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Range of morphological variation within the *Bothriochloa intermedia* complex[1])

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With 95 Figures

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The grass tribe *Andropogoneae* includes a diverse group of genera variously subdivided among subtribes by STAPF 1917: 5—8, BEWS 1929: 82—87, KENG 1939: 274—343, and PILGER 1940: 108, 1954: 367—378. The genus *Bothriochloa* is usually included in the *Andropogoninae*. Although described by KUNTZE 1891: 762, members of *Bothriochloa* are referred to as *Andropogon* L. by HACKEL 1889: 359—651, or treated as members of *Amphilophis* NASH in BRITTON 1901: 71 by STAPF 1917: 171—177. CAMUS 1930: 164, indicates that the species *Bothriochloa anamitica* KUNTZE is identical to *Andropogon glaber* ROXB. which STAPF includes in *Amphilophis*. As the generic name *Bothriochloa* has priority over *Amphilophis*, CAMUS 1930: 163—165, and HENRARD 1940: 520, transferred the Old World representatives of the latter genus to *Bothriochloa*. Similar transfers were made for the American species of *Amphilophis* by HERTER 1940: 134—140, HENRARD 1940: 520, 1941: 456—457, and PARODI 1958: 1—142.

The genus *Bothriochloa* resembles *Andropogon* in that it has spikelets characterized by an obtuse callus and the lower glume 2-keeled with inflexed margins. This genus differs from *Andropogon* conspicuously in respect to lemma characteristics. The bisexual florets have a bilobed lemma with the awn arising from the sinus between the lobes in *Andropogon*; whereas the lemma is entire and forms the hyaline base of the awn in *Bothriochloa*. One American species, *B. exaristata* (NASH) HENRARD, resembles *Hypogynium* NEES, in that it has all florets awnless, and two Australian species

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resemble *Andropogon* in having bilobed lemmas awned from the sinus between the lobes. These three species, however, resemble *Bothriochloa* closely in inflorescence structure.

GARDNER 1952: 329, indicates that no characteristic consistently distinguishes between *Dichanthium* WILLEMET and *Bothriochloa ewartiana* (DOMIN) C. E. HUBBARD, and transfers *B. ewartiana* to *Dichanthium ewartianum* (DOMIN) C. A. GARDNER. Studies by BLAKE 1944: 35, indicate that *B. ewartiana* has oblong-lanceolate lower glume, the pedicel supporting one spikelet of each pair distinctly grooved with all the sessile spikelets bisexual. These are typical *Bothriochloa* characteristics as contrasted to *Dichanthium*, which has more truncate lower glumes, solid pedicels, and the lower 1—6 sessile spikelets male or neuter. Two species of *Capillipedium* STAPF, *C. assimile* (STEUD.) A. CAMUS, and *C. parviflorum* (R. BR.) STAPF, were referred to *Bothriochloa* by OHWI 1947: 1—15. Morphologically *Capillipedium* is characterized by 15 or fewer spikelet pairs per raceme, and the secondary and higher order branches of the panicle each disarticulate individually. Racemes with 20 or more spikelet pairs, a less strongly branched panicle, and a primary raceme complex which disarticulates as a whole characterized *Bothriochloa*. On the basis of these characteristics BOR 1960: 113, refers *B. venusta* (THW.) A. CAMUS to *Capillipedium venustum* (THW.) BOR. Two other species *B. kwashotensis* (HAYATA) OHWI and *B. picta* OHWI, also definitely belong with *Capillipedium*.

HENRARD 1941: 456 points to some objections regarding plants referred to *B. intermedia* (R. BR.) A. CAMUS. The original description of R. BROWN 1810: 202 (*Andropogon intermedius* R. BR. in Prod.), refers to plants from Australia with the primary axis of the inflorescence distinctly longer than the lower racemes. STAPF 1917: 174—175 when transferring *Andropogon pertusus* STAPF (not *A. pertusus* (L.) WILLD.) to *Amphilophis intermedia* var. *acidula*, includes plants with the racemes arranged on a short primary axis. This variety differs from *B. radicans* (LEHM.) A. CAMUS, in having pits present or absent on the lower glume of spikelets in the same raceme. From *B. pertusa* (L.) A. CAMUS, which always has a distinctly pitted lower glume on the sessile spikelet, it differs conspicuously in growth habit.

BLAKE 1944: 37 describes *B. intermedia* as follows. Primary axis of the inflorescence is almost always distinctly longer than the lower racemes, rarely subequal to, or still more rarely slightly shorter than the racemes. The later plants more properly fit the type description of *B. inundata* (F. MUELL.) J. M. BLACK which BLAKE 1944: 37, includes as a synonym of *B. intermedia*.

HENRARD 1941: 456, prefers to include the Malaysian plants with an elongated inflorescence in *B. glabra* (ROXB.) A. CAMUS. STAPF 1917: 172—173, under *Amphilophis glabra* (ROXB.) STAPF, describes this species in detail and cites *Andropogon glaber* ROXB. in: Fl. Ind. 1, 1832: 267 and

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A. intermedius var. *punctatus* subvar. *glaber* (ROXB.) HACKEL as synonyms. ROXBURGH's original description refers to a strongly branched grass with smooth, glossy leaves and panicle branches simple or only sparsely divided, the latter characteristic at variance with the description of both STAPF 1917: 172, and HACKEL 1889: 487. BOR 1960: 106, indicates that both *B. intermedia* and *B. glabra* have elongated inflorescences and refers to *B. intermedia* plants which have all the branches of the panicle simple, or rarely one of the lower divided. Branches of the panicle more or less divided, or if undivided very fine and naked up to over 1.5 cm from the base, characterize *B. glabra*.

Another species *B. odorata* (LISBOA) A. CAMUS, apparently endemic to Bombay State in India, is often difficult to distinguish from *B. intermedia* and *B. glabra*. This species is strongly aromatic, the leaf sheath is terete and the culm always unbranched. The first two characteristics, however, are commonly encountered in the other two species. From Australia *B. ewartiana* (DOMIN) C. E. HUBBARD characterized by a short primary axis of the inflorescence is quite distinct but appears to grade into plants with a long primary axis, apparently due to hybridization. This species, whether having a short or elongated primary axis, differs from *B. intermedia* and *B. glabra* conspicuously in having cauline leaves instead of primarily basal ones.

Bothriochloa caucasica (TRIN.) C. E. HUBBARD, is another species with an elongated primary axis. This plant from Southern Russia was described as *Andropogon caucasicus* TRIN. in: Mem. Acad. Sci. Petersb. Ser. 6, 2, 1832: 286 and treated as *A. intermedius* var. *caucasica* (TRIN.) HACKEL 1889: 486. This is a morphologically distinct species with the upper lemma of the sessile spikelet about half the length of the lower glume and the number of spikelet pairs per raceme reduced to 20 or fewer. In the other species with an elongated primary axis the number of spikelet pairs are more than 25 and the upper lemma is as long as or only slightly shorter than lower glume.

CELARIER & HARLAN 1957: 93—102, indicate that plants usually included in *B. intermedia* form an agamic complex. The specific name *B. intermedia* as referred to in this discussion includes both *B. intermedia* and *B. glabra* as recognized by BLAKE 1944: 39—40, and BOR 1960: 106. CELARIER & HARLAN 1955: 12—21, indicate that natural hybridization takes place between *B. intermedia* and the related *B. ischaemum*. Apparently this hybridization gave rise to *B. ischaemum* var. *songarica* (CELARIER 1957: 737, and CELARIER & HARLAN 1958: 758—759). Morphological data presented by HARLAN & al. 1961: 16—26, suggest that *B. pertusa* may also contribute genes to the *B. intermedia* complex.

The present study is an attempt to determine the range of morphological variation within the *B. intermedia* species-complex.

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TABLE I

MORPHOLOGICAL ANALYSIS CHROMOSOME NUMBERS AND GEOGRAPHIC DISTRIBUTION OF THE MEMBERS OF B. intermedia COMPLEX.

Plant Name	Number	L.P.A.	L.L.R.	No. P.R.	S.R.	Glume	Pr. Node	Sec. Node	2n	Origin
B. longifolia	8298	41.4	65.0	16.2	0.0	B	7.8	0.0	20	Poona, India
	8300	61.9	57.0	23.5	0.4	B	8.8	0.4	20	Sangamner, India
	8301	68.8	58.0	19.8	0.0	B	9.5	0.0	20	Poona, India
B. ewartiana	503	22.3	48.0	9.9	0.0	B	6.1	0.0	50	Queensland, Aust.
	5803	19.6	50.0	7.0	0.0	B	5.0	0.0	50	Queensland, Aust.
	6136	28.0	47.0	10.0	0.0	B	6.2	0.0	60	Queensland, Aust.
	6137	28.6	48.0	9.9	0.0	B	6.4	0.0	60	Queensland, Aust.
B. intermedia X B. ewartiana	6138	59.6	56.0	17.1	1.0	B	9.3	0.6	60	Queensland, Aust.
	7597	47.9	40.0	15.0	14.9	B	9.1	2.0	60	Sydney, Aust.
B. caucasica	1337	90.3	35.0	18.6	25.0	BC	10.8	7.8	40	Tiflis, Russia
	2561	76.0	35.0	14.0	22.0	BC	9.0	2.0	40	U.S.A. Intrd.
	2562	90.0	30.4	26.0	Many	BC	13.0	10.0	--	U.S.A. Intrd.
	2563	95.3	36.1	17.1	48.6	B	10.4	6.3	--	U.S.A. Intrd.
	3238	77.0	30.0	21.0	13.0	BC	10.5	4.0	--	Africa, Intrd.
	4006	90.3	32.0	18.0	27.8	BC	9.8	7.0	40	England, Intrd.
	4595	101.0	45.0	23.5	8.5	BC	11.5	3.5	--	Australia, Intrd.
	5593-b	103.8	42.3	19.4	Many	BC	10.9	10.9	--	Fiji Isls. Intrd.
	6585-b	99.5	33.0	15.5	37.5	BC	11.0	7.0	--	Greece, Intrd.
	7030	88.4	30.5	18.8	35.0	BC	9.4	5.1	40	Africa, Intrd.
	7046	89.9	31.5	19.3	Many	B	11.6	6.9	--	Hungary, Intrd.
	7155	92.6	33.6	17.3	Many	B	10.0	5.6	--	India, Intrd.
	7244	86.3	30.0	19.4	Many	B	10.5	6.2	--	Hungary, Intrd.
	7700	67.0	32.0	13.4	37.5	BC	8.3	4.3	40	Africa, Intrd.
B. odorata	7154	94.1	45.0	25.6	4.0	BC	11.6	1.5	40	Delhi, India
	7232	99.1	42.0	27.6	30.0	BC	12.0	5.3	40	Poona, India
	8295	97.7	32.0	45.2	46.4	BC	12.3	3.6	40	Malavali, India
B. intermedia - B. glabra complex	2560	105.5	60.0	34.5	14.4	B	14.3	3.5	40	U.S.A. Intrd.
	2651	114.0	45.0	41.3	30.3	B	13.5	6.0	40	E. Africa
	2654	89.6	60.0	40.9	8.9	B	12.4	3.9	40	Coimbtore, India
	3726	99.1	51.0	31.6	17.9	BC	13.6	3.5	40	Sydney, Aust.
	3965	154.4	59.0	62.4	10.0	B	16.2	10.0	40	Calcutta, India
	*4087	125.5	40.0	51.5	Many	B	14.5	14.5	40	U.S.A. Intrd.
	4088	113.8	45.0	33.6	16.9	B	13.1	3.1	40	U.S.A. Intrd.
	4090	119.3	50.0	45.4	40.0	B	16.7	9.1	40	S. Africa
	4293	61.1	52.0	25.4	29.8	B	10.5	4.8	60	Trinidad; W. I.
	4394	98.6	40.0	33.5	44.2	B	15.8	9.0	40	Dehra Dun, India
	4596	133.5	65.0	37.6	10.0	B	15.3	2.1	60	Galton, Aust.
	4597	86.3	40.0	26.9	27.0	B	12.1	4.4	60	Galton, Aust.
	*4597-b	135.0	35.0	50.0	Many	B	16.0	16.0	--	Galton, Aust.
	4607	90.1	50.0	34.5	16.5	B	14.1	3.4	80	Lowes, Aust.
	*4633	150.0	43.0	36.0	49.0	B	16.0	12.0	40	Quezon, Philippines
	4896	125.2	60.0	33.5	0.1	B	13.2	0.1	50	U.S.A. Intrd.
	5297	90.3	55.0	30.1	40.1	B	11.8	3.9	40	Lohnavla, India
	5407	110.4	40.0	32.6	60.5	B	15.0	10.9	--	Bhawali, India
	5409	102.5	40.0	30.8	11.1	BC	12.6	3.4	40	Bariely, India
	5410-b	90.0	45.0	36.6	65.5	B	----	---	40	Punjab, India
	5470	116.0	50.0	43.1	32.9	B	14.3	7.1	40	Kenya, Africa
	5752	128.8	----	35.1	7.4	B	13.4	3.0	40	Kedah, Malaya
	5800	62.0	35.0	21.7	11.0	B	10.0	4.0	60	Mayaquez, Porto Rico
	*5825-b	110.3	35.0	30.7	60.0	BC	13.8	13.3	--	U.S.A. Intrd.
	6078	47.5	----	18.0	0.0	B	8.0	0.0	--	U.S.A. Intrd.
	6265	59.0	45.0	25.3	32.0	B	10.3	3.8	50	Mayaquez, Porto Rico
	6363	56.2	30.0	17.5	1.2	B	8.7	1.2	50	U.S.A. Intrd.
	6481	86.0	40.0	25.0	4.0	B	12.0	5.0	--	Delhi, India
	*6511	120.0	30.0	27.2	Many	B	14.7	3.3	40	Australia
	6551	101.4	69.2	34.0	50.0	B	14.0	4.6	40	U.S.A. Intrd.
	*6578	124.1	30.0	47.6	60.0	B	13.4	11.1	--	U.S.A. Intrd.
	6580	64.1	50.0	9.5	0.9	B	6.1	0.9	50	Delhi, India
	6841	112.3	48.0	42.75	35.9	B	13.6	7.1	40	India
	6864	127.0	30.5	23.6	----	B	12.4	6.0	40	Delhi, India
	*6878	76.4	30.0	30.2	50.0	B	16.0	13.2	--	U.S.A. Intrd.
	7010	63.6	40.0	31.5	65.0	B	18.0	16.0	40	Palampur, India
	*7176	131.0	32.0	55.7	22.1	B	18.7	10.0	40	Mindanao, Philippines
	7457	62.5	42.5	16.1	0.6	B	7.0	0.5	40	U.S.A. Intrd.
	*7459	110.0	29.3	21.3	50.0	B	11.0	5.0	--	U.S.A. Intrd.
	7460	77.6	25.0	23.7	0.0	B	9.6	0.0	40	U.S.A. Intrd.
	*7544	109.3	20.0	26.8	37.0	B	13.5	13.5	40	South Africa

Table I (Cont.)

Plant Name	Number	L.P.A.	L.L.R.	No. P.R.	S.R.	Glume	Pr. Node	Sec. Node	2n.	Origin
B. intermedia - B. glabra complex	*7547	137.6	32.0	38.7	60.0	B	14.8	14.8	40	Sydney, Australia
	*7548	99.0	40.0	33.4	60.0	B	16.3	13.3	40	Sydney, Australia
	*7549	101.0	30.0	37.9	60.0	BC	16.1	10.5	40	Sydney, Australia
	*7550	140.7	35.0	33.0	55.5	B	16.9	15.8	40	Sydney, Australia
	*7551	90.0	30.0	32.4	58.5	B	16.6	14.6	40	Sydney, Australia
	*7554	93.8	42.0	31.4	21.6	BC	12.1	3.3	50	Australia
	*7555	170.8	30.0	46.8	60.0	B	17.0	17.0	40	New Guinea
	7556	87.9	28.0	30.1	4.0	BC	14.3	3.4	40	New Guinea
	*7699	142.8	40.0	29.3	37.0	B	11.7	8.7	40	Kenya, Africa
	*7765	110.3	30.0	30.0	60.0	BC	16.6	6.3	40	New Guinea
	7768	120.0	27.5	28.5	----	B	16.5	14.0	--	U.S.A. Intrd.
	8297	102.0	----	22.2	30.3	B	8.8	6.8	40	Nagpur, India
B. intermedia X	5401-a	51.9	60.0	14.8	0.4	B	7.6	0.4	40	Lohnavla, India
	5412	56.4	55.0	16.6	10.0	B	9.8	1.8	--	Tamnar, Morocco
B. ischaemum	6573-b	73.1	41.0	20.7	1.7	B	8.6	0.9	40	Afghanistan
	7055	39.1	35.0	11.6	0.0	B	5.3	0.0	--	Formosa
B. intermedia X	50	67.6	65.0	30.9	4.9	BD	8.3	3.1	50	Australia
	52	87.2	65.0	21.8	24.2	BD	14.0	7.0	50	Australia
D. annulatum (B. grahamii)	2655	61.0	50.0	15.0	1.0	BD	9.0	1.0	40	British Guiana, Intrd.
	2665	56.3	----	15.2	3.0	BD	8.7	0.8	--	Madagascar
	4021-b	46.0	40.0	15.3	0.1	BD	7.6	0.1	40	Ceylon
	4028	43.7	50.0	16.0	2.3	BD	6.8	1.2	40	Mt. Abu, India
	4393	41.5	41.5	15.0	2.5	BD	6.0	1.5	40	Dehra Dun, India
	4600-b	44.3	62.0	11.4	0.0	BD'	6.3	0.0	--	Sargodha, Pakistan
	4806-b	41.5	55.0	14.0	0.0	BD	5.0	0.0	40	Hyderabad, India
	5168-b	56.1	65.0	14.5	2.8	BD'	8.4	1.5	40	South Africa
	5312-b	67.1	52.0	19.8	10.0	BD	9.9	2.8	40	Dehra Dun, India
	5317	47.6	60.0	17.8	0.8	BD	7.1	0.4	--	Dehra Dun, India
	5400	63.8	60.0	19.0	11.9	BD	10.0	2.6	40	Hempur, India
	5400-b	55.3	50.0	16.7	10.2	BD	9.0	2.5	40	Hempur, India
	5400-d	56.1	45.0	21.0	11.0	BD	9.0	2.0	40	Hempur, India
	5404	60.3	65.0	18.0	3.1	BD	8.8	1.3	40	New Delhi, India
	5408	74.9	65.0	22.5	4.0	BD	10.0	1.3	60	Bariely, India
	5408-a	67.0	----	20.8	2.0	BD	9.8	1.6	--	Bariely, India
	5450	74.2	70.0	18.6	8.8	BD	10.2	1.9	40	Delhi, India
	5592	79.8	74.0	17.9	17.0	BD	9.5	2.6	40	Fiji Isls.
	6149	63.3	60.0	18.9	3.1	BD	8.8	0.9	40	Delhi, India
	6176-b	57.6	60.0	14.8	1.3	BD	8.6	0.8	40	West Bengal, India
	7404	69.7	60.0	21.9	14.7	BD	9.4	2.3	--	U.S.A. Intrd.
	7557	69.5	55.0	17.3	7.9	BD'	9.0	1.6	40	New Guinea
B. intermedia X D. caricosum	6482	55.0	45.0	16.2	0.1	BD'	8.8	1.1	40	Laguna, Philippines

*Possible B. intermedia X C. parviflorum derivatives.

Material and methods

Plants investigated were obtained from various parts of the world (Asia, Europe, Australia, Africa, and certain U.S. introductions of these Old World plants) in the form of seeds. These were grown in a uniform nursery following the procedure described by Celarier & Harlan 1956: 184. Plants usually flowered during the first season. Some, however, did not flower before winter and were transferred to a greenhouse. Greenhouse-grown plants differ from field-grown specimens of the same species in morphological features. For this reason, wherever, possible, data from greenhouse material were not used in this study. All the collections studied were not grown the same year; therefore, some environmental variation is to be expected. Both fresh and herbarium specimens were used for the morphological study. The collections studied are listed in Table I.

Eight specimens of each collection were usually studied, and particular attention was given to the following characteristics: 1. Growth habit.

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2. Length and breadth of the third upper-most leaf on the culm. 3. Culm node pubescence. 4. Length of the primary axis of the panicle. 5. Number of node on the primary axis of the inflorescence. 6. Length of the longest panicle branch excluding sterile zone. 7. Length of the longest panicle branch including sterile zone. 8. Number of primary panicle branches. 9. Number of spikelet pairs on the longest raceme. 10. Number of secondary branches. 11. Number of nodes on primary axis of the inflorescence with secondary branches. 12. Length and breadth of sessile spikelets. 13. Shape of sessile spikelets. 14. Pubescence on sessile spikelets. 15. Length and breadth of pedicellate spikelets. 16. Shape of pedicellate spikelets. 17. Pubescence on pedicellate spikelets. 18. Length of pedicellate spikelets. 19. Trichome on pedicel. 20. Pedicel solid or grooved. 21. Awn length.

Character and character combinations (Anderson 1949: 43—48, 1957: 923—927, Sarkar & Stebbins 1956: 297—304) were used to demonstrate natural hybridization between *B. intermedia* and other species of this genus as well as members of the related genera *Capillipedium* and *Dichanthium*. These are presented in pictorialized scattered diagrams (Anderson 1949: 83—86, 1957: 923—927) whereas a comparison of range of these characters is given in tabular form.

Results

The *B. intermedia* species-complex is extremely variable morphologically (Table I). The characters listed are as follows: length of the primary axis of the inflorescence (L. P. A.), length of the longest raceme (L. L. R.), number of primary racemes (P. R.), number of secondary racemes (S. R.), glume characteristics, number of primary nodes on the primary axis of the panicle (Pr. Nodes), number of nodes on the primary panicle branches (Sec. Node) and chromosomes number. In respect to glume characteristics, the lower glume of the pedicellate spikelet may be pilose below the middle (B), pubescent below and scabrid above the middle (BC); these types of glume pubescence are correlated with spikelets which are lanceolate or oblong-lanceolate in outline. Plants with more obovate-truncate glumes are characterized by having the glumes pilose below with longer cilia along

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Explanation of figures 1—21.

Figs. 1—11. Variations in leaf and ligule in the *B. intermedia* complex and related species. One third the original size. — 1. *C. parviflorum*. — 2—3. *B. intermedia* × *C. parviflorum*. — 4—5. *B. intermedia*. — 6. *B. longifolia*. — 7. *B. odorata*. — 8. *B. caucasica*. — 9—10. *B. intermedia* × *D. annulatum*. — 11. *B. intermedia* × *B. ewartiana*.

Figs. 12—21. Variations in nodal hair. Magnification × 3.3. — 12. *B. longifolia*. — 13—16. *B. intermedia*. — 17. *B. intermedia* × *D. annulatum*. — 18. *D. annulatum* × —98. — 19—20. *B. intermedia* × *B. ischaemum*. — 21. *B. ischaemum*.

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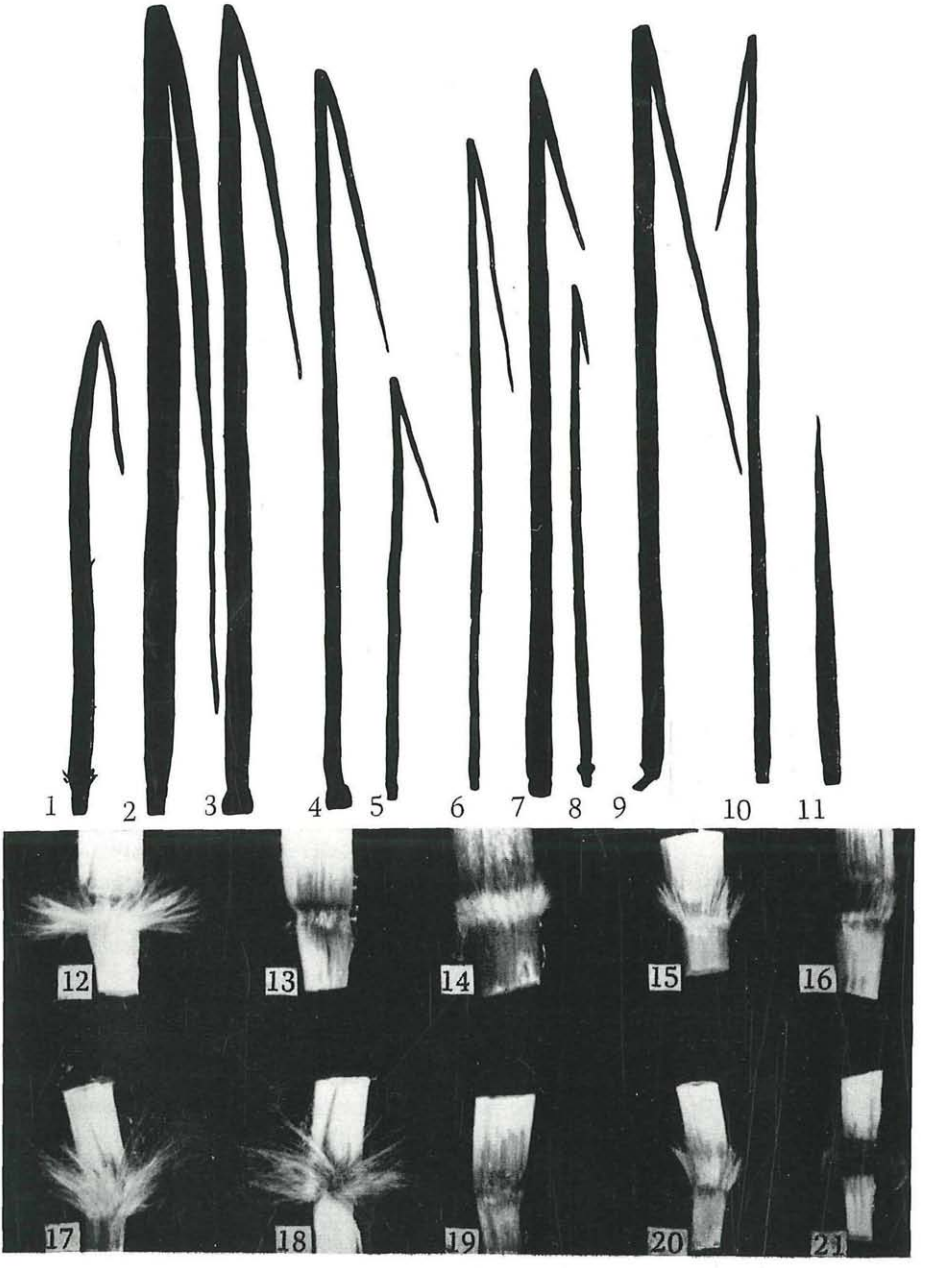

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the margins and near the apex (BD), or the glumes may be glabrous above (BD′). Each one of the characteristics studied will be discussed in some detail.

Growth habit: Plants are erect, or the culms are shortly ascending. One collection was found to be a true creeper. The culms may be branched or simple.

Leaves: Plants studied are characterized by linear-lanceolate leaves (Fig. 1—11), mostly basal, but rarely also cauline. The leaves may be pubescent on both or only one sufrace. Long bulbous-based trichomes are mostly present on the abaxial surface and confined to the base of the leaf. The adaxial surface is usually characterized by the presence of short trichomes. Cilia are always present along the margins of the leaf sheath and are mainly concentrated towards the upper half.

Ligule: This structure is a ciliate membrane in most members of the tribe *Andropogoneae*. This membrane varies from sparsely to densely ciliate.

Culm node pubescence: The nodes are pubescent or glabrous (Fig. 12—21). Typically the node is ciliolate or ciliate. Some plants are characterized by bearded nodes.

Inflorescence structure: The primary axis of the panicle is either subequal in length to or distinctly longer (Figs. 22—55) than the lowest racemes. The panicle branches may be simple, moderately branched or strongly divided.

Spikelet structure: The spikelets are either oblong-lanceolate or oblong-truncate in outline (Figs. 56—90). The lower glumes of the sessile spikelets may be glabrous, pilose below the middle and glabrous above, sparsely pubescent below and scabrid above, or pilose below and with longer cilia along the margins and near the apex. Indentations (pits) may be present or absent on both the sessile and pedicellate spikelets.

Pedicel supporting the pedicellate spikelet: This structure is usually bilaterally ciliate and slightly dorsally compressed. Most plants studied are characterized by pedicels having a distinct translucent middle line. Sometimes, however, the pedicel is solid or only slightly grooved.

Discussion

The grass tribe *Andropogoneae* is one of immense morphological variation, characteristically tropical and subtropical in distribution, with some genera extending into the temperate regions of both the Old and the New Worlds. Gross morphological studies (Hackel 1889: 1—710, Stapf 1917: 4—8, Bews 1929: 82—87, and Pilger 1954: 366—379) indicate that the subtribes, usually recognized, are so interlinked that they form a single coherent group.

The seven genera, *Bothriochloa* O. Kuntze, *Capillipedium* Stapf, *Dichanthium* Willemet, *Euclasta* Franchet, *Eremopogon* (Hack.) Stapf,

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Spathia EWART & DAVIES and *Indochloa* BOR, are morphologically related. Certain members of three of these, *Bothriochloa*, *Capillipedium* and *Dichanthium*, behave like representatives of a coenospecies in the sense of TURESSON 1922: 100—113, 1929: 323—334. Hybrids between certain biotypes of *B. intermedia* and some species of the other two genera are comparatively easy to produce, but *Dichanthium* and *Capillipedium* are genetically isolated (HARLAN & al. 1961: 27). The phylogenetic affinities of *Euclasta*, *Eremopogon*, *Spathia* and *Indochloa* are poorly understood, but morphological data suggest relationships with *Dichanthium*.

CELARIER & HARLAN 1957: 93—102, HARLAN & al. 1958: 3—19, and FARUQI 1964: 280—297 demonstrate that members of these genera form an agamic complex. Diploid (2n = 20) members of this group reproduce sexually, tetraploids are facultative apomicts and higher polyploids are essentially obligate apomicts. Exceptions are some hexaploid Australian and higher polyploid American species of *Bothriochloa* which reproduce sexually. The mechanism of apomixis is gametophytic apospory, and the plants are pseudogamous. The cytologically reduced as well as unreduced female gamete may function sexually or develop parthenogenetically.

It was pointed out by DE WET, MEHRA & BORGAONKAR 1961: 78—82 that in hybrids the chromosomes usually pair preferentially and auto-

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Explanation of figures 22—90.

Figs. 22—55. Panicles of the members of the *B. intermedia* complex showing nature of variation with respect to length of primary axis, length and number of racemes, presence, variation, and absence of branches of the second order and length of sterile zone in primary branches. One fourth the original size. — 22. *D. annulatum* tropical type. — 23. *D. annulatum* mediterranean type. — 24—29. *B. intermedia* × *D. annulatum*. — 30. *B. intermedia*. — 31. *B. intermedia* × *D. caricosum*. — 32. *B. ischaemum*. — 33—35. *B. intermedia* × *B. ischaemum*. — 36. *B. ewartiana*. — 37. *B. intermedia* × *B. ewartiana*. — 38—46. *B. intermedia*. — 47—51. *B. intermedia* × *C. parviflorum*. — 52. *C. parviflorum*. — 53—54. *B. odorata*. — 55. *B. caucasica*.

Figs. 56—87. Variations in pubescence, shape, pit, and relative size of pedicellate and sessile spikelets of the *B. intermedia* complex. Magnification × 4.3. — 56—65. *B. intermedia*. — 66—67. *B. intermedia* × *B. ischaemum*. — 68—69. *B. ischaemum*. — 70—71. *B. intermedia* × *B. ewartiana*. — 72—73. *B. ewartiana*. — 74—75. *B. intermedia* × *D. annulatum*. — 76—77. *D. annulatum*. — 78—79. *B. intermedia* × *D. caricosum*. — 80—81. *D. caricosum*. — 82—83. *B. intermedia* × *C. parviflorum*. — 84—85. *C. parviflorum*. — 86—87. *B. caucasica*.

Figs. 88—90. Members of the *B. intermedia* complex showing pitted, nonpitted, and grooved lower glumes. Magnification × 10. — 88. *B. intermedia* showing pitted glume of the sessile spikelet. — 89. *B. intermedia* × *B. ischaemum* showing smooth glume of the sessile spikelet. — 90. *B. intermedia* × *C. parviflorum* showing a prominent groove in the glume of the sessile spikelet.

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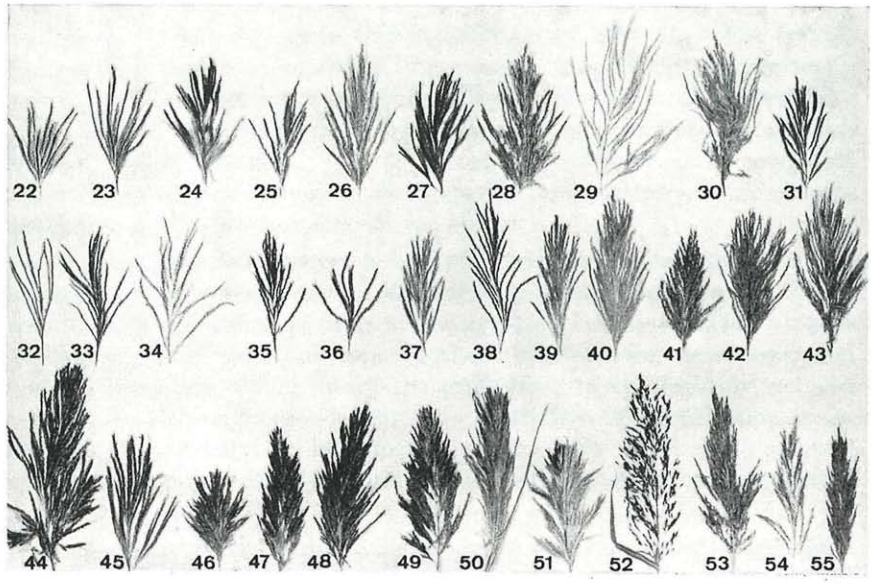

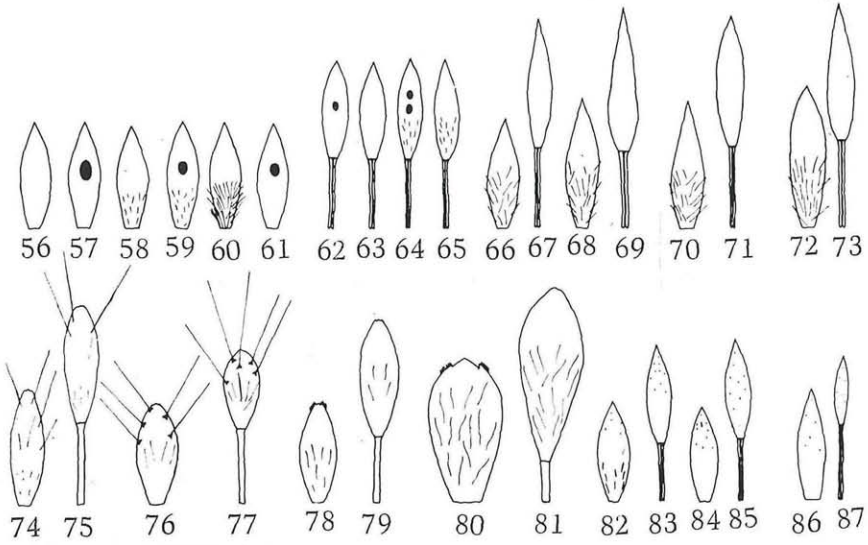

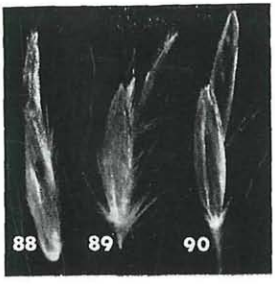

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syndetically to form bivalents. CHHEDA & HARLAN 1962: 461—476, further demonstrate that this mode of chromosome association is genetically controlled. In the dominant condition this gene insures bivalent formation in the natural polyploids. In hybrids this gene induces the chromosomes to pair autosyndetically, and evidence from experimental polyploids indicates that it also induces some degree of nonhomologous chromosome association when close homologues are absent.

Such an apomictic system must have had a far reaching effect on the evolution of this generic-group. Except for species which are genetically isolated from each other, possible hybrid combination can survive by means of its apomictic mode of reproduction. Furthermore, gene-controlled bivalent formation would insure the production of cytologically reduced gametes, and through pseudogamy the possibility for fertilization is increased. Occasionally nonhomologous pairing will result in segmental interchanges and eventually should lead to new arrangements of segmental alloploids.

The polymorphic *B. intermedia* species complex apparently originated through a number of hybridizations among various species of the three genera, *Bothriochloa*, *Dichanthium*, and *Capillipedium*.

Evidence of Intergeneric Hybridization: The concept of *B. intermedia* as referred to in this discussion is recognized as originally described by R. BROWN 1810: 202. This species includes plants with the primary axis of the panicle subequal to or longer than the lower racemes. The panicle branches may be simple, sparsely divided, or strongly branched. Presence or absence of pits on the lower glume of the sessile spikelets is a variable character. Numerous plants are characterized by both pitted and nonpitted spikelets on the same raceme.

On the basis of morphological characteristics in artificially produced hybrids, it can be shown that the range of variation observed in *B. intermedia* must be due to introgression. Primary axis length of the inflorescence is decreased when this species is crossed with either *D. annulatum* or *B. ischaemum* and increased by introgression with *C. parviflorum* or *C. spicigerum* (Table I). Pittedness of the lower glumes disappears in crosses with *D. annulatum*, but not necessarily when introgression with *B. ischaemum* can be demonstrated. Strongly divided panicle branches apparently are a characteristic contributed by *C. parviflorum*, and the presence of aromatic oils is widely distributed among species of both *Bothriochloa* and *Capillipedium*. The *B. intermedia* species-complex is widely distributed, extending almost continuously from southern Africa to China and Australia. Along its complete range of distribution this species is characterized by a robust, erect, and tufted biotype with simple racemes arranged on an elongated primary axis. In Africa, the majority of plants are characterized by moderately to strongly divided panicle branches, and the racemes consist of

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20—35 spikelet pairs. The same variation is obvious among Australian representatives of this species.

The Asiatic material of *B. intermedia* is extremely variable. Two major groups, based on spikelet morphology, may be recognized. First, there are plants with oblong-lanceolate spikelets, characterized by more or less solid pedicels to the pedicellate spikelets, and the lower glumes pilose below with a few longer cilia along the margins and scattered near the apex. Glume shape and pubescence is similar to that characteristic of *D. annulatum*. Furthermore, the racemes and the primary axis of the inflorescence are subequal in length. These plants differ from members of *Dichanthium* only in having the primary axis of the inflorescence slightly elongated, and all the sessile spikelets on a raceme are bisexual and awned. In contrast, typical representatives of *Dichanthium* have the racemes subdigitately arranged on a short primary axis, and the lower 1—6 sessile spikelets are awnless, male, or neuter. Harlan & al. 1961: 16—21, suggest that these plants represent introgression derivatives of hybrids between *B. intermedia* and *D. annulatum*. They are particularly common in the Gangetic plains of India, and Bor 1960: 107, described *B. grahamii* to include them.

The second group of Asiatic plants is characterized by glumes which are lanceolate in outline, and glabrous or scabrid above the middle. These are variously subdivided by Camus 1930: 162—165, Keng 1939: 274—343, Henrard 1940: 456—458, and Bor 1960: 103—106. Plants with 30 or more articulate simple racemes arranged along an elongated primary axis are usually included in *B. intermedia*. When the primary axis and the lower racemes are subequal in length, they are referred to as *B. ischaemum* although typical representatives of this species are characterized by racemes which are subdigitately arranged on a short primary axis. Plants characterized by divided panicle branches are usually included in *B. glabra* and when these plants are strongly aromatic, they are referred to as *B. odorata*.

Morphologically these various biotypes (species as classically recognized) are so interlinked as to form a single coherent group. On the basis of our present knowledge regarding morphology of artificially produced hybrids, it is safe to assume that introgression must have taken place between *B. intermedia* and both *C. parviflorum* and *D. annulatum* to produce this morphologically variable complex. The morphological variation observed in these three species in respect to inflorescence characteristics are graphically presented in Figures 91 and 92. The widely distributed *B. intermedia* biotype with simple racemes arranged on an elongated primary axis may be relics of the original basic species. The tetraploid *B. intermedia* complex being mostly facultative apomictic (Celarier & Harlan 1957: 93—102) cytologically behave like segmental allopolyploids as defined by Stebbins 1947: 403—429. Introgressive hybridization gives rise to a polyploid series with various combinations of *Bothriochloa*, *Capillipedium* and *Dichanthium*

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genomes (FARUQI 1964: 280—297) due to the fact that in the absence of true homologues the gene controlling bivalent formation also induces some degree of pairing between non-homologous chromosomes (CHHEDA & HARLAN 1962: 461—476, FARUQI 1964: 283—286), and that both the cytologically reduced as well as unreduced female gamete may function sexually (HARLAN & al. 1961: 12—15, FARUQI 1964: 286—292). This type of introgression may explain the range of morphological variation characteristic of *B. intermedia*.

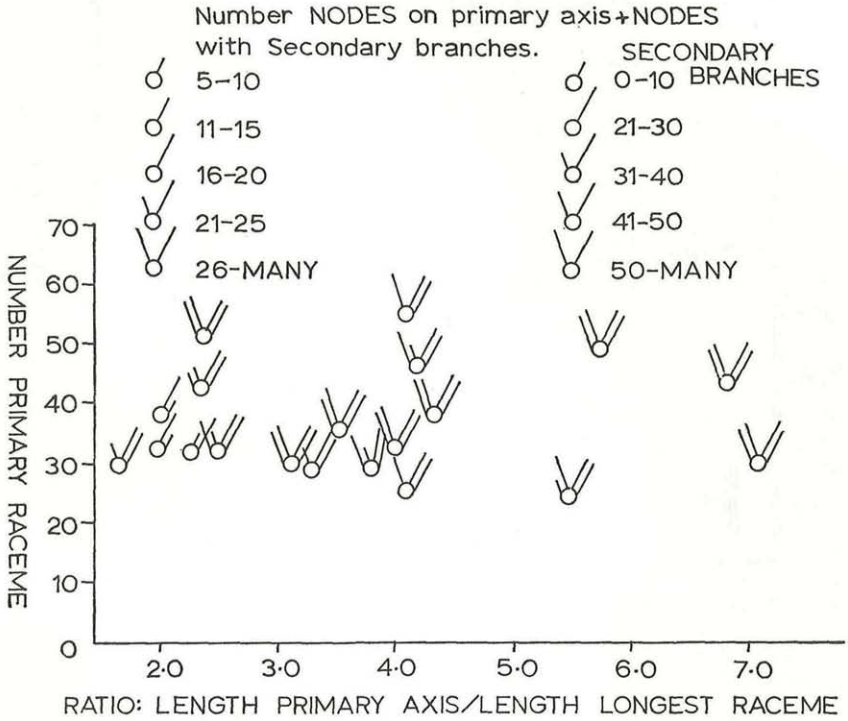

Fig. 91. Pictorialized scatter diagram illustrating the introgression between *B. intermedia* and *C. parviflorum*.

Introgression between *B. intermedia* and *C. parviflorum* can be demonstrated. On the one extreme, we have the assumed residual *B. intermedia* (BBB'B') with simple panicle branches and 30 or more spikelet pairs per raceme. On the other extreme, *C. parviflorum* (CCC'C') is characterized by a strongly branched panicle, and the ultimate racemes consist of a single sessile and two pedicellate spikelets. The hybrid (BB'CC') should be morphologically intermediate between these two species in respect to these

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characters. Introgression with *B. intermedia* will increase the number of spikelets per raceme and will decrease the number of secondary panicle branches. Introgression with *C. parviflorum*, on the other hand, increases secondary and higher order panicle branches and decreases the number of spikelets per raceme (Fig. 91).

B. intermedia and *D. annulatum* hybridized in nature and continuous introgression with both species gave rise to a variable agamic-complex (Fig. 92). The taxonomic picture is further complicated by hybridization between members of these two groups of introgression derivatives, giving rise to biotypes that defy classification (Fig. 95).

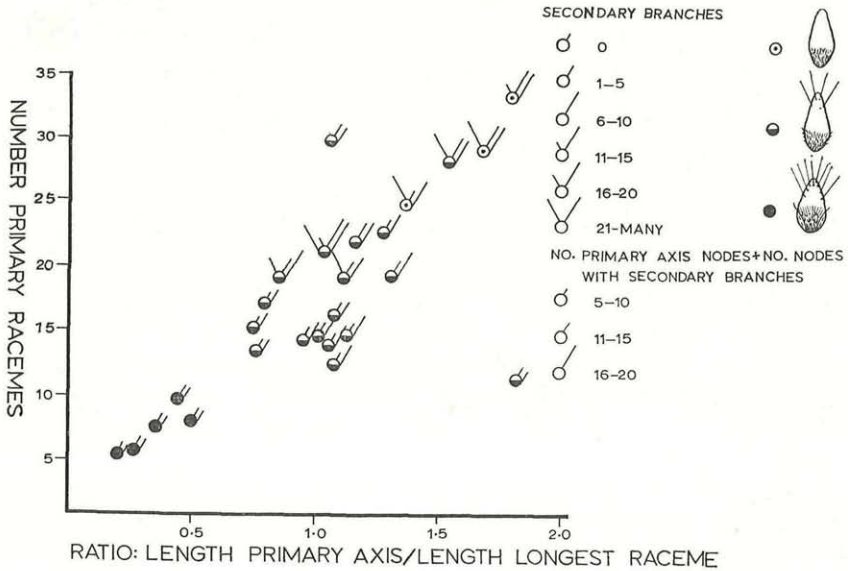

Fig. 92. Pictorialized scatter diagram illustrating the introgression between *B. intermedia* and *D. annulatum*.

Evidence of Interspecific Introgression: The morphological data further suggest that various species of *Bothriochloa* contributed genes to the *B. intermedia* species-complex.

First, *B. intermedia* is sympatric with *B. ischaemum* along the Himalayan region extending from West Pakistan to southern China. Celarier 1957: 729—738, suggests that *B. ischaemum* var. *songarica*, in eastern Asia, may represent a segmental allopolyploid hybrid combining basic genomes of *B. ischaemum* var. *ischaemum* and a foreign basic genome. From Pakistan and India, plants of *B. ischaemum* with an elongated primary axis of the panicle may represent introgression products between this species and

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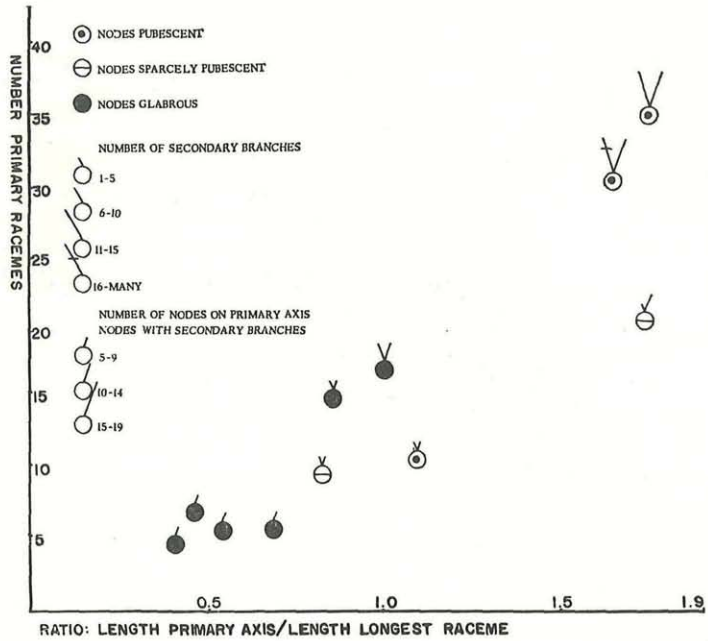

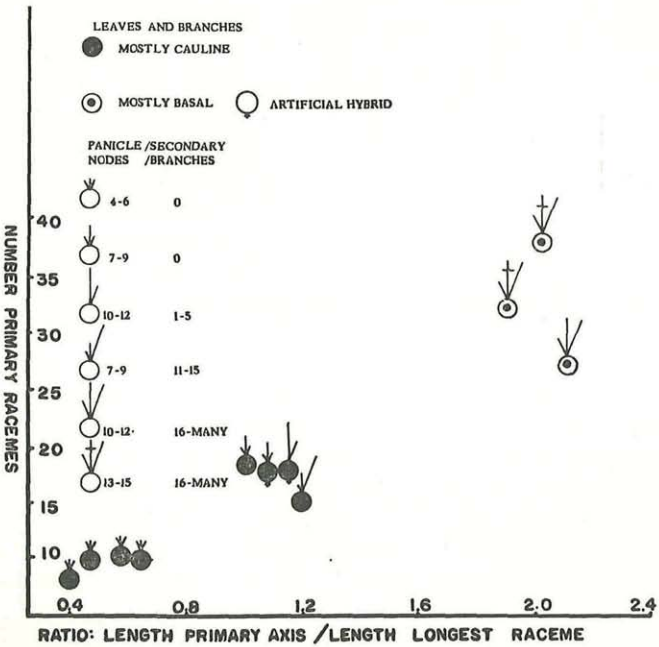

Fig. 93. Pictorialized scatter diagram illustrating natural hybridization between *B. intermedia* and *B. ischaemum*.

Fig. 94. Pictorialized scatter diagram illustrating natural hybridization between *B. intermedia* and *B. ewartiana*.

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B. intermedia at the tetraploid level (Fig. 93). The introgression between *B. intermedia* and *B. ischaemum* is also supported by the studies of HARLAN 1963: 294—300.

Second, morphological evidence of hybridization between *B. intermedia* and the Australian species *B. ewartiana* is present in two of the six specimens of the latter species that were available for study (Fig. 94). *Bothriochloa ewartiana* differs from *B. intermedia* in that the leaves are mostly cauline instead of basal, and the racemes are subdigitately arranged on a short primary axis (BLAKE 1944: 26). The assumed natural hybrids between these two species resemble *B. ewartiana* in detail, but the lower panicle branches and the primary axis are subequal in length. These plants are hexaploids, while those belonging more typically to *B. ewartiana* are either hexaploid or pentaploids. Artificial hybrids between hexaploid *B. ewartiana* and tetraploid *B. intermedia* are all octoploids, suggesting that this Australian species is not only highly apomictic but also the cytologically unreduced female gamete may function sexually to produce hybrids (FARUQI 1964: 286—292).

Third, the hexaploid African and Indian species *B. insculpta* combines morphological characteristics of both *B. pertusa* and *B. intermedia*. The latter species is a typical creeper rooting from the nodes where it forms tufts of leaves, and the culm become decumbent at the time of flowering. The essentially simple racemes in this species are subdigitately arranged on a short primary axis, and the sessile spikelets are always pitted. *Bothriochloa insculpta* is decumbent in growth habit; the racemes are either simple or the lower ones are branched, and the primary axis of the inflorescence is slightly elongated. The sessile as well as pedicellate spikelets of this species are pitted. In spite of thousands of attempts, *B. intermedia* and *B. pertusa* could not so far be crossed.

No matter what happens to the fate of the genera *Bothriochloa*, *Capillipedium* and *Dichanthium*, the variation pattern among the members of the *B. intermedia* complex (Fig. 95) indicates a very clear transgression of all the morphological criteria undertaken in this study. These criteria do not provide any basis for the separation of one group of hybrids from the other. For example the hybrids between *B. intermedia* and *B. ischaemum* are not restricted in the back crossing with either of the parents but they also cross with *Dichanthium* as well as *Capillipedium*. Under these conditions when there are no morphological breaks between one group of hybrids and the other, recognition of the hybrids or their derivatives as distinct species will not be practical from the point of view of herbarium taxonomist. The experimental taxonomist, however, can not ignore the existence of the various hybrid groups. For this reason all the hybrids involving *B. intermedia* are included here as a single species regardless of the other parent, and a key is presented for the identification of various hybrids and their parents.

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The following is a list of synonyms for the *B. intermedia* aggr. or species complex:

B. anamitica KUNTZE 1891: 762. — *B. glabra* (ROXB.) CAMUS 1930: 164. — *B. glabra* subsp. *haenkei* (PRESL) HENRARD 1940: 456. — *B. grahamii* (HAINES) BOR 1960: 107. — *B. haenkei* (PRESL) OHWI 1942: 168. — *B. intermedia* (R. BR.) CAMUS 1930: 164. — *B. intermedia* var. *punctata* (ROXB.) KENG 1957: 249. — *B. inundata* (MÜLL.) BLACK 1936: 163. — *B. odorata* (LISBOA) CAMUS 1930: 165.

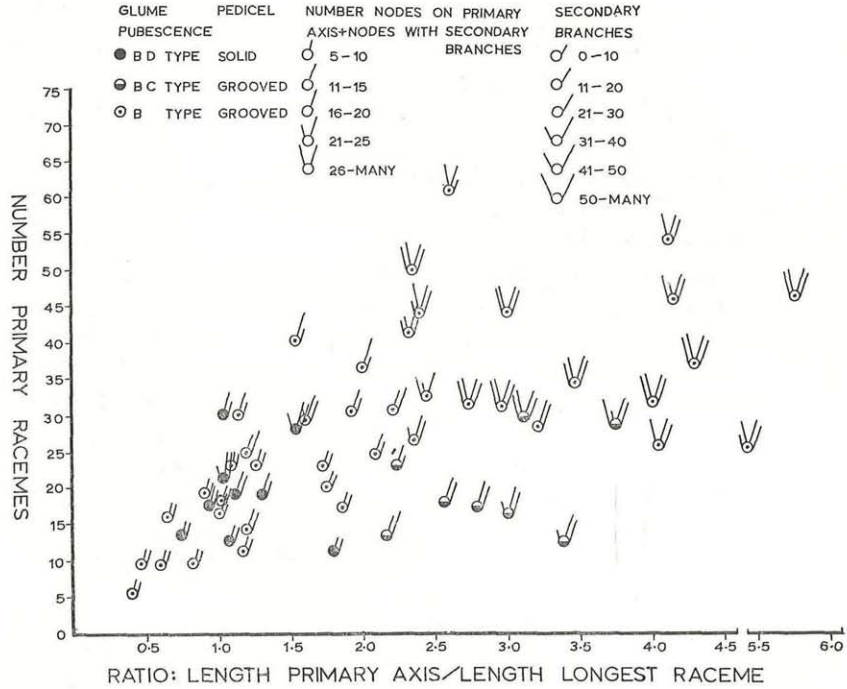

Fig. 95. Pictorialized scatter diagram illustrating morphological variation within the members of the *B. intermedia* complex.

The following names have appeared in the literature as synonyms to the above mentioned species of *Bothriochloa*:

Andropogon glaber ROXBURGH 1820: 271. — *A. punctatus* TRINIUS 1836: 328. — *A. vachellii* HOOKER & ARNOTT 1838: 243. — *A. leptanthus* STEUDEL 1855: 391. — *A. intermedius* var. *punctatus* subvar. *glaber* HACKEL 1889: 487. — *Amphilophis glabra* (ROXB.) STAPF 1917: 172. — *Andropogon grahamii* HAINES 1914: 189. — *A. haenkei* PRESL J. S. ex PRESL K. B. 1830: 340. — *A. intermedius* var. *haenkei* HACKEL 1889: 486. — *A. inter-*

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medius R. Brown 1810: 202. — *A. punctatus* Roxburgh 1820: 268. — *A. perfossus* Nees ex Steudel 1854: 391. — *Amphilophis intermedia* (R. Br.) Stapf 1916: 179. — *Andropogon inundatus* Müller 1852: 444. — *A. odoratus* Lisboa 1889: 123. — *Amphilophis odorata* (Lisboa) Camus 1921: 305.

The following key should be useful in the identification of various hybrids and their parents.

1. Lower 1—6 sessile spikelets on each raceme awnless, male or neuter *Dichanthium*
   2. Lower glumes oblong, narrowly truncate, pilose below the middle with long bulbous based cilia along the margins and near the apex *D. annulatum*
   2*. Lower glumes obovate, broadly truncate, pilose below the middle or glabrous all over *D. caricosum*

1*. All the sessile spikelets on a raceme awned and bisexual.
   3. Racemes 1—15 articulate and disarticulate individually when strongly branched *Capillipedium*
      4. Racemes 1—6 articulate, pancicles lax and open *C. parviflorum*
      4*. Racemes 5—15 articulate, panicles dense and contracted.
         5. Ligule a ciliolate membrane *C. spicigerum*
         5*. Ligule a long ciliate membrane *B. caucasica*
   3*. Racemes 15—30 articulate and disarticulate as a unit when branched *Bothriochloa*
      6. Primary axis distinctly shorter than the lower racemes.
         7. Leaves mostly cauline *B. ewartiana*
         7*. Leaves mostly basal
            8. Leaves linear, sessile spikelets distinctly pitted *B. longifolia*
            8*. Leaves linear-lanceolate, sessile spikelets non-pitted *B. ischaemum* var. *ischaemum*
      6*. Primary axis subequal to, or longer than the lower racemes.
         9. Primary axis distinctly longer than the lower racemes.
            10. Racemes 30 or more articulate, simple or the lower panicle branches divided *B. intermedia*
            10*. Racemes 15 to 30 articulate, panicle branches strongly divided.
               11. Rachis strongly ciliate *B. odorata*
               11*. Rachis less strongly ciliate *B. glabra*
         9*. Primary axis subequal in length to the lower racemes.
            12. Lower glumes lanceolate, acute, pilose only below the middle.
               13. Leaves mostly cauline
                Introgression with *B. ewartiana*

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13*. Leaves mostly basal — Introgression with *B. ischaemum* also *B. ischaemum* var. *songarica*

12*. Lower glumes oblong-lanceolate and truncate, pilose below the middle with a few scattered long hairs near the apex and along the margins — *B. grahamii*

Acknowledgements

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Summary

A detailed morphological study of the polymorphic *Bothriochloa intermedia* complex was undertaken to determine the range of morphological variation. In this study it was established that polymorphism in this group is due to introgression of *B. intermedia* with the species of *Dichanthium* and *Capillipedium* as well as with *B. intermedia*, *B. ewartiana* and *B. pertusa*. The complexity of the variation in this group is also due to the fact that once a species of *Dichanthium*, *Capillipedium* or *Bothriochloa* has been able to hybridize with *B. intermedia* the hybrid could backcross to either of the parents as well as to any other member of the complex. For example, *Dichanthium* and *Capillipedium* seem to be genetically isolated, hybrids between *Dichanthium* and *B. intermedia*, however, could hybridize with *Capillipedium*, and similarly hybrids between *Capillipedium* and *B. intermedia* could hybridize with *Dichanthium*. Under these circumstances morphological breaks cannot be established between the hybrid groups. For this reason *B. intermedia* as well as all the hybrids involving *B. intermedia* are included under one species *B. intermedia*.

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