synthetic)	726 (China)	$\left. \begin{array}{l} 1 \\ 1 \\ 1 \end{array} \right\}$	39
			41
			42
2655 (Br. Guiana)	K. R. (China via Texas)	1	50
<i>B. intermedia</i> , gangetica type (4n) × <i>B. ischaemum</i> (6n)			
2655 (Br. Guiana)	1359 (Turkey)	2	50
		1	70
X750 (Synthetic)	6182 (Burma)	$\left. \begin{array}{l} 2 \\ 3 \\ 2 \\ 1 \\ 1 \\ 1 \end{array} \right\}$	41
			42
			44
			46
			47
			48
<i>B. intermedia</i> , gangetica type (4n) × <i>B. odorata</i> (Lisboa) A. Camus (4n)			
2655 (Br. Guiana)	5409 (India)	2	40
5430b (Senegal)	" "	1	40
<i>B. intermedia</i> , gangetica type (4n) × <i>B. pertusa</i> (4n)			
5168b (So. Africa)	5431 (Senegal)	1	40
		2	60
2655 (Br. Guiana)	" "	1	60
5450 (India)	" "	1	60
X750 (Synthetic)	"	2	40
		1	42
<i>B. intermedia</i> , gangetica type (4n) × <i>B. radicans</i> (4n)			
2655 (Br. Guiana)	3055 (Kenya)	1	60
<i>B. intermedia</i> , gangetica type (4n) × <i>Capillipedium parviflorum</i> (4n)			
2655 (Br. Guiana)	3054 (Kenya)	1	40
5450 (India)	6156 (Japan)	2	40
X750 (Synthetic)	" "	2	40
<i>B. intermedia</i> , gangetica type (4n) × <i>C. spicigerum</i> (4n)			
5450 (India)	4599 (Australia)	2	40
		1	47
		2	40
<i>B. intermedia</i> , gangetica type (4n) × <i>Dichanthium annulatum</i> , tropical type (4n)			
2655 (Br. Guiana)	4099 (India)	9	40
" "	" "	11	60
" "	5398 (India)	1	60
5450 (India)	4099 (India)	2	40
X750 (Synthetic)	"	5	40
		1	60
" "	X98 (Synthetic)	3	40

(Table continued on next page.)

Table 1.—(Continued) Hybrids Produced Experimentally in the Bothriochloineae.

Female Parent	Male Parent	No. F ₁ 's	Chromosome No. F ₁ 's
<i>D. annulatum</i> , tropical type (4n) × <i>B. intermedia</i> , gangetica type (4n)			
4099 (India)	2655 (Br. Guiana)	2	40
X98 (Synthetic)	" "	6	40
<i>B. intermedia</i> , gangetica type (4n) × <i>D. annulatum</i> , tropical type (2n)			
2655 (Br. Guiana)	3242 (India)	1	50
<i>B. intermedia</i> , gangetica type (4n) × <i>D. papillosum</i> (6n)			
X750 (Synthetic)	4083 (So. Africa)	{ 1	40
		{ 1	48
		{ 2	50
<i>B. intermedia</i> , gangetica type (4n) × <i>D. aristatum</i> , mollicomus type (2n)			
X750 (Synthetic)	7199 (India)	5	30
<i>B. intermedia</i> , gangetica type (4n) × <i>D. caricosum</i> (4n)			
X750 (Synthetic)	7208 (India)	1	39
		1	40
<i>B. intermedia</i> , gangetica type (4n) × <i>D. fecundum</i> (4n)			
X750 (Synthetic)	6525 (Australia)	{ 1	38
		{ 1	39
		{ 5	40
<i>B. intermedia</i> (4n) × <i>B. ischaemum</i> var. <i>ischaemum</i> (4n)			
5410b (India)	7162 (USSR)	2	40
<i>B. ambigua</i> (6n) × <i>B. intermedia</i> , gangetica type (4n)			
5643 (Australia)	5450 (India)	2	50
<i>B. ambigua</i> (6n) × <i>B. ischaemum</i> var. <i>ischaemum</i> (4n)			
5643 (Australia)	7162 (USSR)	4	50
<i>B. saccharoides</i> var. <i>torreyana</i> (6n) × <i>B. exaristata</i> (6n)			
2579 (Oklahoma)	6591 (Brazil)	8	60
<i>B. saccharoides</i> var. <i>torreyana</i> (8n) × <i>B. decipiens</i> (4n)			
4085 (Hawaii)	6510 (Australia)	1	60
<i>B. saccharoides</i> var. <i>longipaniculata</i> (12n) × <i>B. ambigua</i> (6n)			
3133 (Argentina)	5642 (Australia)	2	90
<i>B. saccharoides</i> var. <i>longipaniculata</i> (12n) × <i>B. erianthoides</i> (6n)			
3133 (Argentina)	4786 (Australia)	1	90
<i>D. annulatum</i> , tropical type (2n) × <i>D. annulatum</i> , tropical type (2n)			
3242 (India)	6180 (India)	1	20
" "	6577 (India)	1	20
<i>D. annulatum</i> , tropical type (4n) × <i>D. annulatum</i> , tropical type (4n)			
X98 (Synthetic)	4099 (India)	2	40
<i>D. annulatum</i> , tropical type (4n) × <i>D. annulatum</i> , tropical type (2n)			
X98 (Synthetic)	3242 (India)	2	30
<i>D. annulatum</i> , tropical type (4n) × <i>D. annulatum</i> , Mediterranean type (4n)			
4099 (India)	4830 (Saudi Arabia)	2	40
X98 (Synthetic)	4390 (Tunisia)	1	40
		1	60
<i>D. annulatum</i> , tropical type (4n) × <i>D. fecundum</i> (4n)			
X98 (Synthetic)	6525 (Australia)	3	40
<i>D. annulatum</i> , tropical type (4n) × <i>D. papillosum</i> (6n)			
X98 (Synthetic)	4080 (So. Africa)	4	50
4099 (India)	" "	3	50
<i>D. papillosum</i> (6n) × <i>D. annulatum</i> , tropical type (4n)			
4083 (So. Africa)	X98 (Synthetic)	2	50

(Table continued on next page.)

Table 1.—(Continued) Hybrids Produced Experimentally in the Bothriochloinae.

Female Parent	Male Parent	No. F ₁ 's	Chromosome No. F ₁ 's
<i>D. annulatum</i> , Senegal type (4n) × <i>D. papillosum</i> (6n)			
5430 (Senegal)	4023 (So. Africa)	1	50
<i>D. annulatum</i> , tropical type (4n) × <i>D. annulatum</i> , Senegal type (4n)			
X98 (Synthetic)	5430 (Senegal)	5	40
		2	60
<i>B. ischaemum</i> var. <i>songarica</i> (5n) × <i>D. annulatum</i> , tropical type (4n)			
6459 (Hong Kong)	X98 (Synthetic)	2	70
<i>D. aristatum</i> , mollicomus type (4n) × <i>D. annulatum</i> , tropical type (4n)			
2571 (Texas-Intro.)	5398 (India)	1	40
<i>D. aristatum</i> , mollicomus type (4n) × <i>D. annulatum</i> , Senegal type (4n)			
2571 (Texas-Intro.)	5430 (Senegal)	1	40
<i>D. aristatum</i> (4n) × <i>D. tenue</i> (4n)			
4084 (Texas--Intro.)	2583 (Malaya)	2	40
		1	60
<i>D. tenue</i> (4n) × <i>D. aristatum</i> (4n)			
2583 (Malaya)	4290 (Trinidad-Intro.)	1	40
" "	4084 (Texas-Intro.)	1	60
<i>D. annulatum</i> , tropical type (4n) × <i>D. tenue</i> (4n)			
X 98 (Synthetic)	5599 (Fiji Isl.)	1	40
<i>D. tenue</i> (4n) × <i>D. annulatum</i> , tropical type (4n)			
2583 (Malaya)	5398 (India)	1	40
<i>D. tenue</i> (4n) × <i>D. aristatum</i> , mollicomus type (4n)			
2583 (Malaya)	4095 (California-Intro.)	1	40
		1	60

Table 2.—Backcrosses Studied Cytologically.

Cross	2n Chromosome Numbers			Number of Backcrosses
	Female Parent	Parent Male (hybrid)	Parent Backcross	
5450 × (4099 × 2655)	40	40	40	1
5450 × (5450 × 5704)	40	40	40	2
5450 × (2655 × 4099)	40	40	40	1
5450 × (2655 × 5295)	40	40	60	1
X98 × (2655 × 5398)	40	40	40	1
X98 × (X98 × 6525)	40	40	40	7
4099 × (5797 × 4099)	40	40	40	1
2655 × (5797 × 4099)	40	60	70	1
				Total 15

5450 and 2655 are *B. intermedia* gangetica types
 4099, 5295, 5398, 5797, and X98 are *D. annulatum* tropical types
 5704 is *B. ischaemum* var. *ischaemum*
 6525 is *D. fecundum*

Second Generation Populations

Open and self pollinated progenies of 267 of the hybrids were grown to test for sexual reproduction in the F₁ generation. Nearly all of the populations were uniform although some of the population sizes were less than desirable. Twenty-two populations showed segregation and 16 of these represented combinations which have some potential for winter hardiness. To date a really winter hardy sexual plant has not been found and this test is particularly encouraging from that point of view. The segregating populations are listed in Table 3.

Table 3.—Segregating F₂ Populations.

Hybrid	Parents	2n	No. of Plants	No. Segregating
55×302-1	D. aristatum 4084 × D. tenue 2583	40	10	4
57×834a-1	D. annulatum 4099 × B. intermedia 5450		13	4
57×955	D. annulatum 5430 × D. annulatum 4099		8	5
58×499-1	B. ambigua 5643 × B. intermedia 5450	50	38	17
58×455	B. ambigua 5643 × B. ischaemum 7162	50	15	3
58×477a	B. intermedia 2655 × B. intermedia 5404		77	12
58×482	B. intermedia 2655 × B. intermedia 6573b	60	72	17
58×489a-1	B. intermedia 2655 × B. intermedia 2655	80	20	5
58×503a	B. intermedia 2655 × B. ischaemum 7162	40	111	20
58×670a-1	B. intermedia 5168b × B. intermedia 3965		42	4
58×675-1	B. intermedia 5168b × B. intermedia 5410b		85	14
58×676-2	B. intermedia 5168b × B. intermedia 5410b	60	41	4
58×676-4	B. intermedia 5168b × B. intermedia 5410b	40	42	4
58×676-5	B. intermedia 5168b × B. intermedia 5410b	60	58	18
58×677-2	B. intermedia 5168b × B. intermedia 5410b	40	44	5
58×685a-1	B. intermedia 5168b × B. ischaemum 7162	43	19	3
58×696-5	B. intermedia 5297a × B. intermedia 5450		12	2
58×768a-1	B. intermedia 5410b × B. ischaemum 7162	60	45	9
58×775-2	B. intermedia 5450 × B. intermedia 3965		20	7
58×785a-1	B. intermedia 5450 × B. intermedia 6587b		30	16
58×798-2	B. intermedia 5450 × B. ischaemum 7162		29	5
58×850a-1	B. intermedia 6573b × B. intermedia 5410b	40	28	5

Morphological Studies

In the second bulletin of this series, certain diploid forms were postulated. Two of these have since turned up in our collection: a basic diploid *Bothriochloa*, and a basic diploid *Capillipedium*. The *Bothriochloa* turns out to fit the description of *B. glabra*, and although they differ somewhat one from the other, three accessions have so far been obtained. In *Capillipedium*, *C. hugelii* appears to be a diploid species,

but more significantly, a diploid race of *C. parviflorum* has also been found.

Our prediction of a diploid *D. aristatum* has also been partially vindicated. We now have such a plant, but the morphological evidence suggests very strongly that this accession is really a polyhaploid derived from a natural *D. aristatum* \times *D. caricosum* cross. We have obtained such polyhaploids experimentally and since the natural $2n$ accession from India shows characters of both *D. caricosum* and *D. aristatum* it is likely that it originated in this way.

If polyhaploids can be successful in nature, there is a possibility that the several $2n$ *D. annulatum* accessions in our collection are also polyhaploids. The ease with which it is possible to scale from one ploidy level to another, both up and down, in this group suggests caution in selecting truly basic diploids upon which to reconstruct the phylogeny of the group. However that may be, a truly basic *Dichanthium* could differ from our $2n$ *D. annulatum* in only a few characters at most. It is with these reservations in mind that a series of morphological characters was worked out for several of the basic genomes in the group. (See Table 4.)

First, the three accessions of *B. glabra* were used to characterize the basic *Bothriochloa* genome, BB. Then, the modified genome B_1B_1 was established by noting the differences between *B. glabra* and *B. ischaemum*. A B_2B_2 genome was also postulated on the basis of the differences between *B. glabra* and *B. pertusa*. The basic *Dichanthium* genome, DD is based upon diploid *D. annulatum* and the modified D_1D_1 upon the differences between *D. annulatum* and *D. aristatum*. The basic *Capillipedium* genome (CC) is based upon the diploid *C. parviflorum*.

Additional characters might be used, but those listed in Table 4 appear to be the most stable and consistent and are adequate to show the relationship between some of the species and genomic combinations. By this system of classification, *B. ischaemum* var. *ischaemum* would have the constitution BB B_1B_1 . Morphologically, this constitution is consistent with the expression of characters in this species. For example, the glumes of *B. ischaemum* are never pitted, but some may be slightly dishd or dimpled especially in the central portions of the racemes. In some cases there is also a faint trace of a groove down the glume or the faintest trace of pungence in the foliage. Such expressions might be expected from a BB B_1B_1 constitution.

Table 4.—Morphological Characteristics.

Character	BB	B ₁ B ₁	B ₂ B ₂	DD	D ₁ D ₁	CC
1. Pedicel groove	yes	yes	yes	no	no	yes
2. Pedicel length	long	long	long	short	V. short	long
3. Glume shape	pointed	pointed	pointed	round	V. round	V. pointed
4. Hairs lower ½ glume	no	yes	yes	yes	yes	few
5. Arc of hairs across tip of glume	no	no	no	yes	no	no
6. Glume hairs bulbous based	no	no	no	yes	no	no
7. Glumes pitted (at least some)	yes	no	yes	no	no	no
8. Glume grooved down back	yes	no	no	no	no	yes
9. Rachis hairs	V. long	V. long	long	med. short	med. V. short	no rachis
10. Axis length (relative to racemes)	long	short	short	short	V. short	V. long
11. Raceme length (relative to axis)	med.	long	long	long	V. long	V. short
12. Peduncle hairs	no	no	no	no	yes	no
13. Length sterile zone	short	short	short	short	short	V. long
14. Lower sessile spikelets bisexual	yes	yes	yes	no	no	yes*
15. Ring of hairs below node	yes	no	yes	no	no	yes
16. Hairs all over node	no	no	no	yes	no	yes
17. Foliage pungent	yes	no	yes	no	no	yes
18. Stature	erect	erect	creep.	decumb.	erect	erect
19. Secondary branching (inflorescence)	V. little	V. little	V. little	V. little	none	much

* In *C. parviflorum* there are but three spikelets per raceme, the sessile one bisexual and the two pedicellate ones male or neuter.

In *B. intermedia* gangetica type, the constitution is presumed to be BBDD. This presumption is based upon the following characteristics of the gangetica type:

1. Pedicel solid (as in DD)
2. Pedicel long (as in BB)
3. Glume pointed (as in BB)
4. Hairs present lower ½ of glume (as in DD)
5. Some hairs across tip of glume (as in BD)
6. A few hairs slightly bulbous based (as in BD)

- | | |
|---|--------------------|
| 7. Glumes not pitted | (as in DD) |
| 8. Glumes round on back | (as in DD) |
| 9. Rachis hairs medium | (as in DD) |
| 10. Axis length intermediate | (as in BD) |
| 11. Raceme length intermediate | (as in BD) |
| 12. Peduncle hairs absent in both parents | |
| 13. Sterile zone short in both parents | |
| 14. Lower sessile spikelets bisexual | (as in BB) |
| 15. Ring of hairs below node intermediate | (as in BD) |
| 16. Hairs over node | (as in BD) |
| 17. Foliage slightly pungent | (as in BD) |
| 18. Stature intermediate | (as in BD) |
| 19. Some secondary branching | (as in $B_x B_x$) |

From this tabulation of characteristics, it is evident that the gangetica type could as well be called a *Dichanthium* as a *Bothriochloa*. Crossing data bear this out.

In the second bulletin in this series as well as elsewhere, we have pointed out that introgression occurs between *B. intermedia* and such species as *Capillipedium parviflorum*, *Dichanthium annulatum*, *B. ischaemum* and *B. pertusa*. The result is a rather extensive variability in the expression of the characters indicated. A generalized genomic constitution of *B. intermedia* might be expressed as $B_x B_x B'_x B'_x$ and the associated characters take on the following variation in expression:

1. Pedicel grooved—or solid in gangetica type
2. Pedicel long
3. Glumes pointed to very pointed
4. Glumes glabrous or with hairs on lower half
5. Upper half of glume glabrous or with a few hairs across tip
6. Glume hairs not bulbous based or some slightly bulbous based

7. Glumes pitted, not pitted, intermediate or variable
8. Glumes grooved, round, or intermediate
9. Rachis hairs short to long
10. Axis medium to very long
11. Racemes medium to short
12. Peduncles glabrous
13. Sterile zone short to medium
14. Lower spikelets bisexual
15. Ring of hairs below node absent, medium or well developed
16. Hairs over node absent to medium
17. Foliage not pungent, to very pungent
18. Stature erect or decumbent
19. Secondary branching none to much.

The extreme polymorphism of *B. intermedia* can be readily explained on the basis of the genetic contributions from the several species with which it crosses in nature. The use of genomic symbols and associated morphological characters has value in demonstrating graphically the origin of certain taxa within the group, but on the whole must be used with some reservations. A large number of the hybrids listed in this bulletin have been studied cytologically. The data are too voluminous to report here, but show clearly that genomes are not clearly defined by pairing behavior. Preferential pairing seems to be the rule within the group. If a chromosome has a homolog, it will usually pair with it although a few univalents are common in most accessions. If a homolog is not present the chromosome will pair, though less frequently, with another similar chromosome. Autosyndesis is common, but there appears to be some slight homology between B and D genomes and perhaps a little homology between B and C genomes.

In a complimentary way, morphological characteristics are not clearcut either. No single character holds up consistently throughout the group. On the other hand, we are not dealing with a freely interbreeding complex. Most accessions can be classified rather easily into one taxon or another. True intermediates that do not fit described species are uncommon although they occur. The forces of cohesion and speciation are

as nicely balanced in the Bothriochloineae as in most natural groups.

With these reservations in mind, the following taxa can be characterized based upon the morphological characters associated with the basic genomes established:

- B. intermedia* $B_x B_x B'_x B'_x$ as indicated
- B. intermedia* gangetica type BBDD as indicated
- B. intermedia* indica type $B_x B'_x B_1 B$ (some *B. ischaemum* characters present)
- B. ischaemum* var. *ischaemum* $BBB_1 B_1$ (by definition)
- B. ischaemum* var. *songarica* $B_x B_x B_x B_1 B_1$ or $B_x B_x B'_x B'_x B_1 B_1$ (allo-pentaploids or allohexaploids between *B. intermedia* and *B. ischaemum*).
- B. pertusa* $BBB_2 B_2$ (by definition)
- B. insculpta* $B_2 B_2 BBB_x B_x$ (allohexaploid between *B. pertusa* and *B. intermedia*)
- C. parviflorum* CCC'C' (by definition)
- C. spicigerum* CC'B_xB_x (This comb. reproduced artificially in our nurseries)
- D. annulatum*, tropical type DDD'D' (by definition)
- D. annulatum*, Mediterranean type DDD'B (This comb. obtained in F₂ populations of *B. intermedia* gangetica type × *D. annulatum*, tropical type)
- D. aristatum* DDD₁D₁ (by definition)
- D. papillosum* DDDD'D'B (Probably a functional unreduced egg of *D. annulatum* tropical type fertilized by *D. annulatum*, Mediterranean type)
- D. caricosum* DDD_xD_x (Or some combination of derived D. genomes)

The morphological characteristics of these taxa are consistent with the genomic designations. Due to the preferential pairing of the chromosomes it is not likely that cytological proof can be developed, and these designations are used primarily to indicate probable relationships of the several species and types.

Problems of Speciation

With the array of successful hybridizations listed in this bulletin, some reevaluation of the taxonomic system is immediately suggested. The fact that a large number of combinations have been obtained, however, does not mean that it was easy or that there are no barriers to genetic exchange. In some cases, literally thousands of emasculations were made to obtain a single hybrid plant. Seed set in wide crosses is often low. The seeds that are set are often of maternal type and do not represent hybrids. In some crosses seeds that do not germinate are produced. Some seeds produced are very poorly developed, hardly amounting to more than swollen ovaries. In some combinations, large seedling mortality is obtained. In the case of *B. intermedia* \times *C. parviflorum* and *B. intermedia* \times *B. caucasica*, delayed lethals are evident. Some of the F_1 plants grew vigorously until the tufts reached 12 inches in diameter and were about four feet high, then as maturity approached, they turned a peculiar shade of yellow and died.

The hybrids of some combinations lived to maturity, but were very weak or dwarfed. Some grew well but proved to be completely sterile and could not produce offspring of any kind. Some of the sexual F_1 's produced a few seeds, but the F_2 generation was entirely weak and nonadapted. Meiosis was highly irregular in many hybrids and provided serious barriers in the sexual plants. When the F_1 reproduced apomictically, this barrier was often overcome.

Some combinations, however, produced vigorous hybrids, sometimes showing marked heterosis, which reproduced freely from seed. Such hybrids were for the most part apomictic, but a few vigorous sexual plants were also obtained in some combinations.

The cross compatibility relationships between the various taxa will be amplified and reported elsewhere, but some of the complex trends can be illustrated by the seed set obtained when non-emasculated inflorescences of x750 were pollinated with various sources (Table 5). It will be noted that when other gangetica type plants were used as males about 12 seeds were set per inflorescence. When *D. annulatum* sources were used, the seed set was about 33 per inflorescence. The crossability between x750 and most accessions of *B. intermedia* was poor (6.6 seeds per inflorescence), but with two accessions from Australia, seed set went up to 50 per panicle. High seed set was also obtained using the diploid *D. aristatum* and intermediate seed sets were obtained from the diploid *D. annulatum* and the hexaploid *D. papillosum*.

Good set is obtained in gangetica plants with combinations involving B or D genomes, but set is relatively low where B_x genomes are involved.

A clue to the rather low set obtained between gangetica types may be provided by a stigma removal study by Dewald and Harlan (1960). Evidence for partial self-sterility was found in a gangetica type plant based both on slower pollen tube growth and on lower seed set. Such genes may be common in the gangetica type and low seed sets may not always reflect phylogenetic differentiation. In fact, the barriers to genetic exchange may sometimes be as strong between some closely related types as between more distantly related forms.

In addition to the 44 successful crossing combinations listed under "Crossing Studies", 80 other combinations were attempted without success. In eight of the 80 combinations, the reciprocals were successful. For example, in the cross *B. pertusa* × *B. intermedia*, 1,213 spikelets were emasculated, 93 seeds and 62 partially developed seeds were obtained, but no hybrids were found in the seeds that germinated. In the reciprocal *B. intermedia* × *B. pertusa*, eight hybrids have been produced and grown to maturity. In the combination *C. parviflorum* × *B. intermedia*, 1,103 spikelets were emasculated but not a single even partially developed seed was produced. The reciprocal has yielded several hybrids although some carried the delayed lethal described earlier. Thirty-eight of the crossing combinations that were tried in both directions failed completely.

In all, over 120 crossing combinations have been attempted counting reciprocals. The size and extensiveness of the study permit some generalizations concerning crossing compatibility and parameters of genetic exchange.

1. The diploid accessions of *D. annulatum* are fully sexual and fully intercompatible. They have not yielded hybrids with anything else when used as females.
2. *D. annulatum* × *D. fecundum* is an easy cross if the female parent is a sexual tetraploid. The reciprocal has failed completely due to apomixis in the *D. fecundum* parent.
3. The next easiest combination is *B. intermedia*, gangetica type × *D. annulatum*. This combination is actually easier to obtain than crosses within the gangetica type or within *D. annulatum*.

4. Genetic exchange is more difficult but quite possible between various members of the *B. intermedia* complex wherever sexuality can be found. About the same level of genetic exchange occurs between various kinds of *B. intermedia* and *B. ischaemum*, *B. odorata*, *B. glabra*, *C. parviflorum*, *C. spicigerum*, and *D. papillosum*.
5. *B. pertusa*, *B. radicans*, and *B. caucasica* are more isolated, but can be crossed with *B. intermedia* if the right parents are selected. *D. aristatum* and *D. caricinum* are also rather isolated from the *B. intermedia* group, but some exchange is possible under exacting conditions.
6. Four F₁ plants have been obtained between Old World and New World species. Whether or not genetic exchange would be possible remains to be determined since these hybrids appear to be completely sterile. *B. ambigua* appears to bridge the gap between New and Old World types. It has been crossed with *B. intermedia* and *B. ischaemum* of the Old World and *B. saccharoides* of the New World. Other Australian species capable of crossing with *B. saccharoides* are *B. decipiens* and *B. erianthoides*. These crosses seem to indicate the extreme limits of crossability within the group.
7. The only extensive attempt to go outside of the three genera was with *Eremopogon foveolatus*. Some 15 combinations were attempted involving 2,609 emasculated spikelets without producing a single hybrid. In the case of *B. intermedia* × *E. foveolatus*, some seeds were stimulated by *Eremopogon* pollen. Of 1,607 emasculated spikelets, 22 seeds and 234 partially developed seeds were produced. Either the seeds contained lethals or were maternal in type. This would appear to represent the extreme limit of genetic affinity. The pollen is sufficiently related to stimulate a small amount of pseudogamous seed without actually producing a hybrid. In other combinations not even this degree of relationship was demonstrable.

At this stage in the investigation, it might be reasonable to conclude:

1. That *D. fecundum* is a race or type of *D. annulatum*.
2. That *Bothrichola*, *Dichanthium*, and *Capillipedium* should be lumped together as one genus.
3. That *Eremopogon* is validly a separate genus.

4. That most of the specific epithets are satisfactory, but
5. that there are somewhat too many species and some lumping is in order.
6. That to revise the taxonomy now would only lead to more revisions as soon as more data are available, and that it would be preferable to wait until most of the planned experimental taxonomy has been completed.

Agronomic Potential

Over 50 accessions or hybrids have been entered into preliminary plot tests. Some have already exhibited insufficient winter hardiness and are being discarded. A few have produced out-standing yields in early tests, but all information obtained so far is highly preliminary.

Of the hybrid combinations studied, the *B. intermedia* \times *B. ischaemum* cross seems to have the most promise. Some of the F₁'s display marked heterosis and reproduce apomictically and should have adequate winter hardiness. Other sources of winter hardiness are less promising. Crosses with *B. caucasica* and *B. saccharoides*, for example, may be too sterile to be of use.

Out of *B. intermedia* \times *B. ischaemum* crosses it should be possible to reconstitute something like King Ranch bluestem, but with rust resistance, more hardiness, more drouth resistance and more specific adaptation. Segregation data suggest that hardy, sexual plants are now available for a crossing program. The fact that the *D. annulatum* \times *B. ischaemum* cross can be made suggests that better forage quality might be incorporated into adapted materials.

Field observations in Iran, Afghanistan, Pakistan, and India in 1960 have added considerably to our knowledge of the ecological behavior of various members of the group. In areas of monsoon influence where some summer rainfall occurs, the Bothriochloineae are among the most common and most important of the forage grasses. In desert areas or in areas of winter moisture, only *B. ischaemum* and *D. annulatum* were found, the former generally at upper elevations and the latter in lowland desert regions.

The germ plasm obtained by plant exploration in 1960 should add substantially to the plant breeding resources of the Old World bluestem improvement program.

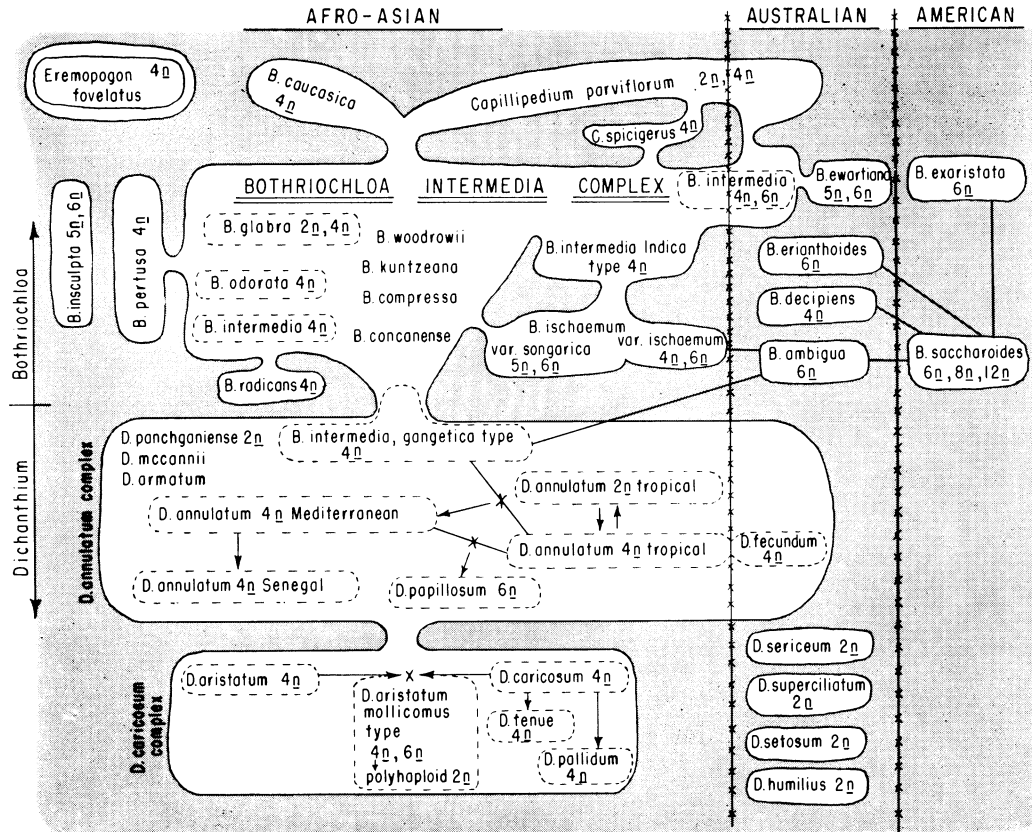


Figure 1. Chart of Relationships among the Bothriochloinae. This chart is based upon extensive crossing studies designed to evaluate the possibilities of gene exchange among and between various taxa. In general, some gene exchange is possible between taxa enclosed by the same solid line. The ease of exchange varies enormously with the most nearly related taxa being placed closest together. For example, genetic exchange between forms within the *Dichanthium annulatum* complex is easier than between this complex and another complex. Crosses between *B. intermedia* and *Capillipedium* are fairly easy, but we have not been able to cross *Capillipedium* with any *Dichanthium* sp. Gene exchange may not be possible between American and Australian species because the hybrids are completely sterile. Lines connecting these taxa indicate such hybrids have been obtained. *Eremopogon* appears to be completely isolated genetically although the pollen can stimulate a small amount of pseudogamous seed to set in *B. intermedia* gangetica type plants. Taxa without chromosome numbers given have not yet been studied experimentally and are placed in their appropriate complexes on the basis of morphology only.

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