CYTOGEOGRAPHY OF THE

Bothriochloa intermedia

COMPLEX

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INTRODUCTION

The grass tribe Andropogoneae includes a diverse group of genera variously subdivided among subtribes by Stapf (1917), Bews (1929), Keng (1939), and Pilger (1940, 1954). The genus Bothriochloa is usually included in the Andropogoninae. Although described by Kuntze (in Rev. Gen. Pl. 2, 762, 1891) members of Bothriochloa are referred to Andropogon Linn. by Hackel (1889) or treated as members of Amphilophis Nash (in Britton, Man. Fl. North. United States 71, 1901) by Stapf (1917). Camus (1931) indicates that the type species of Kuntze, Bothriochloa anamitica, is identical to Andropogon glaber Roxb. which Stapf includes in Amphilophis. As the generic name Bothriochloa has priority over Amphilophis, Camus (1931) and Henrard (1940) transferred the Old World representatives of the latter genus to Bothriochloa. Similar transfers were made for the American species of Amphilophis by Herter (1940), Henrard (1941, 1942), and Parodi (1958).

The genus Bothriochloa resembles Andropogon in having 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 having all florets awnless, and two Australian species 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) indicates that no characteristic consistently distinguishes between Dichanthium Willemet and Bothriochloa ewartiana (Domin) C. E. Hubbard. Studies by Blake (1944) indicate that B. ewartiana has oblong-lanceolate lower glume, the pedicel supporting one spikelet of each pair distinctly grooved, and all the sessile spikelets bisexual. These are typical Bothriochloa characteristics in contrast 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). 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, characterize Bothriochloa. On the basis of these characteristics Bor (1960) refers B. venusta (Thw.) A. Camus to Capillipedium. Two other species, B. kwashotensis (Hayata) Ohwi and B. picta Ohwi, definitely also belong with Capillipedium.

Henrard (1940) points to some objections regarding plants referred to B. intermedia (R. Br.) A. Camus. The original description of R. Brown (Andropogon intermedius R. Br. in Prod. 202, 1810) refers to plants from Australia with the primary axis of the inflorescence distinctly longer than the lower racemes. Stapf (1917) when transferring Andropogon pertusus Stapf (not A. pertusus (Linn.) Willd. in Sp. Pl. 4, 922, 1806) 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 (Linn.) A. Camus which always has a distinctly pitted lower glume on the sessile spikelet, it differs conspicuously in growth habit.

Camus (1931) and Blake (1944) describe this species 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 latter plants more properly fit the type description of B. inundata (F. Meull.) J. M. Black which Blake (1944) includes as a synonym of B. intermedia.

Henrard (1940) prefers to include the Malaysian plants with an elongated inflorescence in B. glabra (Roxb.) A. Camus. Stapf (1917) under Amphilophis glabra (Roxb.) Stapf, describes this species in detail and cites Andropogon glaber Roxb. (in Fl. Ind. 1, 267, 1832) and 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 being at variance with the description of both Stapf (1917) and Hackel (1889). Bor (1960) 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, and the leaf sheath is always terete. Both these 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 longer 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.

Hackel (1889) regards yet another species with an elongated primary axis as belonging to B. intermedia. This plant from southern Russia, B. caucasica (Trin.) C. E. Hubbard, was described as Andropogon caucasicus Trin. (in Mem. Acad. Sci. Petersb. Ser. 6, 2, 286, 1832) and treated as A. intermedius var. caucasica (Trin.) Hack. (in DC. Monogr. Phan. 6, 486, 1889). 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 is 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 the lower glume.

Celarier and Harlan (1957) 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) and Bor (1960). Celarier and Harlan (1955) indicate that natural hybridization takes place between B. intermedia and Dichanthium annulatum. Natural hybridization between B. intermedia and the related B.

ischaemum apparently gave rise to *B. ischaemum* var. *songarica* (Celarier 1957, and Celarier and Harlan, 1958). Artificial hybrids studied by de Wet *et al.* (1962) indicate that *B. intermedia* also hybridizes in nature with members of the related genus *Capillipedium*. Morphological data presented by Harlan *et al.* (1961) 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, and also to determine on the basis of cytological, morphological, and anatomical evidence whether natural hybridization actually takes place as suggested by Harlan *et al.* (1961).

LITERATURE REVIEW

During recent decades taxonomy has undergone marked changes. The taxonomist is no longer satisfied with discovery and description of new taxa. Instead, he is taking a second and more critical look at organisms already known and studied morphologically. Attempts are being made to uncover as many facets of information as possible, and to combine these into a revealing whole. For this reason the experimental taxonomist is borrowing data from various fields of research: paleobotany, ecology, anatomy, physiology, cytology, genetics and many more, and in correlating these with morphological observations attempts to classify living organisms into a system which will express their proved or inferred relationships.

The family Gramineae occupies an advanced position in the system of Monocotyledoneae classification. The flower parts are much reduced and their vegetative characters have reached a high degree of specialization. For these reasons, grasses are difficult to classify and it is not surprising that no other plant group has been more radically affected by this new taxonomic approach (Stebbins, 1956a).

Very early in the history of grass taxonomy some investigators realized that gross morphological characters alone do not always serve to indicate clearly the phylogenetic relationships of the different entities involved. Trecul (1858) notes the organization of starch grains in plants and classified them into simple and compound. These data were employed by Harz (1880) in grass classification. This latter system of classification differs from that proposed by Avdulov (1931), based on cytology and anatomy, only in detail. Duval-Jouve (1875), Grob (1896), and Pee-Laby (1898) demonstrate variations in cell types and chlorophyll distribution in grass leaves. The significance of these characters in taxonomy is fully discussed by Prat (1932, 1936, 1960). Embryo anatomy was investigated by Bruns (1892) and Kennedy (1899), and used extensively in grass taxonomy by Reeder (1946, 1953, 1957). Root hair development, as pointed out by Reeder and von Maltzhan (1953), allows for the subdivision of the Gramineae into two major groups. Other characters studied in relation to taxonomy are: the organization of the shoot apex (Brown, Heimsch, and Emery, 1957), the effect of isopropyl-N-phenyl carbamate on germinating seedlings (Al-Aish and Brown, 1956) and the use of phytoserological data in determining relationships in the Gramineae (Fairbrothers and Johnson, 1959). The major characteristics studied, which may provide data useful in grass classification, are discussed by Stebbins (1956a).

The more important characters are discussed in detail.

1. Cytology

The use of cytology in taxonomy was initiated by the work of Navashin (1912). Later, Newton (1927) and Taylor (1924) demonstrated that a more or less definite constancy of chromosome morphology and number exists in each genus. Lewitsky (1931) and Lewitsky and Araratian (1931) point out that different species of a genus are characterized by different and constant karyotypes (chromosome number and morphology) and that a general karyotype is maintained throughout a genus. When passing from one genus to the other, the karyotype often undergoes a complete transformation. Babcock (1947) demonstrates a range of gross morphological types in Crepis which extends almost continuously from primitive to advanced. This morphological evidence for progressive evolution is correlated with a modification of chromosome number and morphology.

The value of cytology in grass taxonomy is fully discussed by Avdulov (1931), Hunter (1934), and Krishnaswamy (1940). Chromosome number and relative size are the more important characteristics. Chromosomes of grasses are small and their morphology difficult to study. The most significant data on chromosome morphology in the Gramineae are those presented by Tateoka (1953, 1954a, c). The family Gramineae may be subdivided into three major groups on the basis of cytological data. The festucoid group has large chromosomes, mostly in multiples of $n=7$; the panicoid-chloridoid group is characterized mostly by small chromosomes in multiples of $n=9$ or 10 and the arundinoid-danthonioid group has medium-small chromosomes, mostly in multiples of $n=12$.

Additional evidence regarding degree of polyploidy may be obtained from a comparative study of individual cell sizes. Hotchkiss (1955) demonstrates a correlation between chromosome number and pollen size in the Winteraceae. Noggle (1946) relates stomatal length to chromosome number and Muntzing and Akdik (1948) demonstrate such a correlation in Secale. Stebbins (1950, pp. 302-303), however, indicates that the significance of cell size as an indication of degree of polyploidy depends greatly on the group of plants under consideration. In Danthonia, de Wet (1954) points out that stomatal size is dependant, not only on chromosome number, but also on geographical distribution and morphological type. It is necessary, therefore, to correlate cell measurements with similar observations in related groups where chromosome numbers were actually counted. Only if a close correlation between chromosome numbers and increase in cell size exists can such measurements from herbarium specimens be regarded as significant in determining chromosome number.

To determine the basic chromosome number in a polyploid series, Gates (1942) suggests that nucleolus number and differences in size of this structure may be useful. During mitotic telophase diploids are usually characterized by a pair of nucleoli, tetraploids by two pairs and so on. This suggestion is criticized by Stebbins (1950 pp. 362), who indicates that in *Leontodon*, according to Bergman (1935), diploids (2*n*=8) are characterized by four nucleoli. In *Danthonia*, (de Wet, 1953), some hexaploids never have more than two nucleoli, while others have four of these structures. Natural polyploids evidently tend to revert to the diploid cytological condition.

Pathak (1940) from a study of chromosome morphology suggests that the B genome of emmer wheats is contributed by a species of *Aegilops* with one pair of chromosomes having secondary constrictions. Sarkar and Stebbins (1956) on the basis of morphological studies suggest that *A. speltoides* may be the second parent of emmer wheat. This was confirmed by Riley *et al.* (1958) in artificial hybrids between *Triticum monococcum* and *A. speltoides*. In the latter species, the satellite chromosomes are similar to those of emmer as suggested by Pathak. Avdulov (1931) separates the genus *Ehrarta* and its relatives from the Phalarideae. Cytological studies by de Wet and Anderson (1956), Love (1948), Parthasarathy (1939), and Tateoka (1957) support this change.

The studies of Kihara and Lilienfeld (1932, 1937), Lilienfeld and Kihara (1934), McFadden and Sears (1945, 1946), Riley et al. (1958), Riley and Chapman (1958), and various others suggest to Bowden (1959) that the three genera Aegilops, Agropyron, and Triticum should be combined into a single taxonomic unit. Stebbins and Pun (1953a, 1953b), Stebbins and Snyder (1956), Stebbins and Vaarama (1954), Stebbins et al. (1946a, 1946b), and Stebbins and Walters (1949) suggest that all the genera belonging to the tribe Hordeae could be united into a single genus.

2. Leaf anatomy

Duval-Jouve (1875) studied the position of bulliform cells in relation to the nerves in grass leaves. Schwendener (1890) demonstrates that two sheaths surround each vascular bundle, the mestome sheath which has characteristics of an endodermis, and an outer parenchymatous bundle sheath. These sheaths may be well developed or poorly differentiated. The distribution of sclerenchyma between the bundles in relation to taxonomy was also studied by Schwendener (1890). Pee-Laby (1898) indicates that the parenchyma sheath cells may or may not contain plastids. Combining these data Avdulov (1931) recognizes two major types of leaf anatomy in the Gramineae. Brown (1958) after extensive anatomical studies, distinguishes the following major grass groups, recognized by the following leaf anatomical characteristics.

Festucoid type: The mestome sheath is composed of thick-walled cells and is well differentiated; the parenchyma sheath is indistinct and contains chloroplasts similar to those of the loose, irregularly arranged mesophyll cells.

Bambusoid type: The mestome sheath is well developed; the thick-celled parenchyma sheath varies in size from small to large and contains typical chloroplasts; the mesophyll is irregularly arranged around the bundles.

Oryzoid type: Resembles the bambusoid type, but the cells of the parenchyma sheath are larger.

Arundinoid type: The mestome sheath is poorly differentiated; the parenchyma sheath is composed of large cells which are completely devoid of plastids; the chlorophyll containing mesophyll is densely packed and irregularly arranged between the bundles.

Panicoid type: The mestome sheath is absent, or present only around the major bundles; the parenchyma sheath is well differentiated and contains specialized plastids for starch storage, or in some rare instances plastids are absent; the chlorophyll containing cells are to some extent radially arranged, but the cells are not long and narrow, and never tightly packed.

Andropogonoid type: The mestome sheath is absent even from the major bundles. The remaining characteristics are as discussed for the panicoid type.

Aristidoid type: The mestome sheath is absent; two parenchymatous sheaths, each containing specialized plastids, are present and the cell walls are thickened. The chlorenchyma is radially arranged around the bundles and the cells are tightly packed.

Chloridoid type: The mestome sheath is present at least around the major bundles; the large cells of the parenchyma sheath contain specialized plastids; the chlorenchyma is composed of tightly packed, long narrow cells which are strictly radially arranged around the bundles.

An extensive monograph on leaf anatomical features of grasses is presented by Metcalf (1960).

3. Epidermis

Grass epidermis is a complicated structure, characterized by numerous cell types (Grob, 1896). An analysis of shape, size, structure, and distribution of these, may be used to distinguish large groups, or more restricted units and still others the forms caused by environmental factors (Prat,1932, 1936, and Salisbury, 1932).

The epidermal characteristics usually studied are as follows. Siliceous cells: spherical, rod or halfmoon-shaped (Festucoid); dumb-bell-shaped and orientated along the leaf axis (Panicoid) or club-shaped (Chloridoid). A detailed study of bicellular hairs in relation to grass taxonomy was presented by Tateoka, Inoue, and Kawano (1959).

In general, four major types of epidermis, the chloridoid, festucoid, panicoid and oryzoid are recognized. These appear to be closely correlated with internal leaf anatomy. In some genera, however, such as Danthonia and Pentaschistis, de Wet (1954, 1956) demonstrates a panicoid type of epidermis in some species while others are characterized by the festucoid type. Stebbins (1956a) summarizes all known genera where the internal leaf anatomical type is not strictly correlated with the corresponding epidermal type.

4. Culm anatomy

This character is ~~fully~~ discussed by de Wet (1960), who indicates that vascular bundles of the peduncles closely resemble those in the leaf. The parenchymatous outer bundle sheath (or sheaths) is of six distinct types. It may be poorly differentiated and indistinguishable from the other parenchyma tissue (festucoid); in the bambusoid type a sheath is recognizeable, but composed of small cells which contain typical chloroplasts; the panicoid type resembles the bambusoid type in general appearance but the sheath contains specialized plastids; in the arundinoid type the poorly differentiated sheaths lacks plastids; a well developed sheath containing specialized plastids is characteristic of the chloridoid group of grasses and the aristidoid type is characterized by a double parenchyma sheath.

5. Embryo anatomy

The significance of this character in grass taxonomy is pointed out by Bruns (1892), van Tieghem (1897), Kennedy (1899) and Reeder (1953, 1957). The characters studied are as follows: Traces of vascular tissue going to the scutellum and embryonic leaves are separated by an internode (Panicoid), or an internode may be absent (Festucoid); epiblast may be present (Festucoid) or absent (Panicoid); lower part of the scutellum may be free from the coleorhiza (Panicoid) or fused with the coleorhiza (Festucoid); the embryonic leaf is characterized by many bundles and margins which overlap (Panicoid) or few bundles and margins which only meet (Festucoid).

When these characteristics of embryo anatomy are combined Reeder (1957) recognizes six major groups of grasses.

Festucoid type: The traces of vascular tissue to the scutellum and embryonic leaves diverge at approximately the same point, an epiblast is present, the lower part of the scutellum is fused to the coleorhiza and the embryonic leaf has few bundles and its margins only meet.

Genera such as *Bromus*, *Elymus*, *Hystrix* and *Secale* which are typically festucoid in all other characteristics, lack an epiblast (Reeder, 1957).

Panicoid type: A distinct vascular internode is present, the epiblast is absent, a cleft is present between the scutellum and coleorhiza and the embryonic leaf has numerous vascular bundles and margins which overlap.

Chloridoid type: Resembles the panicoid type, except that an epiblast is present, and in seedling leaf anatomy.

Bambusoid type: Basically of the panicoid type, but a well developed epiblast is present. A peculiarity of the Bambusoideae is the presence of more than one vascular bundle in the scutellum and often also in the coleoptile.

Oryzoid type: The vascularization is of the festucoid type and embryonic leaf of the panicoid type. In some genera an epiblast is present, whereas it is absent in others. Similarly the lower part of the scutellum is either free or fused to the coleorhiza.

Arundinoid type: Basically of the panicoid type, but the embryonic leaf has few vascular bundles and margins which only meet.

6. Gross morphology

Most systems of classification are based exclusively on gross morphological characters. Bessey (1917), Bews (1929), Hubbard (1934), Pilger (1954), and

Stebbins (1956a) discuss the more important morphological variations useful in a study of grass phylogeny.

In a study of phylogenetic relationships, however, it is important to realize that a diploid which resembles a tetraploid closely, is not necessarily its sole diploid ancestor. In segmental allopolyploids Stebbins (1947, 1950) indicates that, if component genomes have a majority of segments in common the tetraploid may resemble the one or the other diploid ancestor more closely.

Introgressive hybridization (Riley, 1939, and Anderson, 1949) further tends to confuse the taxonomic picture. By means of this process genes may pass across an effective sterility barrier formed by differences in chromosome numer. The morphological consequences of such a hybridization process is obvious.

Furthermore, in the family Gramineae, spikelets of different genera are often built on the same general lines although these genera are only distantly related. An excellent example was discussed by Tateoka (1959a, b) in respect to the genera Lepturus and Monerma.

7. Root hair development

Sinnot (1939) in a study on plant meristems reports two different types of root hair development among members of the Gramineae. In type A the last division of the surface cells of the meristematic region produces daughter cells of unequal size. Only the cell which is apical, shorter and more densely protoplasmic than its sister cell, can produce a root hair. In type B all the cells are essentially alike and seem to be potentially capable of producing root hairs. In a supplementary paper Sinnot and Bloch (1939) indicate that in the A type, the root hair originates close to the apical end of the trichoblast and projects forward at an angle of 45 degrees from the axis of the root. In the B type, the root hair arises from the middle of the cell and grows nearly straight out from the root at an angle of 90^{o}. Sinnot and Bloch found that Poa, Phleum, and Agrostis have A type, whereas Chloris and Sporobolus have type B root hair development. In a later paper Bloch (1943) reports that in Phalaris arundinacea, an undisputed member of the Festucoideae, the cell development was of type A. Reeder and von Matlzahn (1953) indicate that four undisputed members of Panicoideae, i.e. Panicum capillare, Digitaria sanguinalis, Miscanthus sinensis and Andropogon scoparius are characterized by B type of root hair development. Correlating morphological, cytological, anatomical, and embryological evidence it may be concluded that type A root hair is characteristic of the Festucoideae and type B of the panicoideae. Reeder and Row (1957), from a study of 83 species belonging to 68 genera point out that the alternation of long and short cells (festucoid) vs. equal-sized cells (panicoid) is a more reliable character than either position or angle of the root hairs.

8. Organization of the shoot apex.

Brown et al. (1957) compile all the previous literature on meristems, and studied the shoot apex of 63 species belonging to 21 tribes of the family Gramineae. From the data presented by Thielke (1951) they demonstrate a correlation between these characteristics and the systematic groupings within the Gramineae. In the Festucoideae two tunica layers are common, while only one is usually found in the Panicoideae.

9. Biochemistry

Al-Aish and Brown (1956) demonstrate that grasses differ in their response to a week killing chemical, isopropyl-N-phenyl carbamate (IPC). The germinating seedlings were treated with doses of IPC. Members of the Festucoideae, Danthonieae, and Stipeae are easily killed even by weak doses while the Panicoideae and the chloridoid- eragrostoid group are resistant against this chemical. Members of the Oryzeae, as well as the genera Aristida and Streptochaeta were also found to be strongly resistant to this chemical.

Avers and Gremm (1959) report that the four festucoid grasses investigated, show intensified acid phosphatase activity in the small, hair-producing cells of the root epidermis with loss of activity in the larger cells. Three panicoid grasses on the other hand, show no phosphatase activity in these cells, and all cells are able to produce root hairs.

Cugnac (1931) found that grasses belonging to a restricted group including the Phalarideae, Agrosteae, Avenae, Festuceae, and Hordeae store fructose at least at some stage of their development whereas grasses of other diverse groups never form fructose.

10. Starch grain ontogeny

Harz (1880) was probably the first to use starch grain types as a systematic criterion in the Gramineae. He creates the tribe Brachypodiae on the basis of it being characterized by simple starch grains while in the remainder of the

Festuceae starch grains are compound. Hackel (1887) also uses simple and compound starch grains as a basis for classification. Hackel regards members of the Bromeae and Brachypodeae as a distinct subtribe of the Festuceae, because they have simple starch grains. Later Tateoka (1954b) confirms Hackel's view. In general most of the Festucoideae and members of the chloridoid-eragrostoid complex, the Arundineae and Oryzeae possess complex starch grains. Simple starch grains are found throughout the Panicoideae, in the Hordeae and the genera Brachypodium and Bromus among the Festucoideae.

11. Persistent nucleoli

Brown and Emery (1957) studied 45 species belonging to 39 genera included in 20 tribes of the Gramineae in respect to persistence or non persistence of nucleoli during later stages of mitosis. They find persistant nucleoli in all those members which belong to the sub-family Panicoideae. Among members of the Festucoideae there are no persistent nucleoli. The members belonging to the Phragmitiformes of Avdulov includes plants with and without persistent nucleoli.

12. Ecology

Bews (1929) gives considerable importance to ecology in the evolution of grasses, but does not carry his ideas further in arranging the family into tribes. Harlan (1956) points out that tribes could be arranged into subfamilies on the basis of ecology. This arrangement of Harlan's (1956) is in accord with morphology and cytology. Combining the available data from various fields of study, Prat (1960) and Stebbins (1956b) present systems of classification which differ from each other only in detail. At the same time both systems of classification are perfectly in accord with recent taxonomic treatments based almost exclusively on gross morphological characters, such as those of Hubbard (1934) and Bor (1960).

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 and Harlan (1956b). Plants usually flowered during the first season. However, some 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. Cytological studies were also made from the previous year's flower-bud collections in the absence of fresh material. The collections studied are listed in Table I.

Morphology

Eight specimens of each collection were usually studied, and particular attention was given to the following characteristics. 1. Growth habit. 2. Length and breadth of the third uppermost leaf on the culm. 3. Culm node pubescence. 4. Length of the primary axis of the panicle. 5. Number of nodes 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 pedicel. 19. Trichomes on pedicel. 20. Pedicel solid or grooved. 21. Awn length.

Character and character combinations (Anderson 1957, Sarkar and Stebbins 1956) 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, 1957) while a comparison of range of these characters is given in tabular form.

Anatomy

For the anatomical studies of the glume pit a few plants were selected, and include three collections A-5450, A-5297-a and A-5297-b of B. intermedia, one of B. decipiens (A-7501), one of B. pertusa (A-3704), and four hybrids 56-X-750, 58-X-443-a, 58-X-571-b, and 58-X-696.

Glumes were sectioned after wax infiltration and embedding by means of a dioxane series as recommended by Sass (1958). Leaves and stem were embedded using tertiary butyl alcohol as a dehydrating agent. Stems and leaves were pretreated in hydrofluoric acid for 15 minutes in order to remove silica.

Epidermal cells from surface view were studied in whole cleared mounts of the glumes and leaves. These were prepared by keeping them in a 3% NaOH solution at 50^{o} C for as long as necessary. The transparancies were either prestained with basic fuchsin or stained after clearing with a combination of safranin and haemalum, or safranin and fast green. Fast green was found superior for demonstrating the cell boundries. Clearing technique was found good for a study of glume epidermis. For epidermal study of leaves the technique described by Prat (1948) was also followed, which proved to be superior.

Leaves from herbarium spcimens were placed in a 1:1 solution of glycerine and ethyl alcohol. After 2 to 3 days epidermal slides were prepared by placing a part of the leaf on a glass slide, with the epidermis to be studied facing downward. All the tissue above this epidermal surface was scrapped off with a sharp blade and the remaining epidermal layer was mounted in lactic acid. The coverglass was sealed with transparent nail polish.

Cytology

For the study of chromosomes the flower buds were fixed between 8:30-11:45 A.M. on sunny days in 3:6:1 glacial acetic acid: ethyl alcohol: chloroform. Temporary smears of pollen mother cells were made using acetocarmine, and slides were sealed with a mixture of gum arabic and wax. Usually the slides were kept over night before they were studied and photographed. This provides ample time for the chromosomes to stain sufficiently.

Chromosome numbers were determined from well-spread metaphase and anaphase preparations. First metaphases and first anaphases were scored at random but cells in which the chromosomes were clumped together or poorly stained were not utilized. Whenever necessary, opinions of other colleagues working in the laboratory were also obtained. Usually 20-25 cells were recorded for each stage of meiotic division.

Bridges, fragments, dividing and non-dividing lagging chromosomes, as well as uneven distribution of chromosomes to the two poles were determined from first anaphase.

Usually the second division of meiosis was not analysed in detail. However, in the cases where chromosomal irregularities were commonly encountered during the first division, irregularities of second anaphases, and the number of micronuclei in dyads and tetrads were also recorded.

RESULTS

1. Gross Morphology

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 chromosome 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 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 surface. Long bulbous-based hairs are mostly present on the abaxial surface and confined to the base of the leaf. The adaxial surface

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	6138	59.6	56.0	17.1	1.0	B	9.3	0.6	60	Queensland, Aust.
B. ewartiana	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.

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. caucasica	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

*Possible B. intermedia X C. parviflorum derivatives.

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 -	5407	110.4	40.0	32.6	60.5	B	15.0	10.9	--	Bhawali, India
B. glabra complex	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
	*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

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 -	*7554	93.8	42.0	31.4	21.6	BC	12.1	3.3	50	Australia
B. glabra complex	*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	5401-a	51.9	60.0	14.8	0.4	B	7.6	0.4	40	Lohnavla, India
X	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	50	67.6	65.0	30.9	4.9	BD	8.3	3.1	50	Australia
X	52	87.2	65.0	21.8	24.2	BD	14.0	7.0	50	Australia
D. annulatum	2655	61.0	50.0	15.0	1.0	BD	9.0	1.0	40	British Guiana, Intrd.
(B. grahamii)	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

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	5404	60.3	65.0	18.0	3.1	BD	8.8	1.3	40	New Delhi, India
X	5408	74.9	65.0	22.5	4.0	BD	10.0	1.3	60	Bariely, India
D. annulatum	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

LEGEND TO 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 X C. parviflorum

4-5. B. intermedia

6. B. longifolia

7. B. odorata

8. B. caucasica

9-10. B. intermedia X D. annulatum

11. B. intermedia X B. ewartiana

Figs. 12-21. Variations in nodal hair. Magnification X 3.3.

12. B. longifolia

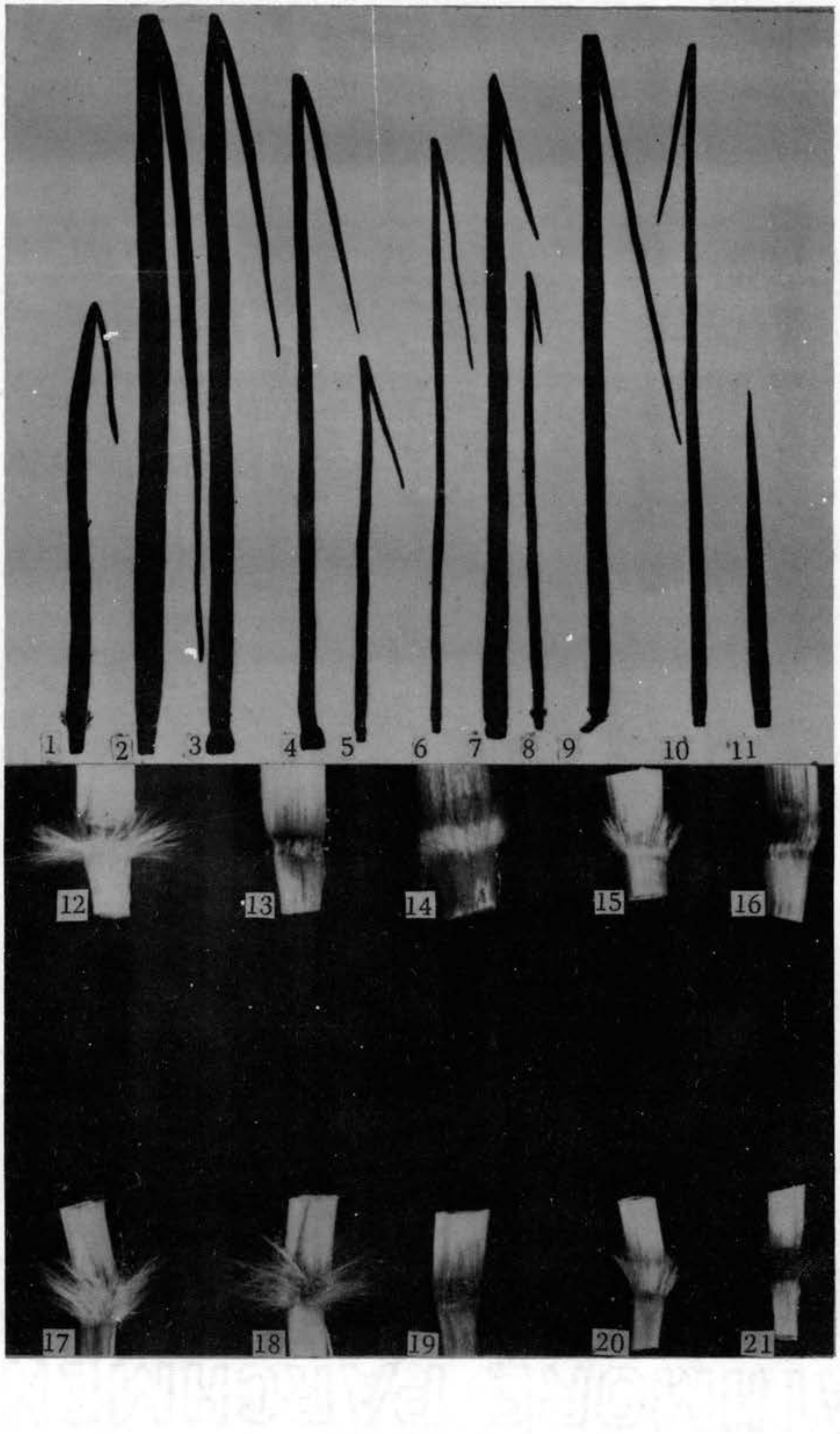
13-16. B. intermedia

17. B. intermedia X D. annulatum

18. D. annulatum X-98

19-20. B. intermedia X B. ischaemum

21. B. ischaemum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is usually characterized by the presence of shorter hairs. 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 may be sparsely to densely ciliate.

Culm node pubescence: The nodes are pubescent or glabrous (Figs. 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. Rarely, however, the pedicel is solid or only slightly grooved.

The species studied are distinguishable, by the following key characteristics.

LEGEND TO FIGURES 22-55

Figs. 22-55. Panicles of the members of the B. intermedia complex showing nature of variations 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 X D. annulatum.

30. B. intermedia.

31. B. intermedia X D. caricosum.

32. B. ischaemum

33-35. B. intermedia X B. ischaemum.

36. B. ewartiana.

37. B. intermedia X B. ewartiana.

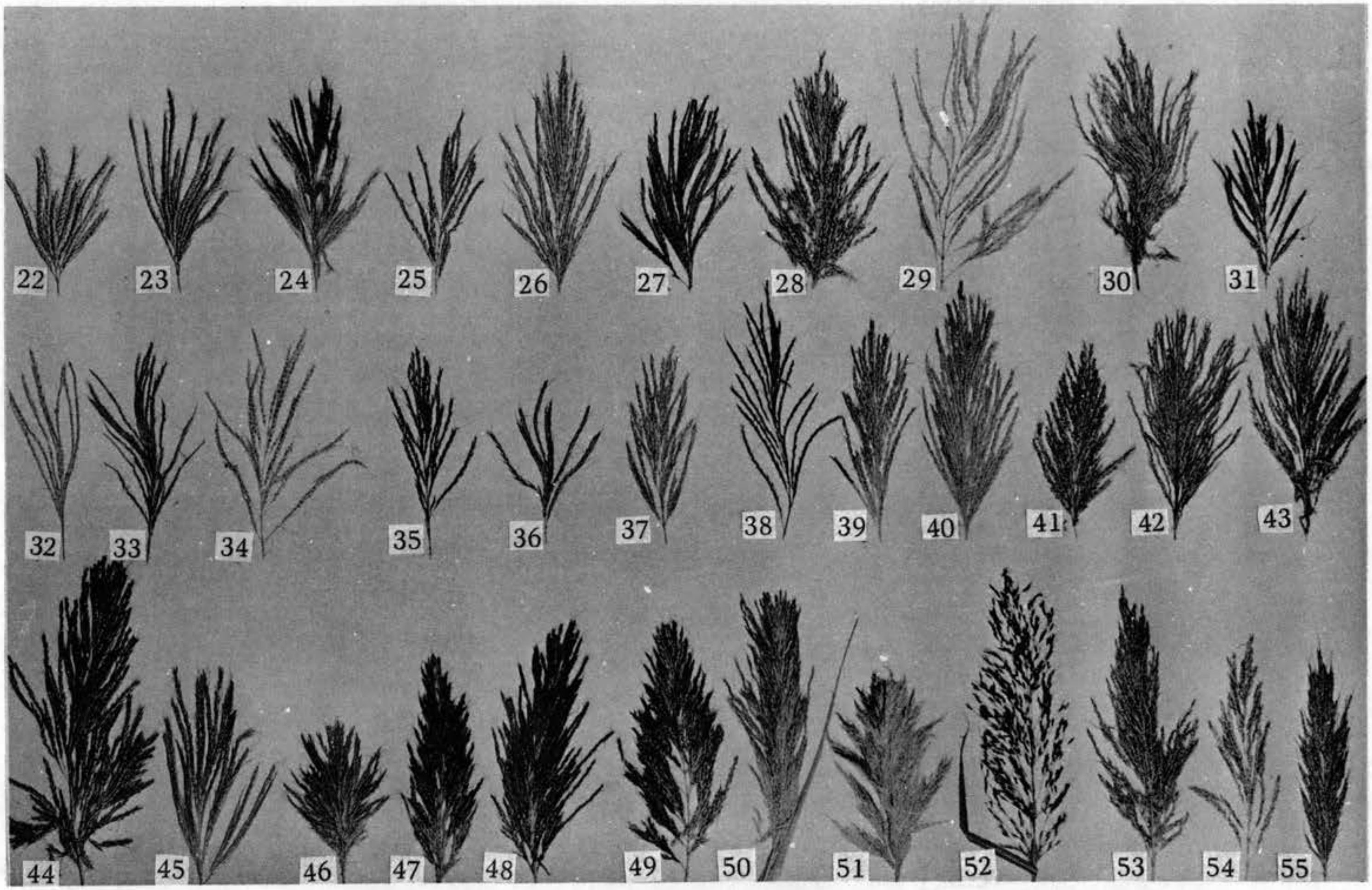
38-46. B. intermedia.

57-51. B. intermedia X C. parviflorum.

52. C. parviflorum.

53-54. B. odorata

55. B. caucasica


22 23 24 25 26 27 28 29 30 31
32 33 34 35 36 37 38 39 40 41 42 43
44 45 46 47 48 49 50 51 52 53 54 55

LEGEND TO FIGURES 56-90

Figs. 56-87. Variations in pubescence, shape, pit, and relative size of pedicellate and sessile spikelets of the *B. intermedia* complex. Magnification X 4.3.

56-65. *B. intermedia*

66-67. *B. intermedia* X *B. ischaemum*

68-69. *B. ischaemum*

70-71. *B. intermedia* X *B. ewartiana*

72-73. *B. ewartiana*

74-75. *B. intermedia* X *D. annulatum*

76-77. *D. annulatum*

78-79. *B. intermedia* X *D. caricosum*

80-81. *D. caricosum*

82-83. *B. intermedia* X *C. parviflorum*

84-85. *C. parviflorum*

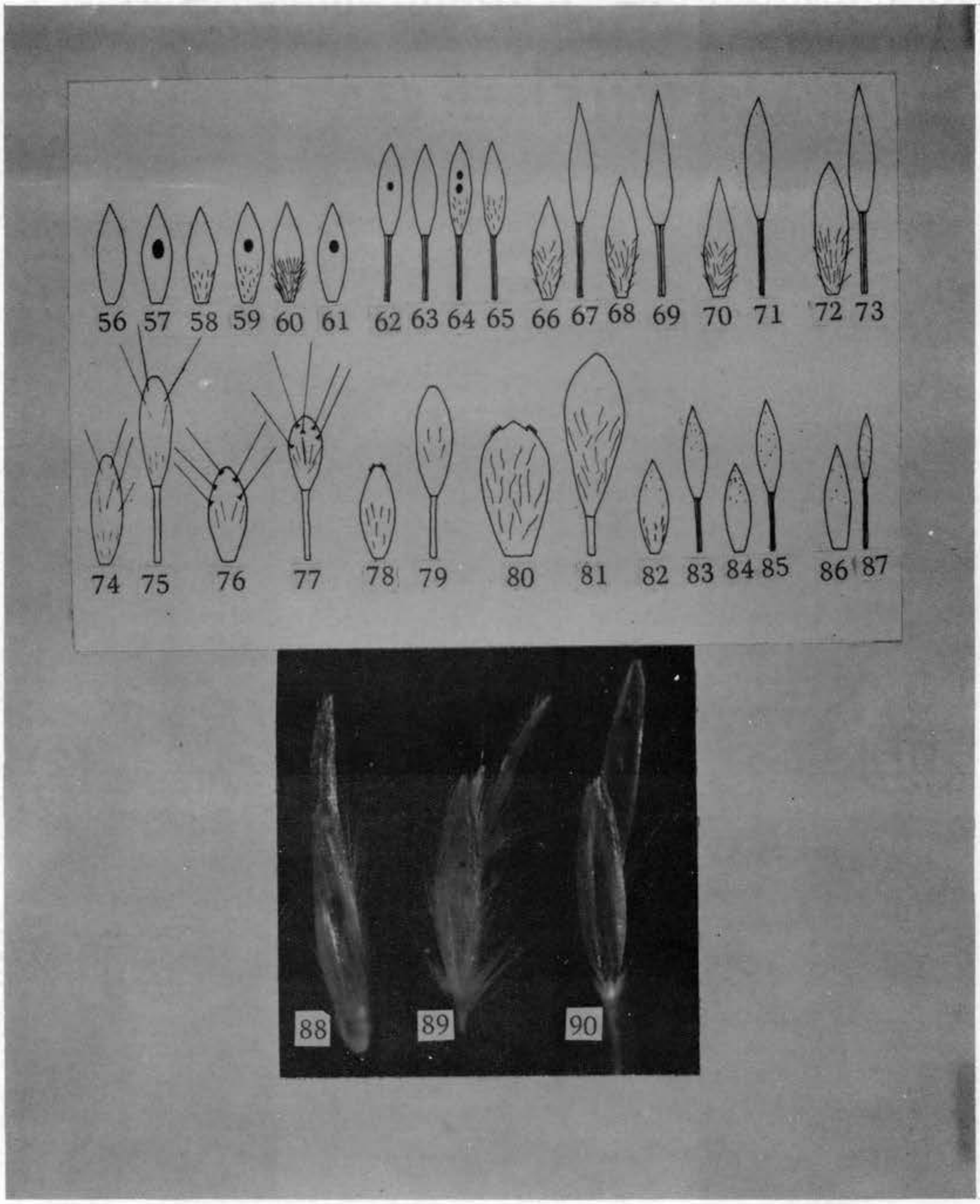
86-87. *B. caucasica*.

Figs. 88-90. Members of the *B. intermedia* complex showing pitted, nonpitted, and grooved lower glumes. Magnification X 10.

88. *B. intermedia* showing pitted glume of the sessile spikelet.

89. *B. intermedia* X *B. ischaemum* showing smooth glume of the sessile spikelet.

90. *B. intermedia* X *C. parviflorum* showing a prominent groove in the glume of the sessile spikelet.


56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73
74 75 76 77 78 79 80 81 82 83 84 85 86 87
88
89
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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, panicles 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*

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 longer hairs near the apex and along the margins — *B. grahamii*

2. Cytology

Avdulov (1931) reports 2n=60 chromosomes for B. intermedia. Oke (1950) records 2n=40 and 2n=60 chromosomes, and indicates morphological differences between plants of these two chromosome races. De Wet (1954) reports 2n=40 chromosomes in B. glabra from South Africa. Celarier and Harlan (1955, 1956a) and Harlan et al. (1961) record 2n=40, 50, 60 and 2n=80 chromosomes in the members of this species complex.

Eighty collections of the B. intermedia were studied cytologically. These include three diploids (B. longifolia), sixty tetraploids, seven pentaploids, nine hexaploids and one octoploid. The geographic distribution of these chromosome races is presented in the Figure 125.

Meiotic behavior: The three diploids are mostly characterized by ten bivalents at diakenesis and metaphase I (Fig. 91). One of the ten bivalents sometimes has only a single chiasmata, and consequently an early separation into two univalents (Fig. 92). At anaphase I the two univalents are often present as laggards. These could be seen lying at the equator of the spindle until late anaphase (Fig. 93). No micronuclei were observed in these diploids, though lagging chromosomes are seen as late as early telophase. The laggards consequently merge with the main body of the daughter nuclei. Bridges and fragments were never observed.

The tetraploids (Figs.95-103), both natural species and assumed hybrids, show cytological abnormalities of more or less the same nature. The difference of cytological abnormalities between certain morphological types are only quantitative. Cells at diakenesis and metaphase I regularly show twenty pairs, but

LEGEND TO FIGURES 91-102

Figs. 91-102. Meiotic behavior of chromosome among the members of the B. intermedia complex. Magnification X 1350.

91. Metaphase I showing ten bivalents in the diploid B. longifolia.

92. Metaphase I showing nine bivalents and two univalents in the diploid B. longifolia.

93. Anaphase I showing two dividing laggards in the diploid B. longifolia.

94. Telophase I showing regular division in the diploid B. longifolia.

95. Metaphase I configuration of tetraploid B. intermedia X C. parviflorum.

96. Metaphase I configuration of tetraploid B. intermedia.

97. Metaphase I configuration of tetraploid B. intermedia X C. parviflorum.

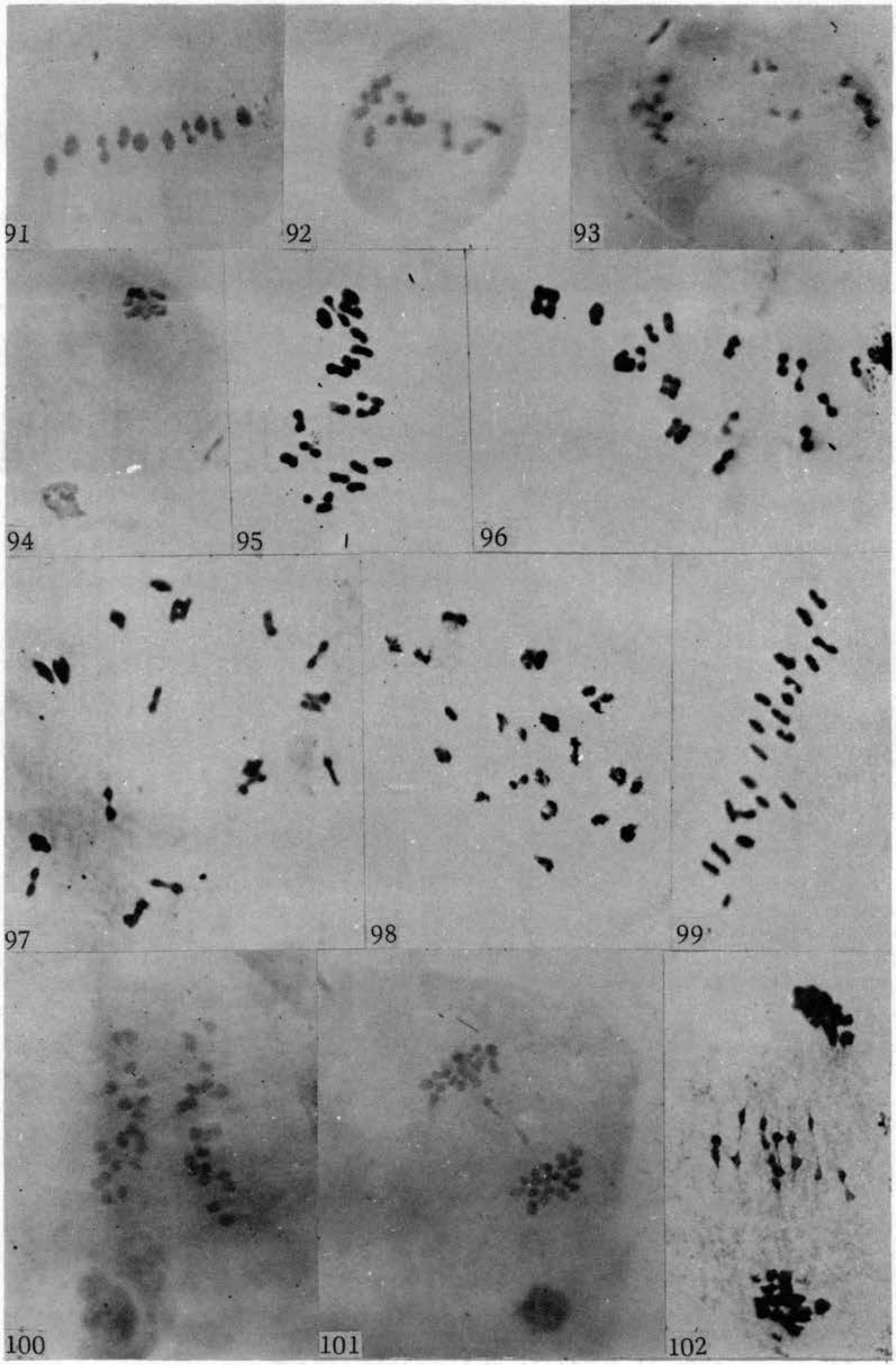
98. Diakenesis in B. caucasica.

99. Metaphase I configuration of tetraploid B. intermedia X D. annulatum.

100. Anaphase I in a tetraploid B. intermedia X B. ischaemum.

101. Anaphase I showing a bridge in the tetraploid B. odorata.

102. Anaphase I showing lagging chromosomes in the tetraploid B. caucasica.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often a few univalents are present (Figs. 95, 98, and 99). Trivalents and quadrivalents are also observed. Anaphase I may be regular (Fig. 100) where all the chromosomes are equally distributed to the two poles. Usually a few laggards remain at the equator of the spindle (Figs. 101, 102). These may divide or move to either pole undivided. Dividing laggards are more common than nondividing ones. Sometimes bridges and fragments may also be found (Fig. 103). Micronuclei may or may not be present at the dyad and tetrad stages. Not withstanding these abnormalities, normal and viable pollen is produced in these tetraploids. Among the different morphological biotypes, B. caucasica is cytologically more irregular than any of the others. On the other hand it seems very interesting to note that hybrids between B. intermedia X Dichanthium are comparatively more regular in their cytological behavior (Fig. 123) than some representatives of B. intermedia (Fig. 122) or B. intermedia X Capillipedium hybrids (Fig. 124).

The seventeen collections representing pentaploids, hexaploids and the octoploid, are characterized by cytological abnormalities of the same nature as those found in tetraploids, but in a higher frequency. Quadrivalents and univalents were observed at diakenesis and metaphase I (Figs. 104, 105, 110). Anaphase abnormalities (Figs. 106-109, 112-114) are also comparatively more common than in the tetraploids. Dyad and tetrad stages may possess micronuclei (Fig. 115). The octoploid (Figs. 116-118) represented by a single collection is characterized on the average, by 8.27 univalents, 31.13 bivalents, 0.36 trivalents, and 1.95 quadrivalents.

LEGEND TO FIGURES 103-115

Figs. 103-115. Meiotic behavior of chromosomes among the members of the *B. intermedia* complex. Magnification X 1350.

103. Late anaphase I showing bridges, and fragments in a tetraploid *B. intermedia*. X *D. annulatum*.

104. Metaphase I in a pentaploid *B. intermedia*.

105. Metaphase I in a pentaploid *B. ewartiana*.

106. Anaphase I showing laggards and bridges in a pentaploid *B. intermedia*.

107. Anaphase I in a pentaploid *B. intermedia* X *D. annulatum*.

108. Anaphase I showing a dividing laggard in a pentaploid *B. intermedia* X *D. annulatum*.

109. Anaphase I chromosomes in a pentaploid *B. intermedia*.

110. Diakenesis in a hexaploid *B. intermedia*.

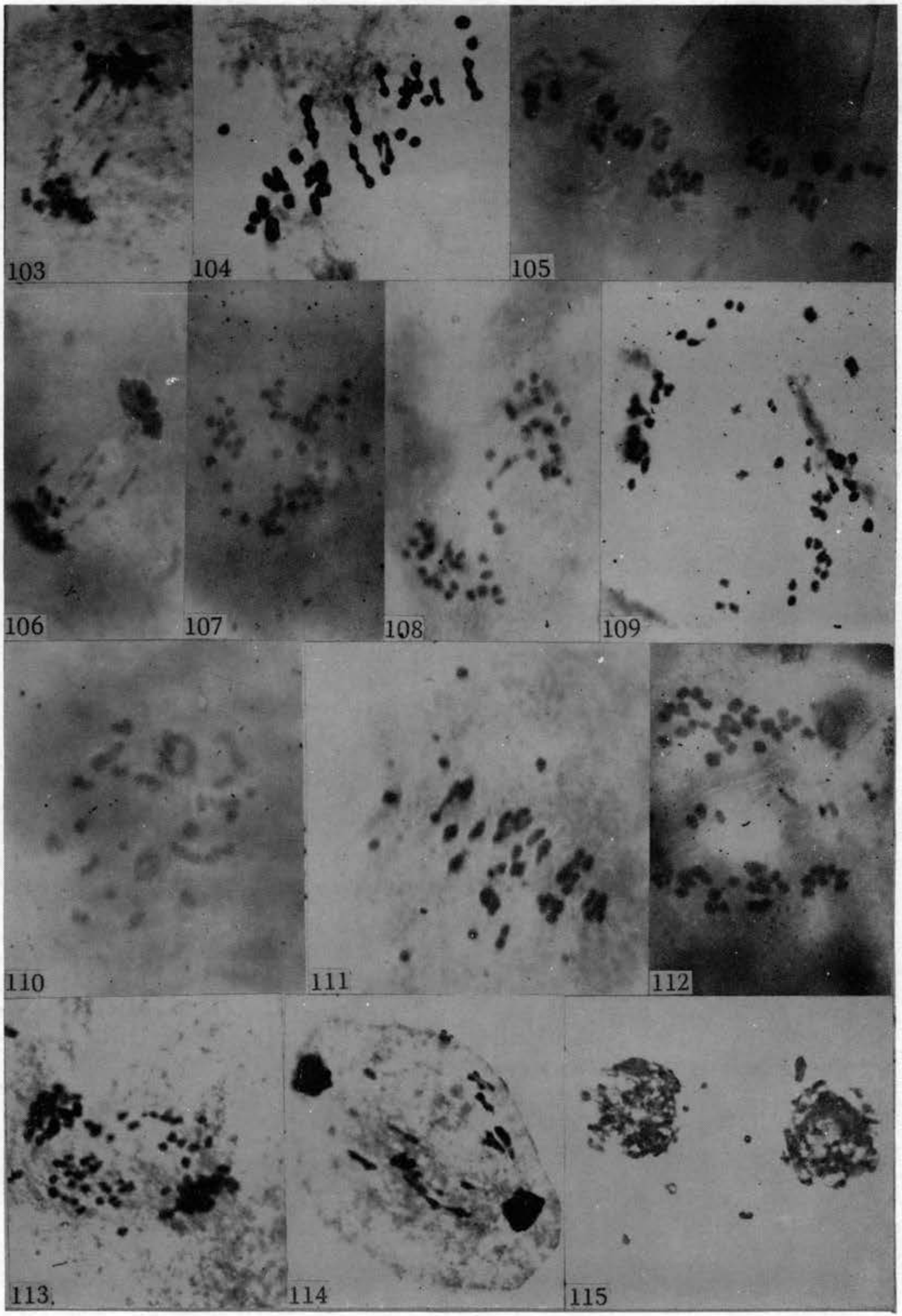
111. Metaphase I in a hexaploid *B. intermedia* X *D. annulatum*.

112. Anaphase I in a hexaploid *B. ewartiana*.

113. Anaphase I showing dividing and non-dividing laggards in a hexaploid *B. intermedia*.

114. Late anaphase I showing non-dividing laggards mostly concentrated to one pole in a hexaploid *B. intermedia*.

115. Telophase I showing micronuclei in a hexaploid *B. intermedia*.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LEGEND TO FIGURES 116-124.

Figs. 116-118. Meiotic behavior of chromosomes in a octoploid *B. intermedia*. Magnification X 1350.

Figs. 119-124. Frequency histograms showing the average number of bivalents per cell of tetraploid plants with respect to morphological types and geographic distribution.

119. Frequency histogram of bivalent chromosomes of the Indian tetraploid *B. intermedia* complex.

120. Frequency histogram of bivalent chromosomes of the Australian tetraploid *B. intermedia* complex.

121. Frequency histogram of bivalent chromosomes of African tetraploid *B. intermedia* complex.

122. Frequency histogram of bivalents in *B. intermedia*.

123. Frequency histogram of bivalents in *B. intermedia* X *D. annulatum*.

124. Frequency histogram of bivalents in *B. intermedia* X *C. parviflorum*.

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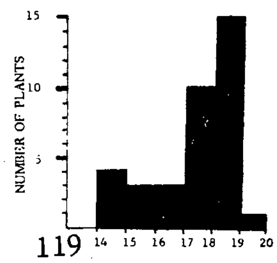

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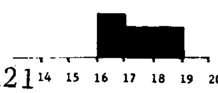

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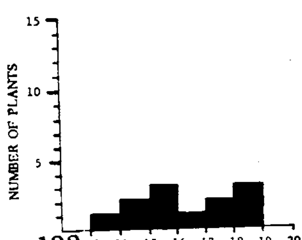
AVERAGE NUMBER OF BIVALENTS PER CELL



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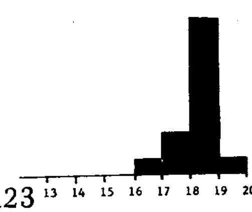

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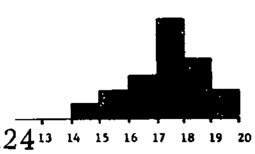


124

AVERAGE NUMBER OF BIVALENTS PER CELL

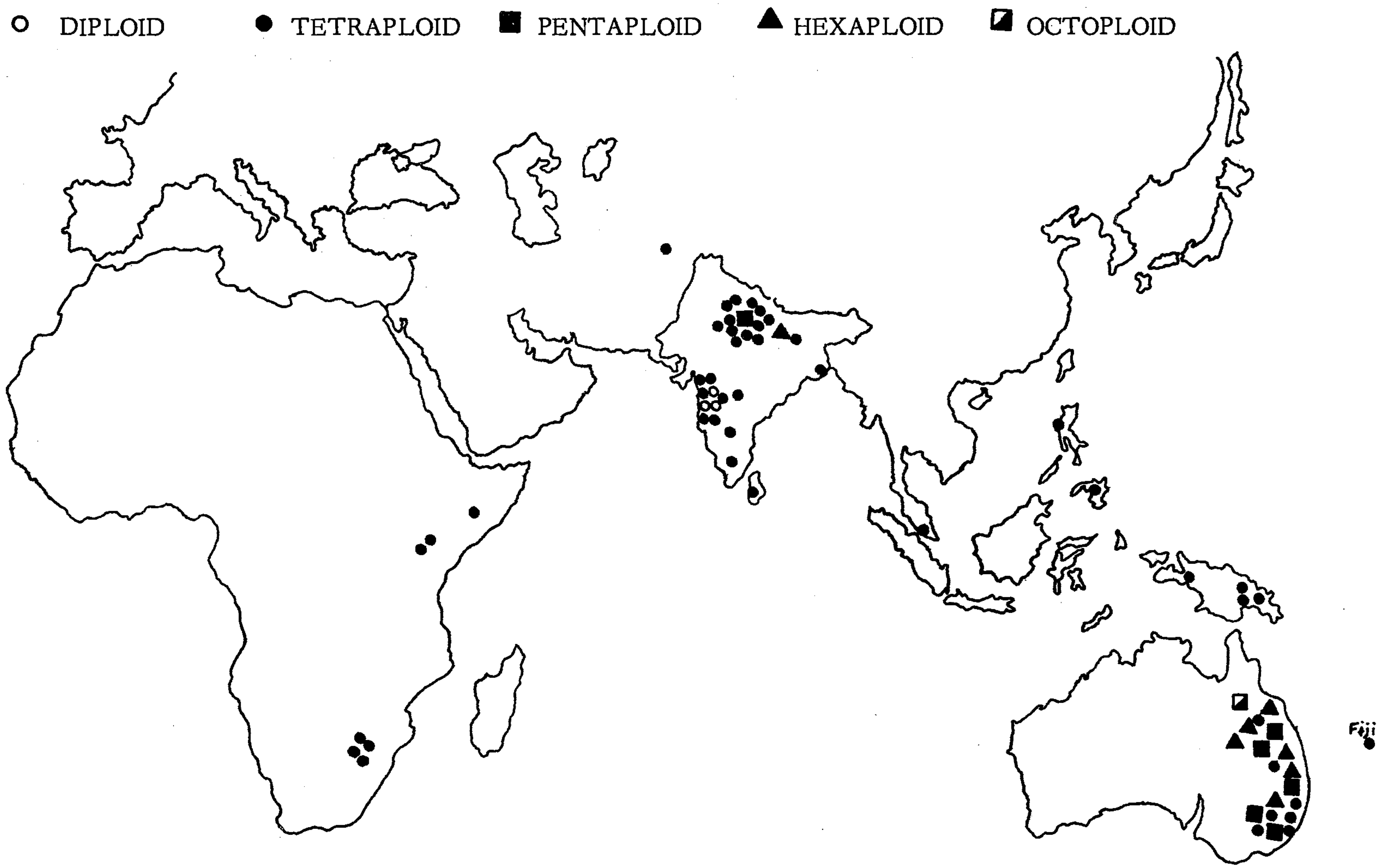


Fig. 125. Cytogeography of the B. intermedia complex.

Meiotic abnormality and geographic distribution: Average number of bivalents in the tetraploid plants representing Indo-Pakistan and Australia (Fig. 120) are plotted in frequency histograms (Figs. 119-124). A comparison of these two geographic locations indicate more cytological regularity in Indian plants than in Australian.

3. Anatomy of the Leaf and Culm

Leaf anatomy of some species belonging to Bothriochloa, Capillipedium, and Dichanthium is described by Sabnis (1921), Vickery (1934), Prat (1937), and Metcalf (1960). Studies on the internal structures of culm are still meager and culm anatomy of Capillipedium is not yet known. The descriptions of leaf anatomy of B. decipiens, B. erianthoids, B. glabra, and B. intermedia by the above mentioned workers indicate remarkable similarities between these species. The recent work of Metcalf (1960) indicates similar conclusions within the members of the three genera in respect to anatomical characters.

Leaf epidermis surface view: The leaf epidermis of grasses is composed of a number of cell structures discussed by Prat (1936 and 1948). Among these, the shape of siliceous cells is a variable characteristic (Figs. 127-130). These cells may be either narrow (Fig. 130) as in B. longifolia and B. ischaemum (Table II) or broad as in B. caucasica (Figs. 127, 128). The shape may also vary from narrow to broad in the same plant, as is common among the rest of the species studied.

Short cells and long cells (Fig. 131) are present both over the veins and between the veins in the epidermis. In D. annulatum and B. intermedia X D. annulatum short cells are longer than broad (Fig. 132), and may be up to five in a row. In the other species stud ed they are either solitary (Fig. 139) or in pairs (Fig. 131) and broader than long or equidimensional. Long cells may be pitted or unpitted (Table II).

The interstomatal cell may be short and broad (Fig. 134) or long and narrow (Fig. 135) but usually both the types are present in the same species (Fig. 139),

LEGEND TO FIGURES 126-143

Figs. 126-139. Leaf epidermis among the members of the *B. intermedia* complex. Magnifications for figures 126-137 X 275; 138-139 X 180.

126. "A" type prickle hairs in *B. caucasica*.

127-128. Broad silica cells in *B. caucasica*.

129. Broad silica cell in *B. intermedia* X *D. annulatum*.

130. Narrow silica cell in *B. longifolia*.

131. Long-cells and short cells in *B. longifolia*.

132. Long-cell and short cell in *D. annulatum*.

133. Short cell modified in "B" type prickle hair in *B. longifolia*.

134-135. Interstomatal cells in *B. longifolia* and *C. spicigerum* respectively.

136-137. Bicellular microhairs in *D. annulatum* and *B. odorata* respectively.

138-139. A portion of leaf epidermis in *B. ischaemum* and *B. odorata* respectively.

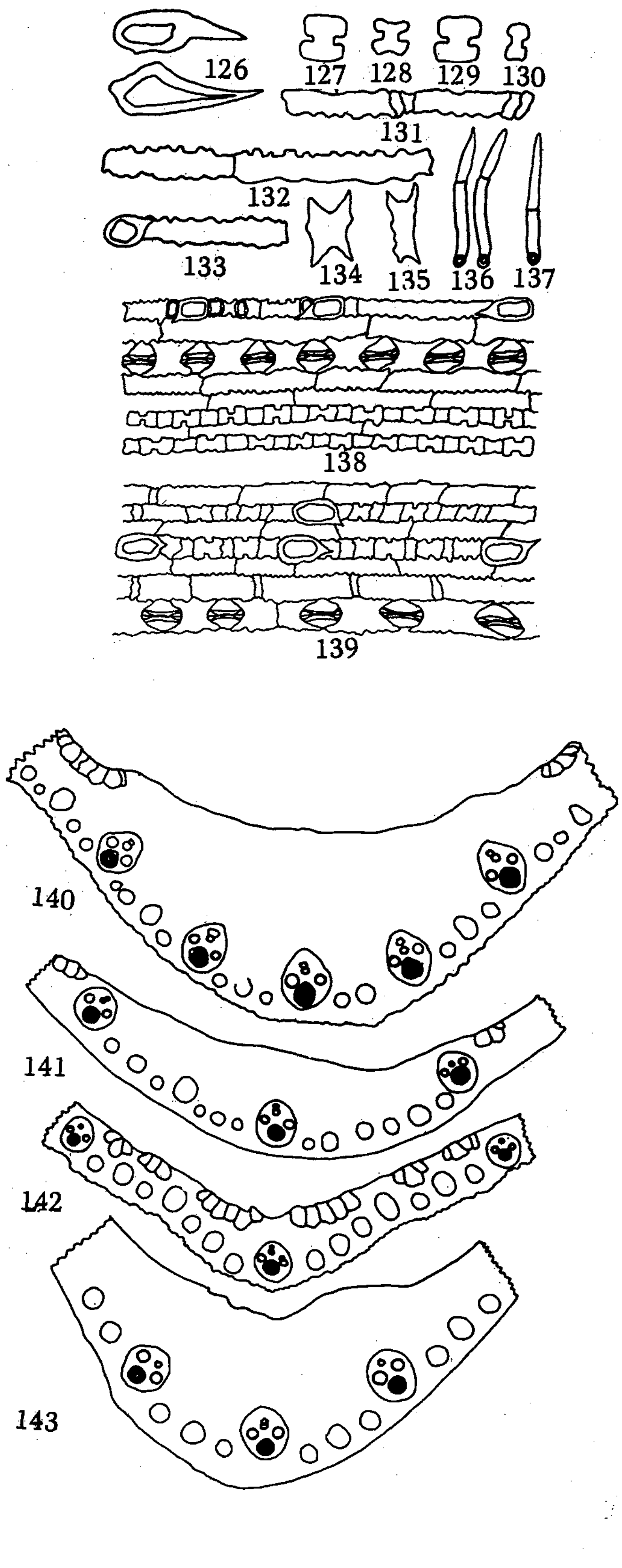
Figs. 140-143. Cross sections of leaf in the *B. intermedia* complex to note the thickness of keel and number of vascular bundles in the keel. Magnification X 60.

140. *B. longifolia*

141. *B. intermedia* X *B. ewartiana*.

142. *B. ewartiana*

143. *B. intermedia* X *D. annulatum*.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hence it is not a very reliable character. Short interstomatal cells are abundant in B. longifolia, B. ewartiana, B. ischaemum, D. annulatum, and C. spicigerum. The rest of the species studied have a greater frequency of long interstomatal cells.

Bicellular microhairs are found in all the species of the three genera studied. Vickery (1935) and Metcalf (1960) did not find bicellular microhairs in members of the genus Capillipedium. Two species, C. spicigerum and C. parviflorum, were checked with respect to this character and bicellular microhairs were present in both. The two species also possess long macrohairs which may overshadow small microhairs. This may be the reason why previous workers did not notice bicellular hairs. The ratio of basal/distal cell length is highest in D. annulatum. In B. longifolia, B. ewatiana, B. caucasica, and B. intermedia X D. annulatum this ratio is more than 1.00 (Fig. 136, Table II). In the other species studied, this ratio is less than 1.00 (Fig. 137 and Table II).

Prickle hairs with swollen bases and curved tips are unicellular. These could be divided into two types according to their position and distribution. Type "A" (Fig. 126) originates over the veins from the same rows as cork cells and silica cells. These are present in B. caucasica, C. spicigerum and D. annulatum. Type "B" (Fig. 133) originates from the short cells in the region between the veins and it is present in B. longifolia, B. ischaemum and B. ewartiana. The rest of the species have both types of the prickle hairs. However, there are differences in the size and relative abundance of the two types of hairs in different species. The presence and relative abundance of these two types of microhairs are represented by plug signs (Table II). The "A" type prickle hairs are also relatively

TABLE II

AN ANALYSIS OF LEAF EPIDERMIS
WITHIN B. intermedia COMPLEX

Name	Short cells	Long cells	Bicellular microhairs: Mean length in mms.	Bicellular microhairs: Ratio:basal/ distal cell	Prickle hairs: 'A' type	Prickle hairs: 'B' type	Silica cells: Ratio: length/ breadth
B. longifolia (Hack.) Bor	short 1-2	-	0.041	1.36	-	+	2.00
B. ischaemum (L.) Keng	do	Pitted	0.055	0.77	-	++	2.00
B. int. X B. isch.	do	-	0.050	0.78	+	++	1.22
B. ewartiana (Domin) C.E.Hubbard	do	-	0.057	1.25	-	+	1.44
B. intermedia (R.Br.)A.Camus	do	-	0.060	0.84	+	+	1.32
C. spicigerum S. T. Blake	do	Pitted	0.070	0.85	++	-	1.60
B. int. X Capillipedium	do	-	0.063	0.83	++	+	1.33
B. caucasica (Trin.) C.E.Hubbard	do	Pitted	0.056	1.28	++	-	1.09
B. odorata (Lisboa) A. Camus	do	do	0.060	0.79	++	+	1.48
D. annulatum (Forsk.) Stapf	short-long 4-5 in row	do	0.073	1.80	++	-	1.69
D. int. X D. ann.	short-long 1-5 in row	do	0.058	1.20	++	+	1.33

larger than the "B" type. In this respect B. odorata and B. intermedia X Capillipedium are similar to B. caucasica and Capillipedium species.

Leaf in cross section: The single layer of upper epidermis is modified into thin-walled bulliform cells between the primary bundles, but is usually interrupted by vascular bundles of the second order. The three genera Bothriochloa, Capillipedium, and Dichanthium in this respect, are very similar, as usually there are a maximum of two bands of bulliform cells interrrupted by normal epidermal cells between the two primary vascular bundles (Figs. 144-148). An assumed natural hybrid involving B. intermedia and Capillipedium forms a single continuous layer of bulliform cells between the two primary bundles (Fig. 149). This condition was observed neither in the true Capillipedium species studied nor in B. intermedia. On the other hand, B. ewartiana and its assumed natural hybrids with B. intermedia are characterized by having three to four bands of bulliform cells between the primary bundles (Fig. 151). This is due to greater number of vascular bundles of the second order in B. ewartiana. In the rest of the species studied there is only one vascular bundle of the second order between two first order (primary) bundles. The lower epidermis has regular thickened cells.

Sub-bulliform cells are commonly present below the bulliform cells. These may form 1-2 or 3 layers in most of the species (Figs. 144-149). In B. ischaemum, B. ewartiana, and B. intermedia X B. ewartiana these cells form a single layer (Fig. 151). In B. caucasica the sub-bulliform cells are entirely absent (Fig. 150). In all the species studied a single tier of parenchyma cells is present between the vascular bundles and connects the upper epidermis to the lower epidermis.

LEGEND TO FIGURES 144-151

Figs. 144-151. Cross section of lamina in the members of the *B. intermedia* complex showing number of bulliform cell bands, presence, absence, and variation of sub-bulliform cells, number of vascular bundles of the second order and number of intercalary bundles. Magnification X 125.

144. *B. longifolia*.

145. *B. intermedia*.

146. *B. intermedia*.

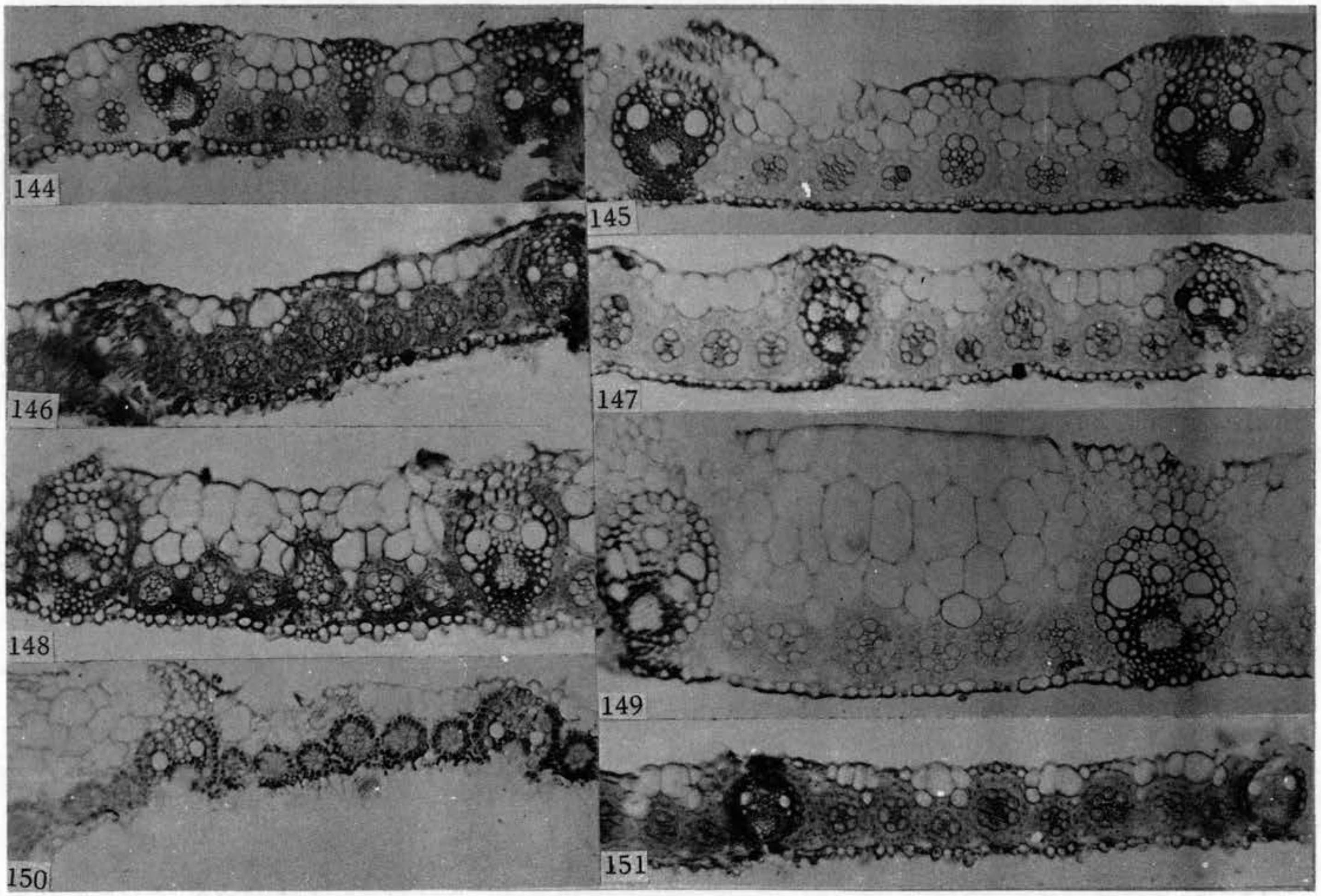
147. *B. intermedia* X *D. annulatum*.

148. *B. odorata* A-~~7232~~.

149. *B. intermedia* X *C. parviflorum*.

150. *B. caucasica*

151. *B. intermedia* X *B. ewartiana*.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The classification of veins is discussed in detail by Pee-Laby (1898) who recognizes five categories in the cross-section of grass leaves. Reynolds (1959), working with the leaf blade anatomy in Andropogoneae, has pointed out the difficulties in the recognition of fourth and fifth order veins in this group. Pee-Laby's classification is based upon type of thickening in the protoxylem vessel, presence and absence of a lacuna, and number and type of metaxylem elements. Reynolds (1959) on the other hand relies on size differences. Following Reynolds, the veins are classified into three categories according to their size. The primary bundles include those of the largest size category, which also possess at least two prominent metaxylem vessels and a lacuna in the protoxylem. These characteristics are absent from other categories of vascular bundles. The second order vascular bundles are present between two primary bundles. These can be recognized also on the basis of size, being smaller than the primary, while larger than other categories. As mentioned earlier, usually bulliform cells are replaced by normal epidermis above the primary and second order vascular bundles. The remaining bundles not included as primary or second order bundles are termed as third order bundles. Intercalary bundles as referred to in this discussion include all the bundles between two primary bundles. These include second and third order bundles.

In some of the species, the keel has a solitary median vascular bundle, but some of the adjoining bundles may also be included in the keel. In this respect the majority of species studied have three primary bundles in the keel (Fig. 143, Table III), but there is only one in B. ewartiana (Fig. 142), B. intermedia X B. ewartiana (Fig. 141), and B. caucasica. In B. longifolia primary keel bundles are five in number (Fig. 140).

The intercalary bundles include all the categories of vascular bundles between the two primary bundles. Due to the variation of intercalary bundles at different situations of the lamina, counts are restricted to the bundles at either side of the median bundle of the keel. In most of the species studied these bundles are three to four in number. Bothriochloa ischaemum has five such bundles, while B. intermedia X B. ischaemum has only three. Maximum number of intercalary bundles is seven in B. ewartiana, and its hybrid varies from five to six (Table III).

The vascular bundles are surrounded by a parenchyma sheath in each case. Chlorenchyma cells are also present around the vascular bundles, but they are not elongate and obviously radially arranged, being typically panicoid in this respect (Stebbins 1956a, Brown 1958). In B. caucasica (Fig. 150) the chlorenchyma cells are smaller in size than any other species studied.

Sclerenchyma is present above and below the primary vascular bundles. In the vascular bundles of the second order, this is true only in B. longifolia (Fig. 144). In B. ischaemum and B. intermedia sclerenchyma is only on the upper side, while in Capillipedium and B. odorata towards the lower side only.

Culm in cross section: Metcalf (1960) points out small epidermal cells with moderate thickenings in the culms of B. caucasica (Fig. 157) and D. aristatum. Such epidermal cells are also present in B. odorata, B. ischaemum (Fig. 154), B. ewartiana, and C. spicigerum (Fig. 158). Another type of epidermis includes a group of long, radially arranged, thin walled cells alternating with a group of small equidimensional cells with moderate thickenings (Figs. 152,

TABLE III

ANATOMICAL FEATURES OF LEAF
IN CROSS SECTION WITHIN
B. intermedia COMPLEX.

Plant Name	Sub-Bulliform cell layers	Parenchyma in keel	No. primary vbs. in keel	No. intercalary vbs. in keel	No. of bulliform bands between two primary bundles.
B. longifolia	1-3	⧸⧸⧸	5	3	2
B. ischaemum	1-2	⧸⧸⧸	3	5	2
B. int. X B. isch.	1-3	⧸⧸⧸	3	3	1-2
B. ewartiana	1	⧸	1	7	3-4
B. int. X B. ewart.	1	⧸⧸	1	5-6	3-4
B. intermedia	1-2	⧸⧸⧸	3	4	1-2
C. spicigerum	1-2	⧸⧸⧸	3	3-4	1-2
B. int. X Capillipedium	1-3	⧸⧸⧸	5	3	1-2
B. caucasica	0	⧸⧸⧸	1	5-6	2
B. odorata	1-3	⧸⧸⧸	5	3-4	1-2
D. annulatum	1-3	⧸⧸⧸	3	3	1-2
B. int. X D. ann.	1-2	⧸⧸⧸	3	3	1-2

153, 155). In the diploid B. longifolia (Fig. 152) the number of radially elongated cells far exceeds the short ones, the ratio being more or less 25:5 including the two guard cells which are also located in this region. The polyploid members of the B. intermedia complex on the other hand may either possess only the equidimensional cells in the epidermis (Fig. 156) or may include the radial ones as well (Figs. 153, 155). In no case are the radial cells as many or more in number than the equidimensional ones (Table IV).

A single layered hypodermis (Figs. 152, 155) is present in all the species mentioned above. However, these cells are comparatively more thickened in plants with radial epidermal cells.

Bothriochloa longifolia, B. intermedia, B. odorata, D. annulatum and C. spicigerum possess three categories of vascular bundles according to size, and these are arranged in three different rings. In B. ischaemum, B. ewartiana, and B. caucasica the differences between the two inner rings are small. In this way vascular bundles belong to two size categories in these three species. These vascular bundles form a single ring in B. ischaemum (Fig. 154) and B. ewartiana and two in B. caucasica (Fig. 157).

The vascular bundles of the outermost ring or the ones belonging to the smallest size category in the species with less than three distinct rings are broader than long (Table IV, Figs. 152, 153-155) in most of the species of the genus Bothriochloa. However, in the genera Dichanthium and Capillipedium these are longer than broad, or round. In B. caucasica (Fig. 157) these are more or less round with little variation. Dichanthium annulatum and C.

LEGEND TO FIGURES 152-159

Figs. 152-159. Culm in cross section to show types of epidermis, categories of vascular bundles according to size and shape and the number of rings the vascular bundles are arranged. Magnification X 125.

152. B. longifolia.

153. B. intermedia X B. ischaemum.

154. B. ischaemum.

155. B. intermedia X B. ewartiana.

156. B. intermedia X C. parviflorum.

157. B. caucasica.

158. C. parviflorum.

159. D. annulatum.

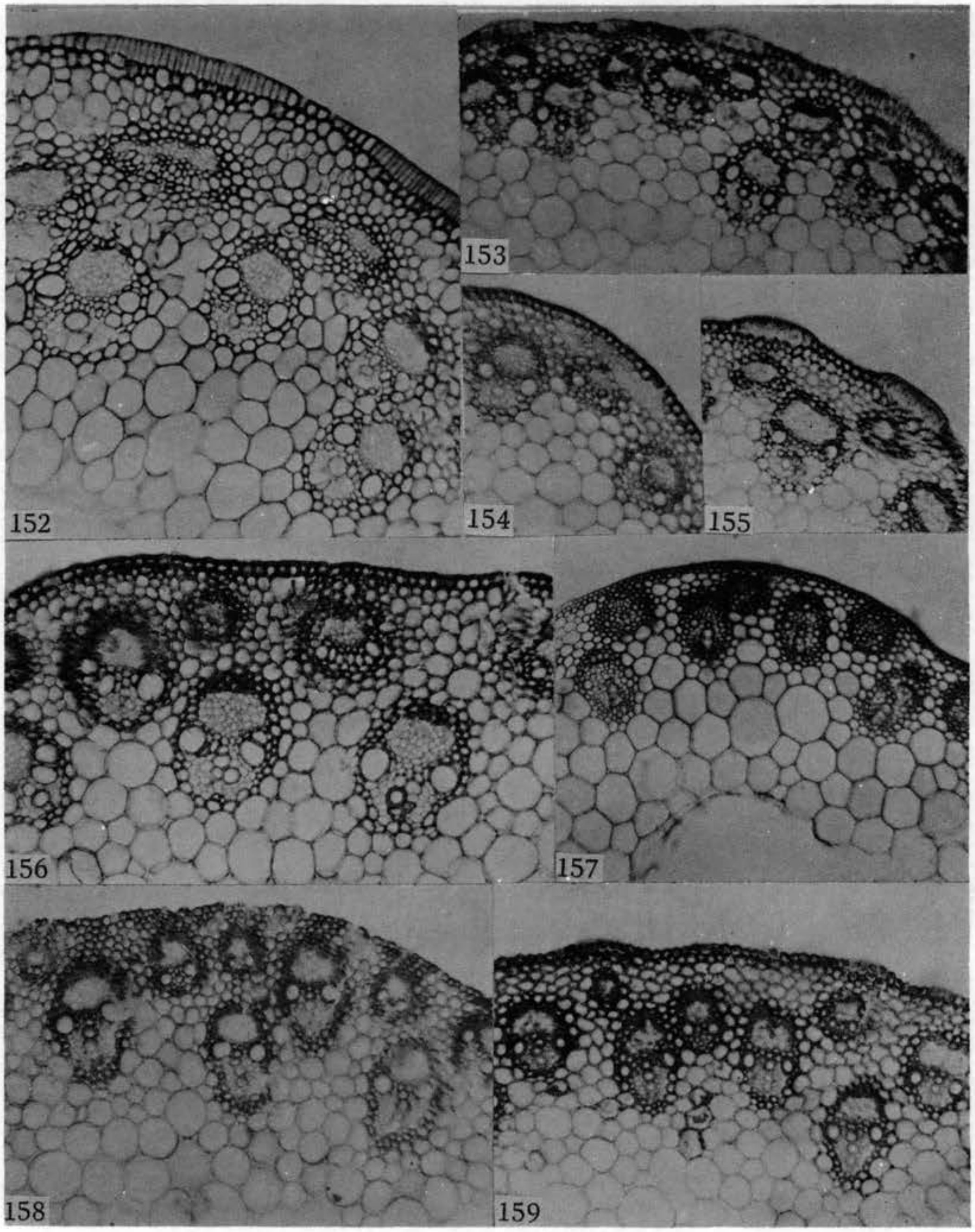
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TABLE IV

ANATOMICAL FEATURES OF CULM IN CROSS SECTION WITHIN B. *intermedia* COMPLEX

Plant Name	Epidermis		Hypodermis	Size Categories of Vascular bundles	No. Vascular bundle rings	Shape of outer ring bundles	Internode
	Radial	Short					
B. *longifolia* (Hack) Bor	//	/	conspicuous	3	3	Broad	Hollow
B. *ischaemum* (L.) Keng	-	///	inconspicuous	2	1	Broad	Solid
B. *int.* X B. *isch.*	- or /	/// or //	inconspicuous or conspicuous	3	3	Broad	Solid
B. *ewartiana* (Domin) C. E. Hubbard	-	///	inconspicuous	2	1	Broad	Solid
B. *int.* X B. *ewart.*	/	//	conspicuous	3	3	Broad	Solid
B. *intermedia* (R. Br.) A. Camus	- or /	/// or //	inconspicuous or conspicuous	3	3	Broad	Solid
C. *spicigerum* S. T. Blake	-	///	inconspicuous	3	3	Narrow	Solid
B. *int.* X *Capillipedium*	-	///	inconspicuous	3	3	Round	Solid or Hollow
B. *caucasica* (Trin.) C. E. Hubbard	-	///	inconspicuous	2	2	Round	Hollow
B. *odorata* (Lisboa) A. Camus	-	///	inconspicuous	3	3	Round	Solid
D. *annulatum* (Forsk) Stapf	- or /	/// or //	inconspicuous or conspicuous	3	3	Narrow	Solid
B. *int.* X D. *annulatum*	- or /	/// or //	inconspicuous or conspicuous	3	3	Oval	Solid

spicigerum have slightly narrow vascular bundles.

Hollow internodes are present in *B. longifolia* and *B. caucasica*. The rest of the species studied possess solid internodes (Table IV). However, the collection number 6511 *B. intermedia* complex has hollow internodes.

4. Anatomy of the Glume Pit

The surface view of glume epidermis (Fig. 164) shows long cells, silica cells and cork cells in a horizontal line. The cells at the margin of a pit are more or less alike, so that the three types of epidermal cells cannot be distinguished easily (Fig. 160). Here the long cells are shorter and short cells and siliceous cells longer than their usual size. Within the pits these epidermal cells show little elongation in the direction of the long axis (Figs. 161, 163) and tend to grow radially (Figs. 165-167). Elongation of the pit cells both in the direction of the long axis or at its right angle is quite variable within the hybrids of B. intermedia (Figs. 166, 167, 169). The cells of the pit epidermis have a dense cytoplasm and prominent nucleus. At early stages of their development these cells are more prominent, larger radially and have a more prominent nucleus than the cells of normal epidermis.

Crystals are also associated with pits (Figs. 161-163) which may be few to many, and fill the entire cavity. When heated on a direct flame no physical change could be observed in these crystals except in color from white to light brown which may be due to over heating. The material is readily soluble in water.

Within B. intermedia pits vary from a few cells with more or less no depression (Fig. 163) to many cells with fully developed pits (Figs. 166, 167, 169). There seems to exist a direct correlation between the size and structure of pit cells and amount of crystals present.

A vein may be present under a pit, or absent, but veins never open inside a pit.

LEGEND TO FIGURES 160-169

Figs. 160-164. Surface view of the glume and glume pit in the genus Bothriochloa. Magnification X 675.

160. Cells at the pit margin in the B. decipiens A-7501.

161. Cells of the pit in B. decipiens A-7501 in continuation with the Figure 160. Note some crystals.

162. Crystal packed pits of B. pertusa A-3704.

163. Cells of the pit in the hybrid 58-X-371-b2.

164. Normal glume epidermis of the hybrid 56-X-750-1.

Figs. 165-169. Cross sections of the glume and glume pit in the genus Bothriochloa.

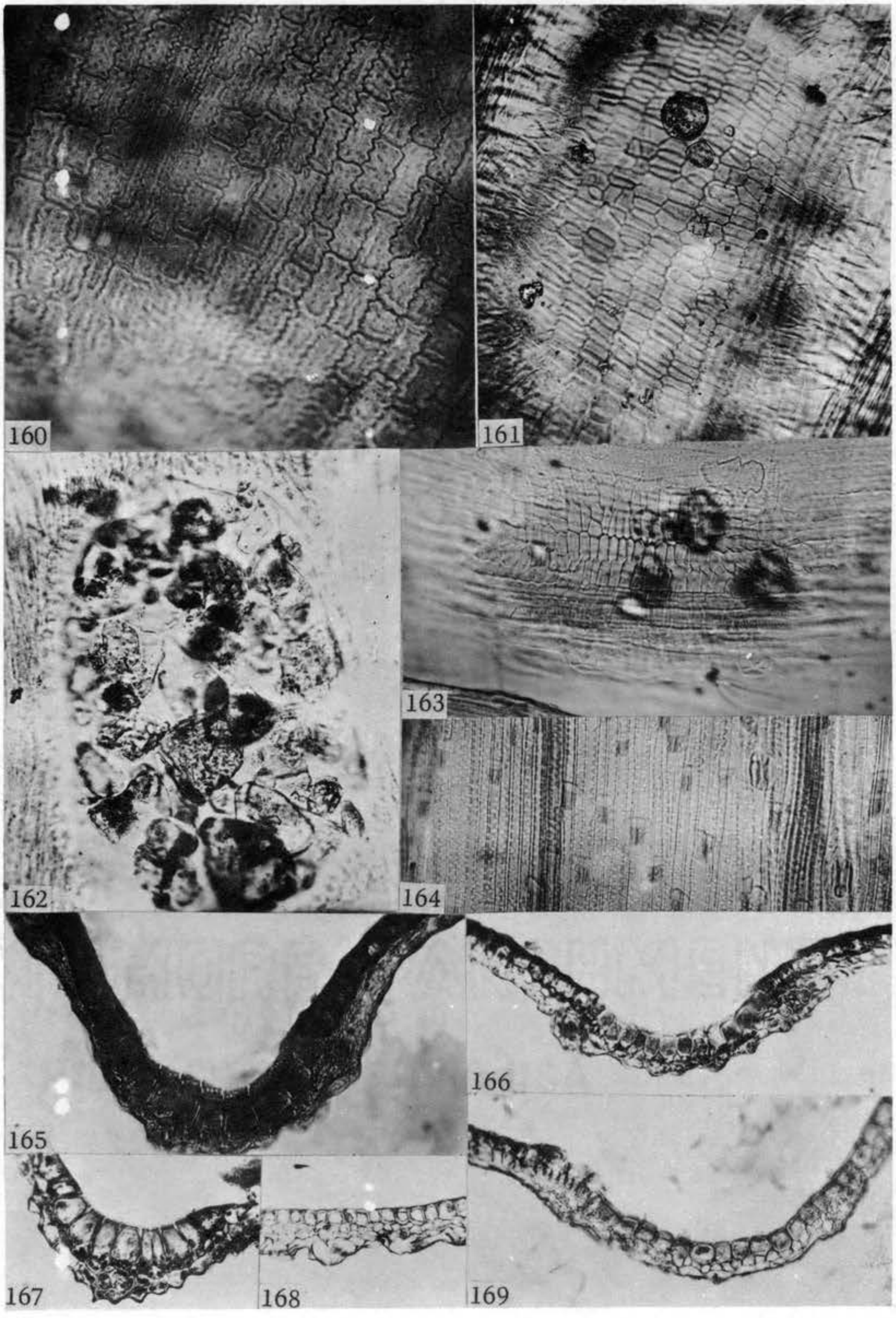
165. Glume pit in B. pertusa A-3704.

166. Glume pit in B. intermedia A-5297-a.

167. Glume pit in the hybrid 58-X-371-b2.

168. Normal glume cells in B. decipiens. A-7501.

169. Glume pit in B. intermedia A-5297-b.


160
161
162
163
164
165
166
167
168
169

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, Stapf 1917, Bews 1929, and Pilger 1954) 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, Spathia Ewart et 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, 1929). 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 et al. 1961). The phylogenetic affinities of Euclasta, Eremopogon, Spathia and Indochloa are poorly understood, but morphological data suggest relationships with Dichanthium.

Celarier and Harlan (1957) and Harlan et al. (1958) 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. Both the cytologically reduced as well as unreduced female gamete may function sexually or develop parthenogenetically.

It was pointed out by de Wet, Mehra, and Borgaonkar (1961), that in hybrids, the chromosomes usually pair preferentially and autosyndetically to form bivalents. Harlan and Chheda (1962) 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 polyhaploids 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, any possible hybrid combination can survive by means of its apomictic mode of reproduction. Furthermore, gene-controlled bivalent formation will insure the production of cytologically reduced gametes, and through pseudogamy the possibility for fertilization is increased. Occasional 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 Robert Brown (1810). 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 non-pitted 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. 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 is 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 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 et al. (1961) 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) describes 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 (1931), Keng (1939, Henrard (1940), and Bor (1960). 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 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 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 artifically 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 170 and 171.

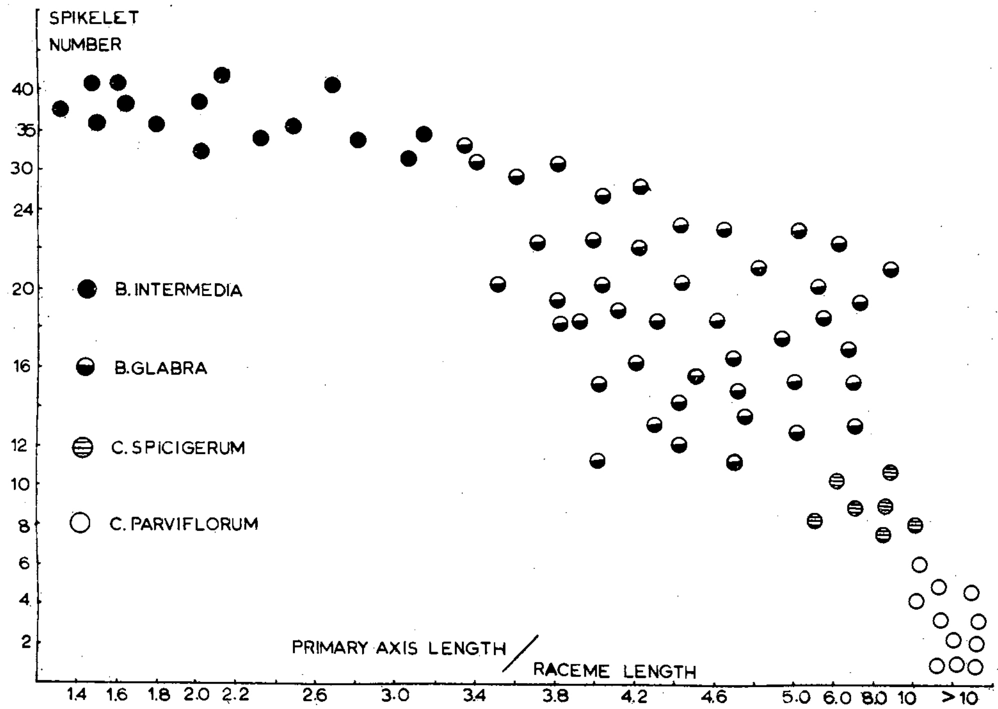
The widely distributed B. intermedia biotype with simple racemes arranged on an elongated primary axis may be relics of the original basic species. Celarier and Harlan (1957) demonstrate that members of the B. intermedia complex are mostly facultative apomictic tetraploids. Cytologically these tetraploids behave like segmental allopolyploids as defined by Stebbins (1947). Harlan and Chheda (1962) demonstrate that chromosome pairing is genetically controlled and takes place autosyndetically. Furthermore, the gene controlling bivalent formation also induces some degree of pairing between non-homologous chromosomes when true homologues are absent.

Experimental evidence, presented by Harlan et al. (1961), demonstrates that both the cytologically reduced as well as unreduced female gamete may

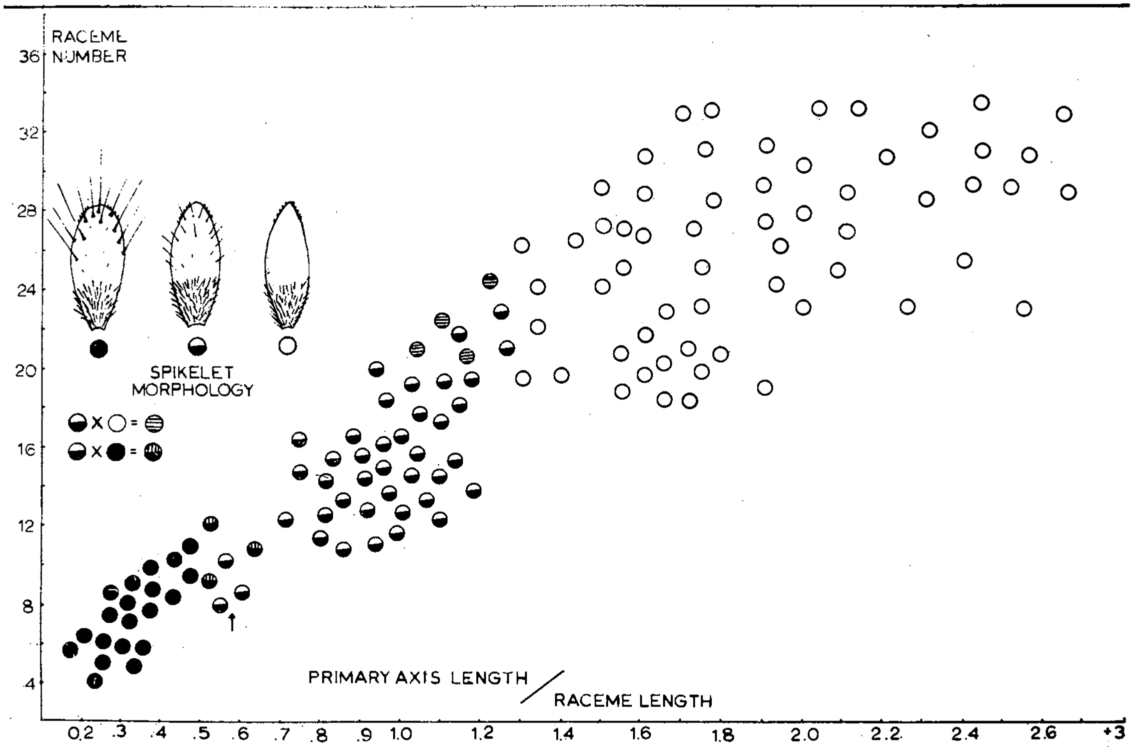
LEGEND TO FIGURES 170-171.

Fig. 170. Pictorialized scatter diagram illustrating the introgression between <u>Bothriochloa intermedia</u> and <u>Capillipedium parviflorum</u>.

Fig. 171. Pictorialized scatter diagram illustrating the introgression between <u>Bothriochloa intermedia</u> and <u>Dichanthium annulatum</u>.


SPIKELET NUMBER
40
35
30
24
20
16
12
10
8
6
4
2
B. INTERMEDIA
B.GLABRA
C. SPICIGERUM
C. PARVIFLORUM
PRIMARY AXIS LENGTH / RACEME LENGTH
1.4 1.6 1.8 2.0 2.2 2.6 3.0 3.4 3.8 4.2 4.6 5.0 6.0 8.0 10 >10

170


RACEME NUMBER
36
32
28
24
20
16
12
8
4
SPIKELET MORPHOLOGY
PRIMARY AXIS LENGTH / RACEME LENGTH
0.2 .3 .4 .5 .6 .7 .8 .9 1.0 1.2 1.4 1.6 1.8 2.0 2.2 2.4 2.6 +3

171

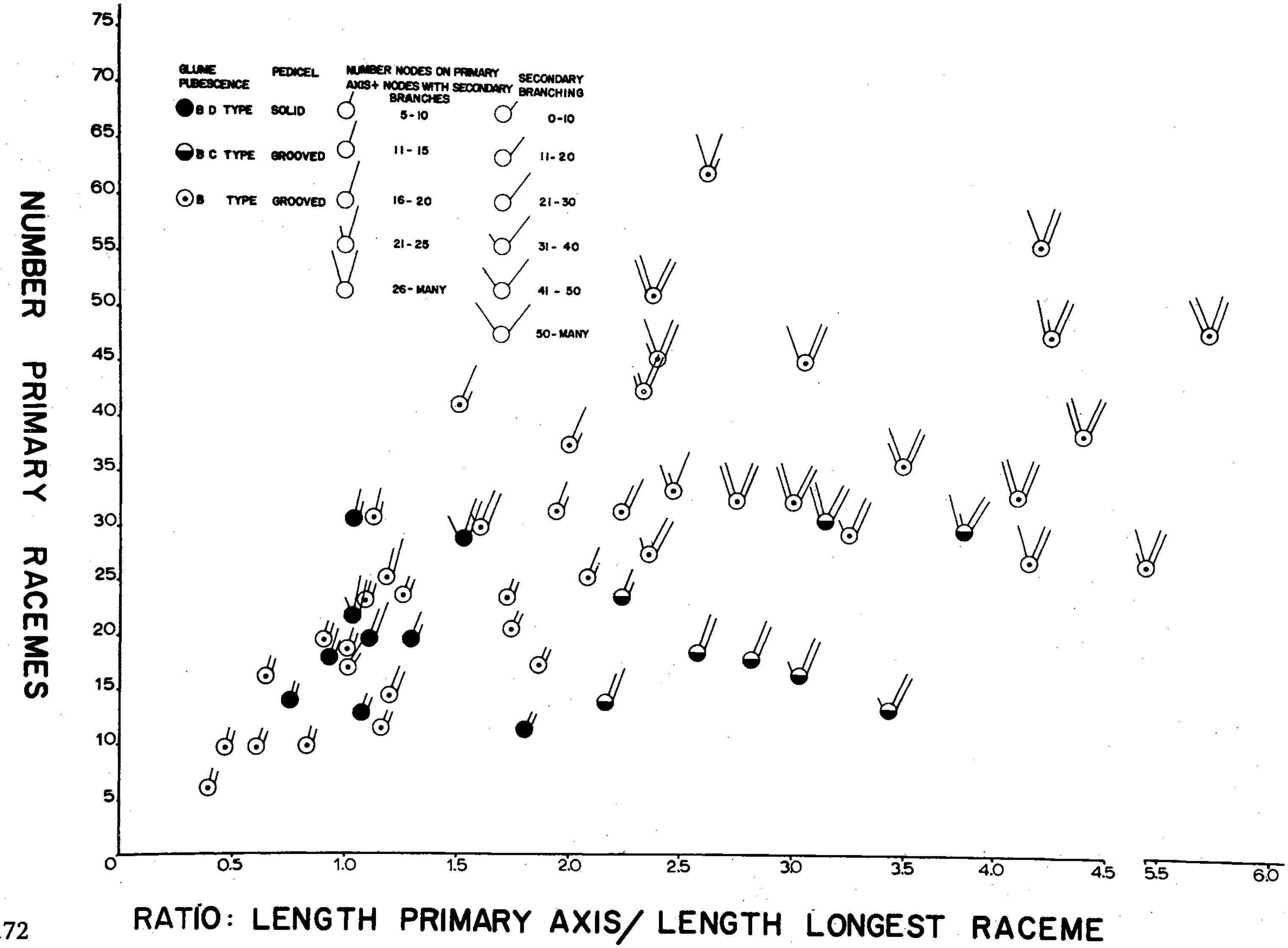
function sexually. Introgressive hybridization should therefore give rise to a polyploid series with various combinations of *Bothriochloa*, *Capillipedium*, and *Dichanthium* genomes. This type of introgression can explain the range of morphological variation characteristic of *B. intermedia*.

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 characters. Introgression with *B. intermedia* will increase the number of spikelets per raceme and decreases 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.

B. intermedia and *D. annulatum* hybridized in nature and continuous introgression with both species gave rise to a variable agamic-complex. The taxonomic picture is further complicated by hybridization between members of these two groups of introgression derivatives, giving rise to biotypes that defy classification (cf. Fig. 172).

LEGEND TO THE FIGURE 172.

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


GLUME PUBESCENCE
PEDICEL
NUMBER NODES ON PRIMARY AXIS + NODES WITH SECONDARY BRANCHES
SECONDARY BRANCHING
B D TYPE
SOLID
B C TYPE
GROOVED
B TYPE
GROOVED
5-10
11-15
16-20
21-25
26-MANY
0-10
11-20
21-30
31-40
41-50
50-MANY
NUMBER PRIMARY RACEMES
RATIO: LENGTH PRIMARY AXIS/ LENGTH LONGEST RACEME
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.5
6.0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75

Evidence of Interspecific Introgression

Although less conclusive than evidence for intergeneric hybridization, morphological data 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) 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 B. intermedia at the tetraploid level. An extensive collection of plants from West Pakistan, Kashmir, and northern India is now being studied in this laboratory and the data will be presented elsewhere.

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. Bothriochloa ewartiana differs from B. intermedia in having the leaves mostly cauline instead of basal, and the racemes are subdigitately arranged on a short primary axis (Blake 1944). 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 highly apomictic, but also that the cytologically unreduced female gamete may function sexually to produce hybrids. A detailed cytomorphological study of B. ewartiana should prove interesting.

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 culms 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. Crosses between B. intermedia and B. pertusa were so far not successful in producing hybrids.

The Significance of Apomixis in Evolution and

Speciation of the Bothriochloininae

Apomixis, although not the most ideal system of reproduction to induce genetic variability, and consequently phylogenetic development, is of common occurrence in plants. Nygren (1954) lists 300 species belonging to 95 genera, including 37 families of both monocotyledons and dicotyledons, that reproduce, at least under certain conditions, asexually. This mode of reproduction is particularly common in the Compositae, Rosaceae, and Gramineae Gustafsson (1946, 1947 a, b.). Brown and Emery (1957) demonstrate gametophytic apomixis in 72 species of the family Gramineae. These belong to 28 genera which are usually included in 11 different tribes. Apomixis is particularly common in the tribe Andropogoneae, a small section of which, the Bothriochloininae, is being studied in detail from a biosystematic point of view.

The monotypic genus Euclasta Franchet is present in both tropical Africa and tropical America. African material of E. condylotricha (Hochst.) Stapf is tetraploid with 2n=40 chromosomes and apparently reproduces apomictically. Eremopogon (Hack.) Stapf is characterized by two species. The one, E. tuberculatus (Hack.) A. Camus endemic to Madhya Pradesh, India, is unknown cytologically. The other, E. foveolatus (Del.) Stapf is an apomictic tetraploid extending along the drier regions from southern India to tropical Africa. The monotypic Spathia Ewart, endemic to north-central Australia, and Indochloa Bor with two locally endemic species in India are unknown cytologically. The remaining three genera, Capillipedium Stapf, Dichanthium Willemet, and Bothriochloa O.

Kuntze are widely distributed throughout the tropics and subtropics of the Old World. Representatives of the latter genus also extend into southern Europe and the warmer parts of the Americas.

Each of these three genera are characterized by diploids which are endemic to localized ecological niches, and more widely distributed polyploid species. A survey of mode of reproduction (Celarier and Harlan, 1957) indicates that they follow the classical pattern where diploids (2*n*=20) are sexual, tetraploids are facultative apomicts and higher polyploids essentially obligate apomicts. Some Australian hexaploids and the American species of *Bothriochloa* with 2*n*=60, 80, 120, and 180 chromosomes reproduce sexually. The apomictic mechanism is evidently pseudogamous apospory. Sexual embryosacs apparently are always formed but these are usually crowded out by one to several apomictic ones. From one to several of these may contain developing embryos at the time of anthesis, but the endosperm does not appear to form until pollination. Cytogenetical data indicate that both a reduced as well as unreduced female gamete may function sexually or develop parthenogenetically to produce viable offspring.

At the Oklahoma State University, approximately 1500 different collections, including the majority of species belonging to *Bothriochloa*, *Capillipedium*, and *Dichanthium* have so far been studied cytologically and morphologically. Over 600 hybrids, involving 57 parents representing 44 different combinations of 21 species belonging to these three genera were so far produced. These include not only intra- and interspecific hybrids, but it was found that some biotypes of *B. intermedia* may be crossed with members of both *Capillipedium* and

Dichanthium (Harlan et al. 1961). The latter two genera appear to be genetically isolated. The fact that a large number of hybrid combinations was obtained, however, does not mean that there are no barriers to genetic exchange. Often, literally thousands of emasculations were necessary to obtain a single hybrid. In some combinations seeds that do not germinate are produced, often a large percentage of seedling mortality is obvious and in some crosses delayed lethals, effecting well developed plants are evident. Other cross combinations, on the other hand, produce vigorous hybrids. These are usually apomictic although a few highly sexual hybrid combinations were also obtained. Approximately 80 different combinations attempted, produced no hybrids at all. Classically, apomixis was regarded as the mechanism leading to a phylogenetic dead end. This may be true in obligate apomicts where genetic variability is limited to mutation. Whether true obligate apomicts are common in nature however, is doubtful, and even in these, as pointed out by Ostenfeld (1921) for Hieracium, mutations play a major part in speciation. In the essentially obligate apomicts belonging to the Bothriochloininae, fertile pollen is always produced, and under experimental conditions this can fertilize sexual gametes of facultative apomicts to produce viable offspring.

Apomixis, as pointed out by Clausen (1954), should be regarded as a potential source of genetic variability which may become available in time of need. Apomictic clones which are adapted to a certain ecological condition can become established in a limited time as inummerable replicas of itself can be produced. Should the requirements change, the available genetic variability, through limited recombination, may lead to newly adaptive clones that again are quickly multiplied. Clausen (1961) demonstrates that in the genus *Poa*, facultative apomixis actually provides a means for increasing genetic variability through introgressive hybridization.

Natural hybridization, as was shown in previous sections, are commonly encountered between *Bothriochloa intermedia* and *B. ischaemum*, *Capillipedium parviflorum* as well as *Dichanthium annulatum*. At the diploid, sexual level, the genera *Bothriochloa*, *Capillipedium*, and *Dichanthium* appear to be genetically isolated. Experimental evidence indicates that intergeneric hybrids can be produced only when some biotype of *B. intermedia* is used as the one parent. Although *D. annulatum* and *C. parviflorum* are sympatric over most of their ranges of geographic distribution from southern Africa to Australia through India and China, no natural hybrids were ever collected; nor can these two species be crossed under experimental conditions. *Bothriochloa ischaemum* extends from southern Europe through northern India to China. From West Pakistan eastward this species is often sympatric with both *D. annulatum* and *C. parviflorum* without forming natural hybrids. Similarly artificial hybridization between them appears to be impossible. The morphologically variable species, *B. intermedia* extends over all the tropical and subtropical regions of the Old World.

Taxonomically, the *B. intermedia* species-complex, including genes from at least one other species of *Bothriochloa* as well as the widely distributed *C. parviflorum* and *D. annulatum*, is variously subdivided into species by different taxonomists. This is not surprising, as such an apomictic system will be characterized by a number of distinct biotypes, with some adapted to particular ecological niches. The B. intermedia complex, is not an agamospecies in the usual sense of the word. In reality it represents a converging point of three, apparently distinct genera. The term compilo-species from the Latin "to rob or to plunder" seems an appropriate name to describe such an intergeneric complex. Genetic variability is increased by continuous introgression, as well as hybridization between various biotypes. In this way the original B. intermedia became swamped and at present it is difficult to decide exactly what this species looked like originally.

Polyploid basic species within these three genera behave like segmental allopolyploids as defined by Stebbins (1947). Morphological and genetical evidence indicate that Bothriochloa is closer to Dichanthium than to Capillipedium, and that the latter two genera are only distantly related. Polyploidy and apomixis provided mechanisms which facilitate hybridization, giving rise to the compilo-species we know today. As these plants are all pseudogamous apomicts, some system insuring the formation of fertile pollen is essential.

Cytologically, intra- and interspecific, as well as intergeneric hybridization has little effect on mode of chromosome pairing. The chromosomes usually associate into bivalents, with some chromosomes often failing to pair or these combine into multivalents. It was suggested by de Wet, Mehra and Borgaonkar (1961) that bivalent formation is due to preferential autosyndetic chromosome pairing. Harlan and Chheda (1962) demonstrate that this mode of pairing is controlled by a single dominant gene.

Tetraploid B. intermedia, when self pollinated, gives rise to tetraploid and occasionally hexaploid offspring. Morphological data suggest that hexaploids originated from the fertilization of a cytologically unreduced female gamete. On selfing, the tetraploids often produce 2n=20 polyhaploids, and the hexaploids give offspring with 2n=30 chromosomes, indicating that the cytologically reduced female gamete may also develop parthenogenetically.

The tetraploid, B. intermedia, behaves cytologically like a segmental allopolyploid as defined by Stebbins (1947). The following genomes, BBB'B' may therefore be assigned to these plants. These genomes usually associate into 20 bivalents, although as many as 10 chromosomes sometimes fail to pair or produce multivalents. This tetraploid, when self pollinated, may produce polyhaploids (BB') characterized by 10 bivalents, or occasionally two univalents. It also gives rise to hexaploids (BBB'B'BB') which were expected to be characterized by a high frequency of trivalents. The chromosomes of this hexaploid, however, associate into as many as 26 bivalents, and never more than two multivalents were observed. The polyhaploid derived from such a hexaploid is characterized by as many as 13 bivalents. These cytological data indicate that preferential pairing can take place. Usually, homologous chromosomes pair with each other, but in the absence of homologues, pairing can also take place between non-homologous chromosomes. Chheda and de Wet (1961), and Harlan and Chheda (1962) further demonstrate, that in some crosses approximately one in every four hybrids are characterized by some degree of chromosome desynapsis. This may best be explained on the basis of gene controlled bivalent formation. The idea that chromosome pairing must be genetically controlled is well demonstrated by Rees (1961).

The mechanism of insuring bivalent formation must have influenced the evolutionary pattern of the group. First, it insures the formation of viable pollen, and provides a means for the development of sexual embryo sacs. Secondly, very wide crosses become possible without extreme changes in the cytological mechanisms. Such a system will naturally have a selective advantage in nature, and may be widespread among apomictic groups in the Andropogoneae.

The gene controlling preferential autosyndetic pairing, and which induces pairing between homoeologous or nonhomologous chromosomes, also provides a means by which the plants may change their ploidy level. Under experimental conditions at least, a tetraploid plant was obtained as the result of the fertilization of an unreduced female gamete of a diploid by normal pollen of a tetraploid race of the same species. Diploids are commonly produced by the parthenogenetic development of a cytologically reduced female gamete of a tetraploid. Hexaploids are often encountered in crosses between tetraploids, and pentaploids arise from hybrids between tetraploids and diploids, or hexaploids and tetraploids. All these plants behave like segmental allopolyploids cytologically. Two examples may suffice to demonstrate that these mechanisms also operate in nature. First, morphological and cytogenetic data suggest that B. intermedia X D. annulatum (B. grahamii) combines 20 chromosomes of D. annulatum and 20 chromosomes of B. intermedia. The first mentioned species (Mehra and Celarier 1958) is characterized by two morphologically distinct ecotypes, the one confined mainly to tropical India and the other extending from West Pakistan to North Africa. Hybrids between Tropical D. annulatum and B. intermedia X D. annulatum resemble the Mediterranean ecotype of D. annulatum in morphological characteristics. When the Mediterranean and Tropical ecotypes of D. annulatum are crossed, hexaploid hybrids resembling the tropical Arican 2n=60 chromosome species D. papillosum in detail were obtained. Furthermore, 2n= 20 chromosome polyhaploids obtained from tropical D. annulatum resemble the diploids in detail morphologically. Second, Celarier (1957) and Celarier and Harlan (1958) demonstrate that B. ischaemum var. songarica represents a hexaploid hybrid between tetraploid B. intermedia and tetraploid B. ischaemum. This hexaploid, back crossed to tetraploid B. intermedia further gave rise to pentaploids which, due to preferential autosyndetic chromosome pairing, resemble the hexaploid hybrids closely in morphological characteristics.

Taxonomically the compilospecies here described includes the morphologically "basic" species Bothriochloa ischaemum (Linn.) Keng, Capillipedium parviflorum (R. Br.) Stapf and Dichanthium annulatum (Forssk.) Stapf as well as hybrid-complex involving these three species of three different genera. Classically this hybrid-complex is subdivided into numerous species. Thus, Andropogon glaber Roxb., A. punctatus Trin., A. haenkei Presl., A. vachellii Hack. et Arn., A. lepthanthus Steud., and A. intermedius var. punctatus subvar. glabra Hack. were later transferred to B. glabra (Roxb.) A. Camus. Ohwi (1947) described a new species B. haenkei (Presl.) Ohwi to include plants among this complex, characterized by non-pitted spikelets. Camus (1931) combined the species Andropogon intermedius R. Br. A. punctatus Roxb. and A. perfossus and described B. intermedia (R. Br.) A. Camus. Andropogon caucasicus Trin. and A. intermedius var. caucasicus (Trin.) Hack. are synonyms of B. caucasica (Trin.) C. E. Hubbard, and A. grahamii Haines became the type for B. grahamii (Haines) Bor. The recently described Capillipedium spicigerum S. T. Blake (1944) evidently also represents a distinct biotype of the hybrid-complex. This probably is also true of plants included in B. odorata (Lisboa) A. Camus.

The taxonomic status of the genera Bothriochloa, Capillipedium, and Dichanthium still remains to be discussed. It seems logical to assume that they constitute one large comparium in the sense of Danser (1929). Morphological similarities suggest to Ohwi (1942, 1947) that Capillipedium and Bothriochloa could more naturally be combined into a single taxonomic unit. Gardner (1952) and Roberty (1960), on the other hand, combine Bothriochloa and Dichanthium but retain Capillipedium as a distinct genus. From a classical, as well as experimental, view point the latter seems to be the most logical solution. However, these genera are quite distinct, and for the most part genetically isolated. To revise the taxonomy of this generic group at the present time would only lead to more revision later, and it is preferable to wait until the planned experimental taxonomy is completed.

The following is a list of synonyms for the B. intermedia species-complex.

Bothriochloa intermedia (R. Br.) A. Camus in Soc. Linn. Lyon 1930, 76, 164, 1931.

Recognized to include:

Bothriochloa anamitica Kuntze in Rev. Gen. Pl. 2, 762, 1891.

B. glabra (Roxb.) A. Camus in Ann. Soc. Linn. Lyon 1930, 76, 164, 1931 et subsp. haenkei (Presl.) Henr. in Blumea 3, 456, 1940.

B. grahamii (Haines) Bor in Grasses Burma, Ceyl. Ind. Pakistan 107, 1960.

B. haenkei (Presl.) Ohwi in Acta Phytotax. Geobot. Kyoto 11, 168, 1942.

B. intermedia var. punctata (Roxb.) Keng in Clav. Gram. Prim. Sin. 249, 1957.

B. inundata (F. Meull.) J. M. Black in Trans. Proc. Roy. Soc. So. Austral. 60, 163, 1936.

B. odorata (Lisboa) A. Camus in Ann. Soc. Linn. Lyon 1930, 76, 165, 1931.

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

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Andropogon grahamii Haines in Kew Bull. 1914, 189, 1914.

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Cytogeography

The meiotic behavior of the chromosomes in the tetraploids is slightly irregular, characterized by occasional univalents, trivalents, and tetravalents. This suggests the plants to be segmental allotetraploids as defined by Stebbins (1947). The low frequency of univalents and multivalents in B. ischaemum complex whose cytological behavior is more or less similar to B. intermedia complex is suggested to be a cause of genome differentiation (Celarier 1957). Further cytological interpretations in the genera Bothriochloa, Capillipedium, and Dichanthium are in favor of autosyndetic or preferential pairing (Borgaonkar and de Wet 1961, Celarier et al. 1961, de Wet et al. 1961).

Thus, the chromosome pairing may be gene controlled. Genic influence on the chromosome pairing is demonstrated by Riley and Chapman (1958) in Triticum vulgare. Formation of tetravalents and trivalents do show some chromosomal homologies between the member of this species complex. Chromosomes may be completely homologous, or homeologous (Kihara and Lilienfeld 1937, Lilienfeld and Kihara 1934), or may only represent a translocated segment. The types of tetravalents usually encountered show a ring type structure indicating chromosomal homologies. Bridges and fragments, on the other hand, do indicate segmental interchange and consequently suggest that structural differences in the chromosomes have been produced. It is also possible that some of the tetravalents represent translocations.

The frequency histograms based upon average numbers of univalents in tetraploid plants indicate more irregularity in B. intermedia X Capillipedium materials than in B. intermedia X Dichanthium. This may indicate a closer relationship of B. intermedia to Dichanthium than to Capillipedium. This is also favored by morphological and anatomical similarities which will be discussed later.

Chromosome number and meiotic behavior of chromosomes suggest that hybridization has taken place in B. intermedia complex. Cytological data in this group often do not provide a means of determining genomic relationships in the manner demonstrated in Nicotiana (Goodspeed 1954), Triticum (McFaden and Sears 1945, 1946, Lilienfeld and Kihara 1934) or Gossypium (Beasley 1940, Stephens 1957). This apparently is due to polyploidy correlated with gene controlled preferential pairing of chromosomes. Harlan and Chheda (1962), however, demonstrate that this mode of chromosome pairing is genetically controlled, and in the homozygous recessive state compulsion for non-homologous pairing breaks down. In these hybrids only closely homologous chromosomes can pair.

The plants included in this complex are represented by tetraploids, pentaploids, hexaploids and one octoploid based on $n=10$. Due to apomixis unreduced female gametes may be fertilized by a reduced male gamete. This is the way a hexaploid could be produced from two tetraploids. The pentaploid on the other hand may have originated when a reduced female gamete of a hexaploid plant is fertilized by a reduced male gamete of a tetraploid plant. The plants with eighty chromosomes may involve an unreduced female gamete of a hexaploid plant and a reduced male gamete of a tetraploid. Due to apomixis the unreduced gamete could be contributed more easily from the female side.

Aneuploids are found in the artifically produced hybrids of Bothriochloa intermedia (Chheda et al. 1961, Borgaonkar, unpublished). However, in the eightly collections studied, no aneuploid could be found, indicating either absence of aneuploidy in nature or its rare occurrence. In case aneuploids are able to compete in nature they should be at least locally common due to apomictic mode of reproduction. It seems, therefore, that plants with incomplete genomic sonstitution are not able to compete with plants having a complete genome.

Cytogeographic data may provide clues to certain important aspects of evolution. Such interpretations, however, are possible only when both diploid and polyploid types are fully understood. When diploids and polyploids of certain genera are found in nature the line of evolution usually starts from the diploids while the higher ploidy levels represent derived forms. This picture has never been read in the reverse order, as the diploids that may be produced by polyploid ancestors are physiologically weak, lethal or sterile and incapable of competition in nature. However, studies in the genera Bothriochloa, Capillipedium, and Dichanthium indicate that the cytologically reduced female gamete may develop parthenogenetically to produce viable offspring (Brown and Emery 1957, Brooks 1958, Celarier and Harlan 1956a, 1958). Harlan et al. (1961) synthesized a polyhaploid derived from a natural hybrid of D. aristatum X D. caricosum which is similar to certain diploids from India showing characteristics of both D. aristatum and D. caricosum. Mehra (1960) through extrapolation suggested certain natural diploids of D. annulatum from India to be polyhaploids. Origin of diploids from polyploids deserves consideration in this group, as there are also records of rather regular meiosis in polyhaploids of other plant groups. Elliott and Wilsie (1948) report a polyhaploid in *Bromus inermis* and Duara and Stebbins (1952) in a hybrid between induced autotetraploid *Sorghum vulgare* var. *sudanense* and tetraploid (2n=40) *S. halepense* where high degree of pollen fertility and comparatively regular meiosis were observed. For these reasons some of the diploids in the *Bothriochloa-Capillipedium-Dichanthium* complex may represent polyhaploids.

Cytologically, the diploid *B. longifolia* has regular meiosis, and 100 per cen pollen fertility. Morphologically *B. longifolia* cannot be placed with any hybrid types, rather it shares certain common features with *B. pertusa*, *B. insculpta* and *B. foulkesii.* Large vascular bundles and thin walled radially arranged epidermis of culm suggest it to be adapted to tropical climates. Geographically *B. longifolia* is confined to Bombay State of India. Here certain other species of this genus are also endemic (Bor 1960) and the tribe Andropogoneae in general also shows concentration in this area (Hartley 1958). Thus the correlative evidence from cytology, anatomy, morphology and geographic distribution all favor the assumption that the species *B. longifolia* should be regarded as a basic species.

It was pointed out earlier, that representative of *B. intermedia* behave cytologically like segmental allopolyploids (Stebbins 1947). Whether the diploid *B. longifolia* could be the direct ancestor seems to be unlikely. However, certain morphological features, and especially the distribution of thin walled radial cells of culm epidermis in the hybrid populations involving *B. intermedia* does suggest a close ancestral affinity with B. longifolia, which is the only known basic species with radially arranged epidermal cells of the culm. The ancestral diploids that gave rise to tetraploid B. intermedia were most probably tropical in origin like B. longifolia. The present day wide distribution of B. intermedia may be an outcome of the aggressive nature of polyploids to new environments. Whether the diploids had a restricted distribution in the geologic time and new areas were taken over after polyploids originated or the diploids were widely distributed and due to change of climate were replaced by the tetraploids would be mere speculation in the absence of fossil records. There exists enormous controversy regarding the distribution of diploids and polyploids and various views are presented by Hagerup (1932), Shimatomai (1933), Tischler (1937), Sokolovskaja and Strelkova (1938), Flovic (1940), Clausen et al. (1945), and Love and Love (1956). Available data show that either diploid or polyploid could extend to extreme ecological habitats. Stebbins (1950), out of one hundred small taxonomic groups studied, found sixty taxa with wider distribution of polyploids than their diploid ancestors, seven with about an equal area, and thirty three others in which diploids occupy a larger area than the polyploids. Faruqi (1961) indicates that polyploid Heliotropium species extend to more recent habitats such as saline soils, sand dunes, and limestone hills, whereas the diploid is reported from ricefield margins. However, no hard and fast rule can be laid down for the distribution and ecological tolerance of polyploids. Cain (1944) and Stebbins (1950) suggest certain generalizations with reservation: Polyploids, in general, have a different geographical distribution than their diploid relatives, and their area of distribution is usually greater than that of the diploids. They are generally adapted to new regions open to colonization, and often show more tolerance to extreme conditions. The polyploid B. intermedia are widely distributed in the tropics and subtropics of Africa, Asia, and Australia, and show a greater ecological plasticity than the known basic diploid.

Anatomy of the Leaf and Culm

Bothriochloa intermedia is characterized by longer primary axis than the longest raceme, secondary branches in the inflorescence are absent and if present only basal racemes are sparcely divided. Anatomically these plants have short cells of leaf epidermis, single or paired, both A and B type prickle hairs, and variable siliceous cells. In the cross sectional view the leaf of B. intermedia has three vascular bundles in the keel, number of bulliform bands between two primary bundles of the lamina are usually two and number of intercalary bundles three to four. Bothriochloa intermedia in the cross sectional view of the culm may be characterized by equidimensional cells with moderate thickenings in the epidermis, such epidermal cells may be interupted by small bands of thin walled, radially elongated cells. However, in the B. intermedia these radial cells are never as numerous as the equidimensional cells. The vascular bundles in this species are grouped into three orders according to their size and are arranged in three rings. The internode is solid.

The diploid B. longifolia is confined to Bombay State of India and among the species of the genus Bothriochloa included in this study it is morphologically similar to Eurasian B. ischaemum and Australian B. ewartiana in the characters of its glume and inflorescence. Narrow siliceous cells and exclusively B type of prickle hairs over the leaf epidermis are characteristic to this species. In the former characteristic it is similar to B. ischaemum and in the latter to both B. ischaemum and B. ewartiana. The similarities in morphology and the preceeding anatomical characteristics suggest a close ancestral relationship among these three species. In B. longifolia the culm epidermis in cross section is mostly made up of thin walled elongated cells which are radial in arrangement. Among all the species studied such an epidermis exclusively composed of these cells is unique in B. longifolia. Such cells are only present in the certain collections of B. intermedia and in some of its suspected natural hybrids, and are absent in all the other species studied. This again points to a close relationship of B. longifolia and B. intermedia. Other important anatomical features of B. longifolia are a hollow internode, large vascular bundles of the culm arranged in three rings, five primary bundles in the keel of the leaf, and well developed mesophyll parenchyma. In general the anatomical attributes of B. longifolia may be correlated with an adaptation to tropical type of climate.

The culm epidermis of B. ischaemum is composed of equidimensional cells with moderate thickenings and the vascular bundle in a single ring, exclusive presence of B type prickle hair and narrow siliceous cells. The assume natural hybrids are more like B. intermedia, however, these hybrids possess a greater frequency of B type prickle hair.

Bothriochloa ewartiana has variable siliceous cells, a flat keel with little mesophyll tissue, numerous intercalary bundles, bulliform cells in 3-4 bands between two primary bundles and usually the vascular bundles of the second order about three in number. All these anatomical features in this species are unique and are also found in the assumed hybrids of B. intermedia X B. ewartiana. Anatomical features in cross section of stem and leaf indicate that though morphological and epidermal similarities do exist between B.

ewartiana, B. ischaemum, and B. longifolia, the Australian B. ewartiana shows marked differences with respect to the internal anatomy of leaf and stem.

Bothriochloa odorata is a species similar to B. intermedia in morphology, and is chaeacterized by being strongly aromatic, unbranched culms, panicle branches divided and number of spikelet pairs per raceme ranges from 15-17. Anatomical characteristics of this species are very similar to B. intermedia except that the leaf epidermis has A type of hair in a greater frequency than B type.

The species distributed in the Caucasus of Russia is B. caucasica. The branches of the panicle in this species are more strongly divided than in B. odorata and the spikelet pairs per raceme range from 10-15 in number. The leaf is devoid of sub-bulliform cells and chlorenchyma cells, though typically panicoid, are somewhat smaller than the other species and slightly regular. Leaf epidermis bears A type of hair and broad siliceous cells. The vascular bundles of the culm are oval, quite small and in two rings. The stem also has a hollow pith. This plant is quite different in a number of anatomical features of leaf and stem from any other species of the genus Bothriochloa.

Capillipedium spicigerum is characterized by two bands of bulliform cells in the lamina, sub-bulliform cells present, and keel with ample of meso-phyll-tissue. The culm in the same way has vascular bundles in three rings. In all these characteristics both B. intermedia and D. annulatum are similar to C. spicigerum. Taking all these characters into account B. intermedia, B. longifolia, C. spicigerum and D. annulatum show many more common features than B. intermedia or B. longifolia share with any other species of the genus Bothriochloa studied. From the point of view of ecological phytogeography B. intermedia, B. longifolia, D. annulatum and C. spicigerum are all tropical or sub-tropical in distribution whereas B. caucasica, and B. ischaemum are distributed in comparatively colder or drier regions of the world. Therefore it seems that ecological adaptation has played an important role in the anatomical modifications of stem and leaf, and do not always indicate clearly phylogenetic relationships. However, leaf epidermis is in accord with morphology and seems to be less affected by ecological adaptation. Narrow siliceous cells in B. ischaemum and B. longifolia and B type hair in B. ischaemum, B. longifolia, and B. ewartiana are also correlated with morphological similarities, whereas these three species are distributed in completely different ecogeographical situations. In the same way, presence of A type prickle hair in B. caucasica, both A and B type in B. odorata with type A more frequent than type B, may be used to show the relationship of these two species of the Bothriochloa to C. spicigerum and C. parviflorum. The suspected natural hybrids of B. intermedia X C. parviflorum are also like B. odorata in the characteristic of the siliceous cells.

The leaf epidermis of D. annulatum with respect to short cells and bicellular microhairs is very characteristic. Short cells are 4-5 in a row and longer than broad in contrast to 1-2 and broader than long in the species of Bothriochloa and Capillipedium studied. The assumed natural hybrids of B. intermedia X D. annulatum have short cells 1-5 in a row and longer than broad.

In conclusion, there are limitations as to the use of leaf and culm anatomy to demonstrate relationships within this group of plants. Nevertheless, certain anatomical features are of more value than others, and in this respect leaf epidermis should be regarded as a good criterion to use. However, to demonstrate natural hybridization, the anatomy of both culm and leaf are of significance. The parental species and hybrids can be identified with the same confidence as with the help of morphology. Following is a key by which parents and assumed natural hybrids of B. intermedia complex can be identified.

1. Number of primary bundles in the keel five.

    2. Siliceous cells of leaf epidermis twice as long as broad, culm epidermis mainly composed of thin walled radial cells ..... B. longifolia

    2. Siliceous cells of leaf epidermis less than twice as long as broad, culm epidermis with no radial cells.

        3. Prickle hairs of leaf epidermis A type and long cells pitted ..... B. odorata

        3. Prickle hairs of leaf epidermis both A and B type, and long cells unpitted ..... B. intermedia X C. parviflorum

1. Number of primary bundles in the keel less than five.

    4. Number of primary bundles in the keel three.

        5. Siliceous cells of leaf epidermis twice as long as broad, in culm, epidermis with no radial cells and vascular bundles in a single ring ..... B. ischaemum

5. Siliceous cells of leaf epidermis less than twice as broad, in culm, epidermis with or without radial cells and vascular bundles in three rings.

6. In leaf epidermis, short cells 1-2, broader than long.

7. Both A and B type prickle hairs present.

8. B type prickle hair more frequent than A type

B. intermedia X B. ischaemum

8. B type prickle hair as common as A type

B. intermedia

7. Only A type prickle hairs present C. spicigerum

6. In leaf epidermis, short cells up to five and longer than broad.

9. Short cells 4-5 in a row, and basal cell of bicellular micro-hair 3/4th as long as distal cell D. annulatum

9. Short cells 1-5 in a row, and basal cell of bicellular micro-hair less than 3/2 as long as distal cell

B. intermedia X D. annulatum

4. Number of primary bundles in the keel only one.

10. Sub-bulliform cells present.

11. Leaf with flat keel, number of bulliform cell bands between two primary bundles generally four, and vascular bundles of culm in a single ring B. ewartiana

11. Leaf with more or less flat keel, number of bulliform bands between two primary bundles generally four, and vascular bundles

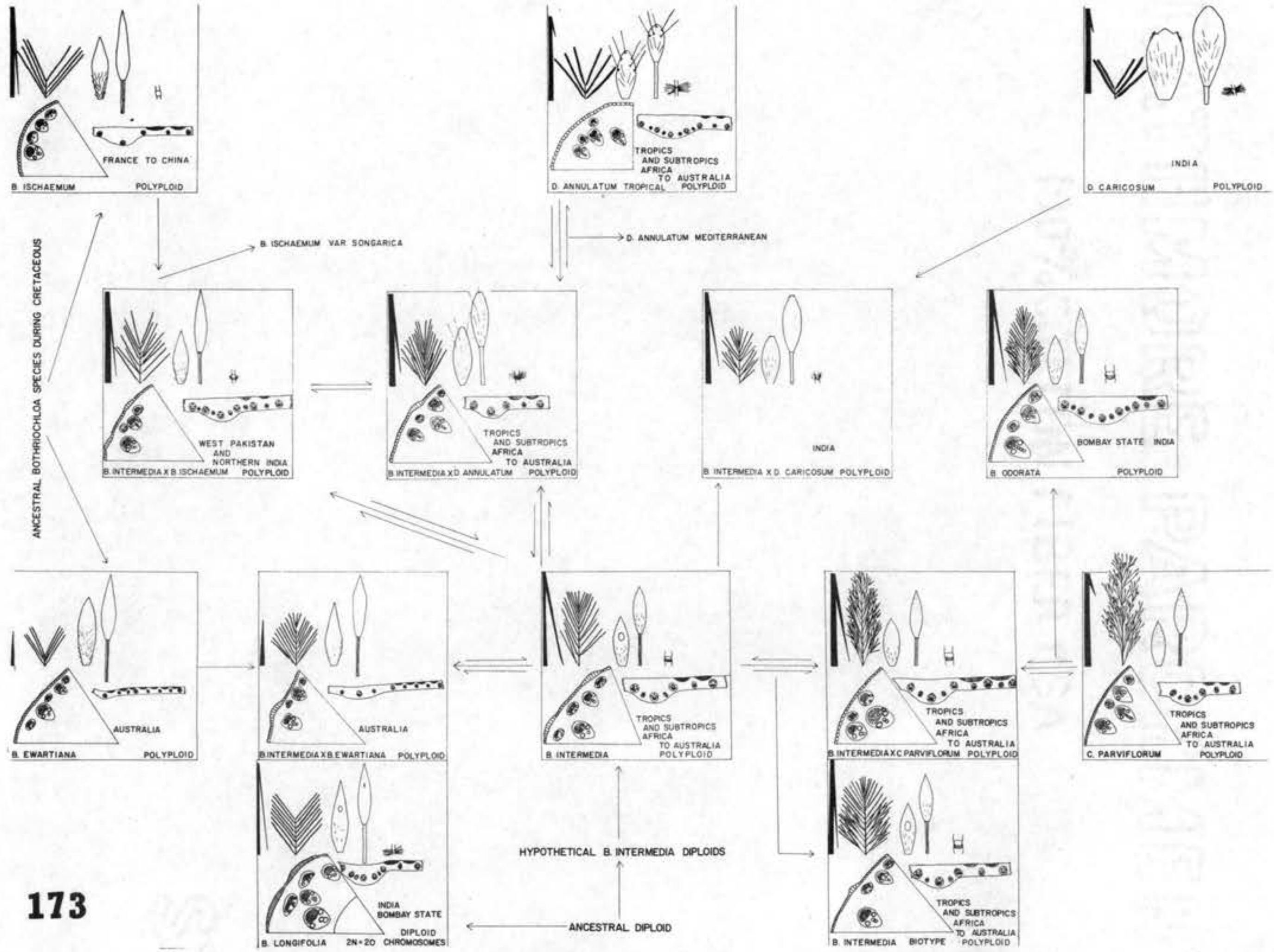
of culm in three rings B. *intermedia* X B. *ewartiana*

10. Sub-bulliform cells absent B. *caucasica*

The evolutionary potential through hybridization in the B. *intermedia* complex is presented in the Figure 173 by combining the evidence from gross morphology, anatomy, cytology, and geographic distribution.

LEGEND TO THE FIGURE 173.

A diagramatic representation of the *B. intermedia* complex illustrating variation, range of hybridization and evolution on the basis of correlative evidence of morphology, anatomy, cytology, and geographic distribution.



B. ISCHAEMUM
FRANCE TO CHINA
POLYPLOID
D. ANNULATUM TROPICAL
TROPICS AND SUBTROPICS AFRICA TO AUSTRALIA
POLYPLOID
D. CARICOSUM
INDIA
POLYPLOID
B. ISCHAEMUM VAR SONGARICA
D. ANNULATUM MEDITERRANEAN
ANCESTRAL BOTHRIOCHLOA SPECIES DURING CRETACEOUS
B. INTERMEDIA X B. ISCHAEMUM
WEST PAKISTAN AND NORTHERN INDIA
POLYPLOID
B. INTERMEDIA X D. ANNULATUM
TROPICS AND SUBTROPICS AFRICA TO AUSTRALIA
POLYPLOID
B. INTERMEDIA X D. CARICOSUM
INDIA
POLYPLOID
B. ODORATA
BOMBAY STATE INDIA
POLYPLOID
B. EWARTIANA
AUSTRALIA
POLYPLOID
B. INTERMEDIA X B. EWARTIANA
AUSTRALIA
POLYPLOID
B. INTERMEDIA
TROPICS AND SUBTROPICS AFRICA TO AUSTRALIA
POLYPLOID
B. INTERMEDIA X C. PARVIFLORUM
TROPICS AND SUBTROPICS AFRICA TO AUSTRALIA
POLYPLOID
C. PARVIFLORUM
TROPICS AND SUBTROPICS AFRICA TO AUSTRALIA
POLYPLOID
B. LONGIFOLIA
INDIA BOMBAY STATE
DIPLOID
2N=20 CHROMOSOMES
HYPOTHETICAL B. INTERMEDIA DIPLOIDS
ANCESTRAL DIPLOID
B. INTERMEDIA BIOTYPE
TROPICS AND SUBTROPICS AFRICA TO AUSTRALIA
POLYPLOID

173

Anatomy of the Glume Pit.

The glume pits in the genus Bothriochloa originate as a result of activities of some epidermal cells which do not differentiate into normal epidermis due to a change in the direction of growth. These cells show a pronounced growth at right angles to the long axis. This change in the direction of growth is not an abrupt activity where epidermal cells outside the pit are normal and inside are different. Rather, this change is gradual and the cells at the margin of the pit and also at the outside show a transition from radially developed thin walled pit cell to elongation in the long axis and thick walls. In the terms of development and biochemical action of genes two processes may be observed that bring about the change from the normal epidermis with three types of cells, to uniform cells of the pit through more or less uniform cells of the pit margin. The first action may be a neutralization of inhibitory effect of the genes responsible for pitting, upon the enzymes responsible for the production of normal epidermis. The cells at the margin of the pits may represent this stage. The other effect of these genes is in the modification of epidermal cells into pit cells. The pit cells of B. intermedia are variable in shape, size and their number. Thus pits are not only present or absent as observed in B. barbinodis by Gould (1959), rather they may be only few-celled with no depression to fully developed pits. Such a variation may be observed in a single raceme of heterozygous B. intermedia and in its hybrids. On the other hand there is a great deal of uniformity in the species B. decipiens and B. pertusa. By crossing the irregularly pitted B. intermedia A-5297 with the nonpitted 56-X-750, the hybrid 58-X-571b-2 was produced. Pit cells in this hybrid are highly specialized. The nonpitted hybrid 56-X-750 is a product of B. intermedia gangetica 5450 and B. intermedia (Table V). On the other hand the hybrid 58-X-696-3 which is also a product of a similar cross as 56-X-750 has quite unspecialized pit cells (Table V). From the study of morphology the assumed natural hybrids of B. intermedia X B. ischaemum, B. intermedia X D. annulatum, and B. intermedia X C. parviflorum are all nonpitted. All this evidence suggest that pitting is controlled by a number of genes which are recessive in nature, and which, in the absence of a complete homozygous set, need certain specific requirements for their expression.

Pit cells have dense cytoplasm, prominent nuclei and thin walls. Associated with these structures certain crystals are also present, which seem to be mostly composed of inorganic material as they are unchanged even under intense heat of direct flame. Though the veins do not terminate in these pits, like the known hydathodes, association of these crystals and appearance of water in the pits are fair indications that the pit cells are secretory in nature and may function as hydathodes in the general sense of the word. Prominent nuclei and dense cytoplasm (Esau 1953) further support this hypothesis.

Blatter (Bor 1960) indicates the presence of a viscous liquid in the glume pit of D. panchganiense and suggested it to play a role in pollination. Heslop-Harrison (1961) demonstrates that in B. decipiens the glume pit acts as an obturator in clastogamous flowers, preventing the exertion of the anther and causing its dehiscence in contact with the stigmas.

TABLE V

FREQUENCY OF PITS IN THE PARENTS AND HYBRIDS OF BOTHRIOCHLOA

Name of species or hybrid	Pits	Accession or hybrid number
B. decipiens	++	A-5701-1
B. pertusa	++	A-3704-1
B. intermedia	+-	A-5297a
B. intermedia	+-	A-5297b
B. intermedia gangetica	-	A-2655
B. intermedia gangetica	-	A-5450
56-X-750-1	-	*B. intermedia* X *B. intermedia* gang A-5450
58-X-421a-1	-	*B. intermedia* A-2655 X B. *intermedia* A-5297
58-X-271b-2	+-	56-X-750-1 X *B. intermedia* A-5297
58-X-433a-1	+-	56-X-750-1 X 58-X-421a-1
58-X-696-3	+-	*B. intermedia* A-5297 X *B. intermedia* A-5450

++ Pits present regularly on each sessile spikelet of the inflorescence.
+- Pits present on some spikelets and absent on others.
- Pits absent.

SUMMARY

A detailed study of the polymorphic B. intermedia complex regarding morphological variations, anatomical characteristics and cytological behavior of chromosomes in meiosis was undertaken in an attempt to explain the range of variation characteristic of this group.

Both morphology and anatomy suggest that in the Gangetic plains of India, B. intermedia hybridizes with D. annulatum. Evidence of hybridization is also found between B. intermedia and C. parviflorum wherever they overlap. However, hybridization between these taxa seems to be more frequent in Australia, than in India or Africa.

In West Pakistan and northern India B. intermedia hybridizes with B. ischaemum and these hybrids probably also cross with other hybrid derivatives.

B. intermedia also hybridizes with B. ewartiana which is exclusively Australian in distribution.

The study has thrown some light on the origin and taxonomic position of certain classically recognized species. In this respect B. glabra is supposed to have originated by backcrossing of B. intermedia X C. parviflorum hybrids with B. intermedia. In the same way the Indian species B. odorata seems to be a product of hybridization between B. intermedia with Capillipedium parviflorum. Morphologically B. caucasica is more like Capillipedium than Bothriochloa. Leaf epidermis and anatomy are also similar to Capillipedium, and B. caucasica would better fit with the genus Capillipedium, than with Bothriochloa.

The cytological studies have shown tetraploids with 2n=40 chromosomes to be the most common chromosome race. However, pentaploids, hexaploids, and one octoploid are also reported. Higher ploidy level plants are more common in Australia, and the single octoploid also comes from this continent. No matter which hybridization group the plants belong to, the nature of chromosomal abnormalities in meiosis, indicates segmental-allopolyploidy and preferential pairing of chromosomes. Higher ploidy level plants, however, show slightly higher frequencies of chromosomal abnormalities.

The diploid B. longifolia is a meiotically regular plant and is confined to Bombay State of India. This species, though more closely related to some other species of the genus Bothriochloa shows certain morphological and anatomical features unique to B. intermedia as it is known today. In this respect it seems that the diploids that gave rise to B. intermedia must have had a close relationship with B. longifolia.

The glume pits are variable in their morphology and anatomy. Anatomical studies suggest glume pits to be secretory in nature. Inheritance of glume pit in the genus Bothriochloa seems to be controlled by a number of genes which are recessive and need certain specific requirements for their expression.

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APPENDIXES

CYTOLOGICAL DATA OF *Bothriochloa intermedia* COMPLEX

CHROMOSOME CONFIGURATIONS*

A. No.	Location	2n	I	II	III	IV	Bridges	Fragments	Dividing laggards	Non-dividing laggards
50	**Australia**	50	6.66	19.88	0.44	0.55	0.21	0.64	0.92	1.92
			3-10	18-22	0-2	0-1	0-2	0-4	0-3	0-8
52	Australia	50	4.68	19.84	0.26	1.21	0.35	0.42	2.14	0.42
			0-10	15-22	0-2	0-3	0-2	0-2	0-6	0-4
503	Queensland, Aust.	50	6.07	20.61	0.23	0.53	0.34	0.34	2.86	1.56
			4-10	19-23	0-1	0-2	0-2	0-3	0-9	0-5
1337	Tiflis, Russia	40	----	-----	----	----	----	----	----	----
2560	U.S.A. Introduced	40	5.87	15.12	0.25	0.68	1.35	0.21	2.21	0.07
			2-10	14-19	0-1	0-2	0-4	0-3	0-8	0-1
2561	U.S.A. Introduced	40	----	-----	----	----	----	----	----	----
2651	E. Africa	40	2.37	18.75	0	0	0.15	0.63	0.57	0.78
			0-6	17-20			0-1	0-2	0-3	0-3
2654	Coimbtore, India	40	0.90	18.22	0	0.63	0	0	0.43	0.30
			0-4	15-20		0-2			0-4	0-2
2655	British Guiana Introduced	40	2.08	18.88	0	0.04	0.11	0.05	1.52	0.41
			0-4	15-20		0-1	0-1	0-1	0-6	0-3

*Range and average listed

A. No.	Location	2n	I	II	III	IV	Bridges	Fragments	Dividing laggards	Non-dividing laggards
3726	Sydney, Australia	40	6.61	16.07	0	0	0.30	0.04	5.00	0
			2-10	13-19			0-1	0-1	4-6	
3965	Calcutta, India	40	0.47	18.30	0.04	0.69	0	0	0.20	0.13
			0-4	16-20	0-1	0-2			0-1	0-2
4006	England, Intrd.	40	----	-----	----	----	----	----	----	----
4021-b	Ceylon	40	1.40	19.15	0.05	0	0.61	0.14	0	0.66
			0-4	16-20	0-2		0-4	0-3		0-4
4028	Mt. Abu, India	40	1.45	19.61	0	0.04	0	0	2.26	0.06
			0-4	18-20		0-1			0-5	0-2
4087	U.S.A. Intrd.	40	0.54	19.54	0	0.09	0.14	0	0.50	0.14
			0-4	18-20		0-1	0-1		0-2	0-1
4088	U.S.A. Intrd.	40	5.13	15.60	0.60	0.86	0	0	3.95	0.10
			2-10	11-18	0-1	0-2			0-9	0-1
4090	South Africa	40	0.92	18.84	0.15	0.30	0.04	0	0.28	0.28
			0-3	15-20	0-1	0-1	0-1		0-2	0-1
4293	Trinidad, British West Indies	60	9.11	24.11	0.44	0.33	0.05	0	2.77	0.16
			2-12	21-29	0-1	0-1	0-1		0-14	0-2
4393	Dehra Dun, India	40	0.66	19.04	0.08	0.25	0	0	0.62	0
			0-2	18-20	0-1	0-1			0-2	

A. No.	Location	2n	I	II	III	IV	Bridges	Fragments	Dividing laggards	Non-dividing laggards
4394	Dehra Dun, India	40	1.10	15.35	1.15	1.25	0	0	0	0
			0-4	9-19	0-2	0-2				
4596	Galton, Australia	60	11.42	24.42	----	----	0.12	0.04	9.40	0.36
			6-22	18-27			0-1	0-1	3-14	0-2
4597	Galton, Australia	60	5.70	27.15	----	----	0.08	0.08	7.66	0.16
			4-8	26-28			0-1	0-1	1-17	0-2
4607	Lowes, Australia	80	8.27	31.13	0.36	1.95	0.28	0.32	8.76	0.04
			3-16	27-34	0-2	0-5	0-1	0-2	6-15	0-1
4633	Quezon, Philippines	40	0.57	18.14	0	0.78	0	0	0.33	0.66
			0-2	16-20		0-2			0-1	0-2
4806-b	Hyderabad, India	40	1.52	19.23	0	0	0.92	0	0.64	0.07
			0-4	18-20			0-2		0-4	0-1
4896	U.S.A. Intrd.	50	6.00	19.20	0.71	0.64	1.17	0.94	4.05	0.41
			2-10	14-23	0-2	0-2	0-4	0-4	0-8	0-4
5168-b	South Africa	40	----	-----	----	----	----	----	----	----
5297	Lohnavla, India	40	0.50	19.02	0.09	0.35	0	0	1.33	0.16
			0-4	16-20	0-1	0-2			1-3	0-1
5312-b	Dehra Dun, India	40	1.87	19.06	0	0	0.05	0.05	0.47	0.21
			0-6	17-20			0-1	0-1	0-2	0-1

A. No.	Location	2n	I	II	III	IV	Bridges	Fragments	Dividing laggards	Non-dividing laggards
5400	Hempur, India	40	0.40	19.40	0	0.2	0	0	1.50	0
			0-2	18-20		0-1			1-2	
5400-b	Hempur, India	40	0.40	19.40	0	0.2	0	0	0	0
			0-4	18-20		0-1				
5400-d	Hempur, India	40	4.40	17.80	0	0	0.09	0.27	2.00	1.09
			0-12	14-20			0-1	0-2	0-4	0-4
5401-a	Lohnavla, India	40	1.00	15.10	0.50	1.70	0.35	0.28	0.14	0
			0-3	11-18	0-1	0-3	0-2	0-3	0-1	
5404	New Delhi, India	40	0.34	19.40	0.02	0.06	0.04	0	0.52	0.09
			0-4	18-20	0-1	0-1	0-1		0-6	0-1
5408	Bareily, India	60	5.80	26.50	0.35	0	0.42	0	3.85	0.09
			2-13	22-29	0-2		0-4		0-10	0-1
5409	Bareily, India	40	3.00	16.91	0.28	0.64	0.30	0.61	1.30	1.84
			1-4	14-19	0-1	0-2	0-1	0-4	0-3	0-12
5410-b	Punjab, India	40	0.35	17.83	0	1.00	----	----	----	----
			0-2	12-20		0-4				
5450	Delhi, India	40	1.88	18.94	0	0.06	0.06	0	1.43	0.37
			0-6	17-20		0-1	0-1		0-4	0-2
5470	Kenya, Africa	40	3.52	17.43	0.05	0.31	0	0.05	0.10	0.21
			0-8	15-20	0-1	0-2		0-1	0-1	0-3

A. No.	Location	2n	I	II	III	IV	Bridges	Fragments	Dividing laggards	Non-dividing laggards
5592	Fiji Islands	40	1.16 0-4	18.74 17-20	0	0.33 0-1	0	0	1.29 0-4	0.29 0-2
5752	Kedah, Malaya	40	1.84 0-6	14.31 9-18	0	2.38 0-5	0	0	1.50 0-4	0.50 0-1
5800	Mayaquez, Porto Rico	60	5.50 5-6	20.50 20-21	0.50 0-1	3.00 3	0.10 0-1	0.10 0-1	2.50 1-5	0.10 0-1
5803	Queensland, Aust.	50	4.30 0-8	19.60 17-23	0.30 0-1	1.50 0-2	0.12 0-1	0	6.12 0-10	1.37 0-7
5803-b	South Queensland, Australia	50	3.91 0-6	21.75 20-25	0.25 0-1	0.50 0-2	0.11 0-2	0	2.27 0-7	0.05 0-1
6136	Queensland, Aust.	60	----	-----	----	----	----	----	----	----
6137	Queensland, Aust.	60	9.00 6-12	25.30 23-27	0	0.10 0-1	0.27 0-2	1.50 0-8	4.55 0-10	1.22 0-5
6138	Queensland, Aust.	60	3.06 0-6	28.20 27-30	0.20 0-1	0.06 0-1	0	0	3.00	0
6149	Delhi, India	40	2.00 0-4	18.89 17-20	0	0.05 0-1	0.23 0-2	0.04 0-1	0.57 0-2	0.61 0-4
6176-b	West Bengal, India	40	2.56 0-6	18.15 15-20	0.23 0-1	0.15 0-1	0.40 0-2	0.20 0-2	0.33 0-3	0.20 0-2

A. No.	Location	2n	I	II	III	IV	Bridges	Fragments	Dividing laggards	Non-dividng laggards
6265	Mayaquez, Porto Rico	50	3.61 0-8	21.28 16-24	0.05 0-1	0.94 0-3	0	0	2.00 1-4	0.07 0-1
6363	U.S.A. Intrd.	40	6.14 2-10	14.57 13-18	0.14 0-1	1.07 0-2	0.06 0-1	0	4.62 3-11	0
6482	Laguna, Philippines	40	3.00 0-10	18.56 15-20	----	----	0.05 0-1	0.05 0-1	1.05 0-5	0.27 0-2
6511	Australia	40	1.75 0-4	19.25 18-20	0	0	0	0	0	0.25 0-2
6551	U.S.A. Intrd.	40	1.76 0-6	19.18 17-20	0	0	0	0	0.18 0-3	0.18 0-2
6573-b	Afghanistan	40	1.33 0-2	18.00 14-20	0.24 0-1	0.52 0-2	0.08 0-1	0.56 0-3	0.08 0-1	0.20 0-2
6580	India	40	0.52 0-2	16.32 14-19	0.04 0-1	1.68 0-3	0	0	0	0
6841	Delhi, India	50	7.00 6-8	18.50 17-20	0	1.50 1-2	----	----	----	----
6864	Delhi, India	40	1.25 0-4	19.37 18-20	0	0	0.50 0-3	0.70 0-3	0.80 0-4	0.55 0-2

A. No.	Location	2n	I	II	III	IV	Bridges	Fragments	Dividing laggards	Non-dividng laggards
7010	Palampur, India	40	0.53 0-4	15.94 14-18	0.13 0-1	1.80 0-3	0	0	1.2 0-2	0
7030	Pretoria, South Africa, Intrd.	40	3.71 0-8	18.14 16-20	0	0	3.23 0-6	0.76 0-4	2.29 0-6	0.23 0-4
7154	Delhi, India, Intrd.	40	3.12 0-6	16.48 13-19	0.28 0-2	0.76 0-2	0.50 0-1	0	2.75 1-9	0
7176	Mindanao, Philippines	40	3.28 0-6	18.42 17-20	0	0	0.38 0-3	0	2.08 0-8	0.15 0-1
7232	Poona, India	40	3.38 0-7	14.85 10-17	0.46 0-2	1.42 0-4	0	0	3.50 0-6	0.10 0-1
7457	U.S.A. Intrd.	40	5.18 2-10	16.36 14-19	0.09 0-1	0.36 0-1	1.08 0-4	1.17 0-6	2.12 0-10	0.54 0-5
7460	U.S.A. Intrd.	40	----	-----	----	----	----	----	----	----
7544	South Africa	40	0	17.63 14-20	0	1.16 0-3	0	0	1.00 0-2	0
7547	Sydney, Australia	40	1.29 0-4	18.33 16-20	0	0.50 0-1	0	0	0	0.5 0-1
7548	Sydney, Australia	40	2.00	17.00	0	1.00	----	----	----	----

A. No.	Location	2n	I	II	III	IV	Bridges	Fragments	Dividing laggards	Non-dividng laggards
7549	Sydney, Australia	40	1.78	16.63	0.53	0.84	0	0	2	0
			0-7	11-19	0-3	0-2			1-3	
7550	Sydney, Australia	40	0.90	19.55	0	0	0.04	0	0.80	0.42
			0-2	19-20			0-1		0-5	0-4
7551	Sydney, Australia	40	0.96	17.61	0.04	0.92	----	----	----	----
			0-5	12-20	0-1	0-3				
7554	Australia	50	7.66	17.22	0.55	1.55	0.09	0.09	5.18	0
			5-10	15-20	0-2	0-3	0-1	0-1	3-8	
7555	New Guinea	40	1.83	17.95	0.08	0.50	----	----	----	----
			0-4	12-20	0-2	0-2				
7556	New Guinea	40	1.00	19.33	0	0.08	0	0	0.23	0.38
			0-4	18-20		0-1			0-2	0-2
7557	New Guinea	40	1.00	18.44	0	0.50	0	0	0.42	0.07
			0-2	15-20		0-2			0-2	0-1
7597	Sydney, Australia	60	----	-----	----	----	----	----	----	----
7699	Kenya, Africa	40	1.66	19.16	0	0	0	0.33	1.00	0.33
			0-4	18-20				0-2	0-4	0-2
7700	South Africa	40	7.46	16.26	0	0	0	0	3.31	0.42
			0-14	13-20					0-6	0-2

A. No.	Location	2n	I	II	III	IV	Bridges	Fragments	Dividing laggards	Non-dividng laggards
7765	New Guinea	40	2.42 0-4	18.89 18-20	0	0	0.50 0-2	0.30 0-3	0.95 0-4	0.60 0-3
8295	Malavali, India	40	3.23 0-6	17.82 14-20	0.16 0-1	0.27 0-2	0.15 0-1	0.10 0-1	1.10 0-4	0.10 0-1
8297	Nagpur, India	40	2.50 0-4	18.21 18-19	0	0.25 0-1	0.31 0-3	0.31 0-3	0.93 0-6	0.25 0-1
8298	Poona, India	20	0.26 0-2	9.96 9-10	0	0	0	0	0	0
8300	Sangamner, India	20	0.46 0-2	9.79 9-10	0	0	0	0.18 0-2	0	0
8301	Poona, India	20	0.20 0-2	9.90 9-10	0	0	0	0	0	0

VITA

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