THE
APPLICATION OF
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TO
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IMPROVEMENT

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FOREWORD

By nature I am a practical man, and I have derived great inspiration from the opportunities I have had to apply genetic knowledge to the problems of crop plant improvement. Both the genetic knowledge and the opportunities to apply it have arisen during my service with the Empire Cotton Growing Corporation, and I take this opportunity to acknowledge my indebtedness to these most enlightened employers.

No one who works on cotton and has not visited the United States Cotton Belt can consider his education complete. I am, therefore, greatly indebted to the National Cotton Council of America and to the Division of Biological Sciences of North Carolina State College, Raleigh, North Carolina, for a joint invitation to tour the United States Cotton Belt and to lecture in the Genetics Faculty at North Carolina State College in the summer of 1954. On the tour I met, in their own fields and laboratories, fellow research workers long known in correspondence. In the Genetics Faculty at Raleigh I had a greatly valued opportunity for discussion of the evolutionary background to cotton breeding problems. These made the American visit a remarkable occasion, for which I should like to express my thanks. What follows is based on the lectures delivered at North Carolina State College, with such additions as have seemed suitable in the light of the work in progress at Namulonge in the years that have elapsed since the lectures were given.

The natural starting-point for a discussion of the world's cottons is Sir George Watt's *Wild and Cultivated Cotton Plants of the World*. He published that classic monograph in 1907, and he made in his introduction an apology that is as valid today as it was in 1907. He wrote:

But as that story [of the Indian cottons] advanced from year to year I found many occasions not only to arrive at conclusions opposed to

those held by many of my predecessors, but to modify and abandon views previously entertained, and even published, by myself....Let me hasten, therefore, to add that I cannot hope to have even now attained finality; but shall be abundantly satisfied if I have succeeded in throwing out suggestions that may tend to elucidate practical results, both commercially and botanically.

Much further progress has been made since 1907 in the study of the cottons, and it is the findings of these fifty years that will be discussed here. It is, however, one of the lasting satisfactions of the genus *Gossypium* that it continues to offer as fascinating a range of problems to the inquirer as were apparent when Sir George Watt summarised the knowledge he had then amassed.

<div style="text-align: right">J. B. H.</div>

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THE RELATIVES OF THE COTTONS

The cotton of commerce is the produce of four species of the genus *Gossypium*. The history and relationships of these four species should be considered primarily with reference to the considerable range of wild species that also belong to *Gossypium*, but some reference must also be made to the genera of the small sub-tribe of the Hibisceae (Edlin, 1935) to which *Gossypium* is related. The collection and study of the wild species of *Gossypium* has gone on for many years. Many were known to Watt as herbarium material, but the acquisition of seed and the establishment of a living collection on which cytogenetic studies could be conducted was only undertaken at a later date. The wild species are all xerophytic, and are generally to be found in rather inaccessible places. Though Kearney, working in Arizona for the United States Department of Agriculture, had some of the American wild species in cultivation in 1926, the acquisition and establishment in a living collection of all those recorded in the botanical literature was not completed until 1949. Even now, it may well be that there remain some undescribed species to be collected in the American region, and quite recently (March 1955) one new species (*G. longicalyx*, Hutchinson & Lee, 1958) was collected in central Tanganyika, and another in the Aden Protectorate.

These wild species are not only inaccessible. Most of them are rare, some very rare indeed. Their rarity, the wide distinctions between them, and the very limited variability to be found within them, have led to the conclusion that they are all of relic status, and may be without the genetic versatility necessary for further evolutionary success. As is so often the case, generalisations are misleading, and though many of the species are restricted in both numbers and distribution, there

are some that must be regarded as well adapted and successful over a considerable range of desert climates.

All the wild species examined in culture save one (*G. tomentosum*) have proved to be diploid, with thirteen pairs of chromosomes. They fall into four natural cytogenetic groups, to which Beasley (1942) assigned the letters *B* to *E*. In general, crosses between species of the same group are fairly easily made. In the F_1 hybrids chromosome pairing is normal or nearly so, and at least some viable gametes are formed. Crosses between species of different groups are difficult to make and often fail completely. If F_1 hybrids are obtained, they exhibit reduced chromosome pairing, and are usually completely sterile.

The *B* group consists of two species, *G. anomalum* and *G. triphyllum*, that are native in desert regions in Africa. *G. anomalum* is widespread on the southern borders of the Sahara, occurring in a range of habitats in the five- to twenty-inch rainfall belt. Smith (1950) has shown that the perennial shrubs and trees of the dry Sudan region occur over such a belt, the ecological situation occupied changing with changing rainfall so that a roughly equivalent moisture regime is experienced wherever the plant grows. Thus, in the northern Sudan where the annual rainfall is five inches per annum, *G. anomalum* is to be found on the tops of dry rocky hills or jebels such as Gebel Merkhayat a few miles from Omdurman. Smith regards the jebel crests as the 'moist habitat' of the region, for there a plant may become established above a fissure in the rock where some moisture is accumulated. In fact, mature plants of *G. anomalum* are confined to such situations, and in the dry weather following good rains, seedlings that have failed to tap a deep source of moisture may be seen dying in considerable numbers. Further south, according to Smith, equivalent moisture conditions are to be found on the clay plains in the twenty-inch rainfall belt in Kordofan, and there *G. anomalum* is found in hollows where water accumulates after rain. That *G. anomalum* is no relic on the verge of extinction is shown by the frequency with which it has been collected in the Sudan in

recent years, and by Chevalier's (1935) record that in parts of the French Sudan it is the main food of camels. The species also occurs in dry regions in the southern parts of Angola and in South-west Africa, in a form scarcely distinguishable from the northern type. There, also, the related *G. triphyllum* grows. *G. triphyllum* does not appear to be common, though it has been collected not infrequently.

The species of the *E* group are distributed over the deserts from Sind to the Sudan, and south to central Tanganyika. Only one of them, *G. somalense*, is at all common, but this has been collected over a great area from northern Kenya, through Somalia and British Somaliland to the Sudan and the north-eastern border of French Equatorial Africa. It is sufficiently variable in Somalia to have been described under five specific names. Elsewhere it is fairly uniform. Of the other species, *G. stocksii* is rare, though it has been collected in Sind, in the mountains of Dhofar, and in Somalia and British Somaliland. *G. areysianum* is confined to a very limited area in the Aden Protectorate. Two other species belong morphologically to this group, though their cytological relationships have not yet been studied. *G. longicalyx* (Hutchinson & Lee, 1958) was discovered in 1955 by Disney near Dodoma in central Tanganyika, and a plant that has been described as *Cienfugosia incana* O. Schwartz, but is certainly a *Gossypium* and morphologically one of the Stocksiana, has been collected in several places from Meifa to Ras Fartak on the coast of southern Arabia in the Aden Protectorate.*

Two Australian species, *G. sturtii* and *G. robinsonii* make up the *C* group. Both are desert plants. The former has been recorded from widely scattered localities in central and south-eastern Australia. The latter is only known from north-western Australia, and is so rare that it was not collected for more than fifty years after the original record in about 1865.

The species found on the western side of Central and South

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* I am indebted to Miss D. Hillcoat for this information. The specimens are in the British Museum herbarium.

America are included in the *D* group. This is the most diverse, and includes the most species, of any in the genus. *G. thurberi,* which occurs in mountain valleys in Arizona and northern Mexico, is the only wide-ranging species with a large population and appreciable variability. Most of the other species are only to be found in small areas, and with very limited populations. A new species, *G. lobatum,* has recently been described from Michoacan, Mexico, by Gentry (1956) and it is not unlikely that other rare, undescribed species exist in western Mexico.

Of the cultivated species, *G. herbaceum* is the cotton of Africa and western and central Asia, and *G. arboreum* the cotton of India, South-east Asia, and the Far East. Both are diploids and belong to Beasley's *A* group. The *A* and *B* groups are related, and crosses between *G. arboreum* and *G. herbaceum* on the one hand and *G. anomalum* on the other are easily made, and give F_1 hybrids in which the chromosome pairing is good, and some viable gametes are formed (Silow, 1941). The *A* and *B* groups are the only two between which fertile hybrids have been made. The species are, in fact, so closely related that they would probably have been regarded as belonging to a single group, had it not been for the vast difference in evolutionary status between the uniform, static wild species and the highly variable, expanding crop plants.

The two cultivated species of the New World and the wild Hawaiian *G. tomentosum* are allopolyploids. There is no reason to postulate more than a single origin for allopolyploidy (see Gerstel & Sarvella, 1956). The allopolyploid complement has been shown to be made up of one chromosome set homologous with the *A* set of the Old World cottons, and one homologous with the *D* set of the wild New World species. The wild species, *G. tomentosum,* is confined to Hawaii. The two cultivated species are *G. barbadense,* the South American cotton, and *G. hirsutum,* which is of Central American origin. Both species have spread widely in the New World and beyond, and in recent times *G. hirsutum* has invaded extensive areas formerly occupied by the Old World diploid species.

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Three other genera of the sub-tribe, *Thespesia*, *Gossypioides*, and *Cienfugosia*, are well enough known for comparisons to be made with *Gossypium*. Of these, *Thespesia* is of particular interest in that it appears to be the one most closely related to *Gossypium*. All species examined have a chromosome number of $n = 13$, the basic number in *Gossypium*, and one species, *Thespesia lampas*, is close enough to show some genetic evidence of relationship. When used as a pollen parent on *Gossypium anomalum*, capsules are occasionally developed, and seeds are formed. The seeds, however, are invariably empty (Hutchinson, 1947).

Exell & Hillcoat (1954) have recently proposed the fragmentation of *Thespesia* into five very small genera. To do so obscures the relationships of the species, and also the existence of parallel evolutionary trends throughout the sub-tribe. The genus *Thespesia* will, therefore, be taken to include the species assigned to it by Hutchinson (1947) with the addition of Exell and Hillcoat's *Thespesiopsis mossambicensis* and Exell & Mendonca's (1954) *Thespesia acutiloba*.

Thespesia is a genus of small trees, and one woody shrub, *T. lampas*. The type species, *T. populnea*, is a circum-tropical strand plant. Related to it are a group of three species native in the islands of the Greater Antilles, and a group of three native on the coasts and hinterland of eastern Africa from Kenya to Natal. Inland in East and Central Africa and the Belgian Congo is to be found *T. garckeana*. *T. lampas* is a shrub of Indian forest lands that has been widely spread as an ornamental.

The species of *Gossypioides* have $n = 12$ chromosomes, one of them, *G. brevilanatum*, having one pair of chromosomes twice as long as the rest, suggesting derivation from $n = 13$. Two species are known. *G. brevilanatum* is very rare in relic forest vegetation in Madagascar. *G. kirkii* is common and successful in dry bush from Portuguese East Africa to Kenya. Both resemble *Gossypium* in many characters and *Gossypioides brevilanatum* is the only plant other than the cottons that bears true lint on the seeds.

Cienfugosia was until recently hopelessly confused with *Gossypium*. In fact it is fairly obviously less closely related to *Gossypium* than are *Thespesia* and *Gossypioides*. Chromosome numbers are known for only two species, *Cienfugosia hildebrandti* $n = 11$ and *C. heterophylla* $n = 10$. *Cienfugosia* is African and Central and South American in distribution, with a considerable range of species in each continent.

A survey of these four genera reveals a pattern of characters which forms what may be regarded as a common denominator for the sub-tribe. This common type may be described as follows:

Leaves: Entire or broadly palmately lobed.

Involucral bracts: Three, large, persistent.

Inflorescence: A many-jointed, sympodial fruiting branch.

Fruit: A dry, brittle, loculicidally dehiscent capsule, with several ovules in each loculus.

In each genus species are to be found that conform in all or nearly all respects to this pattern. Since there is no other pattern that can be regarded as common to the four genera, this may be considered to be the basic pattern from which species differentiation has proceeded.

In leaf shape, all species of *Thespesia* and *Gossypioides* have leaves of the basic pattern, either entire or more often broadly palmately lobed. In *Cienfugosia* and *Gossypium*, species are known with leaves entire or very broadly lobed at one extreme through increasing degrees of dissection to leaves that are digitately divided at the other. Variation in involucral bracts is equally great. *Gossypioides* is the only genus of the four in which all species have bracts of the basic pattern. In *Gossypium* in about half the species the involucral bracts are large and persistent, and in the rest they are reduced to a greater or lesser extent, sometimes caducous, and often no more than minute appendages. Throughout the genus they are three in number. In *Thespesia* and *Cienfugosia* the involucral bracts are, with the exception of those of *Thespesia danis*, always reduced to minute appendages and are often caducous. Frequently they are three in number, sometimes they are arranged in groups of

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three, sometimes there are ten to twelve small appendages not arranged in groups, and in *Cienfugosia argentina* they are absent altogether.

The many-jointed sympodial fruiting branch has been regarded as the characteristic inflorescence of *Gossypium*, but on the one hand it is not universal in *Gossypium*, and on the other, in each of the other three genera there is at least one species in which it is to be found. In *Gossypium* the process of reduction of the fruiting branch is clearly seen, first in species in which there are rarely more than two nodes per branch, and then in species in which only a single node is formed, with its own subtending leaf. Then come forms in which the leaf at the node is reduced and the fruiting branch is no more than a jointed peduncle. Finally, in *G. aridum* from Mexico, the flowers are almost sessile, on short spurs which have lost all resemblance to a sympodial fruiting branch. The same sequence can be followed in each of the other three genera, but whereas in *Gossypium* the fully developed fruiting branch is common, in the other genera, most species have considerably reduced fruiting branches, or simple axillary flowers. In *Thespesia*, moreover, reduction has gone further and the terminal shoots bearing axillary flowers are in one species compressed into terminal panicles.

In fruit type, all species of *Cienfugosia*, both species of *Gossypioides*, and all species of *Gossypium* save a few of the agricultural varieties of *G. herbaceum*, have dry, brittle loculicidally dehiscent capsules. In *Thespesia* one species, *T. lampas*, has capsules of this type, whereas in the other species the capsules are more or less leathery or woody and indehiscent, or nearly so. Some agricultural varieties of *Gossypium herbaceum* also have indehiscent, rather leathery capsules. No reduction in ovule number has gone on in *Cienfugosia*, but in the other three genera species are to be found with ovule number reduced from the characteristic four to six per loculus to two to three, and in some cases to two basal ovules per loculus only.

It will be seen that the potentialities for variation are similar

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throughout the group. There appears to be no correlated variation in the different characters, and in fact the variation between species only fits into a pattern if the basic type is regarded as primitive. In general, the basic characters are to be found in eastern and southern Africa. *Gossypium herbaceum* race *africanum* from the dry country from Angola to Moçambique and *Cienfugosia gerrardii* from the Transvaal and Swaziland are the nearest to the basic type in their respective genera. Both species of *Gossypioides*, from coastal East Africa and Madagascar, are close to the basic type. Only in *Thespesia* is the nearest species, *T. lampas* from India, to be found outside the South and East African region.

The pattern of variation demonstrated among the wild species may now be compared with that to be seen in the cultivated cottons. The course of events in the cultivated cottons can be followed with confidence, since their evolutionary history is well understood, and the identification of the primitive types is supported by historical evidence. The primitive cottons in fact conform closely to the basic pattern of the group of genera as set out above. The cultivated cottons have not followed the pattern of differentiation of the wild species. All the cottons have three large and persistent involucral bracts, their fruiting branches are in general extended, and are never reduced. With few exceptions their leaves are broadly palmately lobed, and their capsules dry, brittle and loculicidally dehiscent. The types of diversity that are to be seen in the wild species are represented in the cultivated cottons by the occurrence of more or less rare, atypical forms, Reduced fruiting branches ('cluster' and 'short branch' mutants) are known in both diploid and allopolyploid cottons. Forms with deeply divided leaves are common in some races of the diploid *Gossypium arboreum*, and occur rarely in both allopolyploid species. And in *G. herbaceum* races *persicum* and *wightianum* agricultural forms are known in Iran and Afghanistan, and in western India, in which the capsules are indehiscent. No form with reduced involucral bracts has been recorded, but deciduous

bract has occurred as a mutant. Thus it is evident that the genetic potentialities exist for the emergence of any of the patterns of diversity to be found in the wild species, but those patterns have not in fact developed.

The differentiation of the cottons has followed other lines. The dominant pattern of change has been the development of annual forms from primitive perennial shrubs. Annuals are not found elsewhere in the sub-tribe, but they have been developed independently in numerous separate stocks in all four species of the cultivated cottons. Capsule size, the number of seeds per loculus, and the amount of the seed-borne hairs have all been greatly increased, and the sympodial fruiting branch has in general been increased in length, rather than restricted as is so often the case in wild species. It is, of course, obvious that the characters in which the greatest change has occurred in a crop plant are those which determine its utility to man. Nevertheless, it does appear to be important to note that the pattern of change under cultivation has been radically different from the patterns that could have been anticipated from a study of the diversity among related wild species. Evidently the pattern of change is not determined by the genetic potentialities of the organism, but rather by the pattern of the selective forces to which it is subject.

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THE ORIGIN AND SPREAD OF THE OLD WORLD COTTONS

It is convenient to distinguish between the true cottons and all other species of the genus *Gossypium*. The name 'cotton' is an agricultural and technological rather than a botanical term, and the cottons may be appropriately defined in terms of their

lint, which is the character that gives them their agricultural and technological value. The seeds of all species of *Gossypium* bear hairs. The seed hairs of the wild species are short, and very firmly attached to the seed. In most wild species they are circular in cross-section and unconvoluted when mature, and remain closely appressed to the seed. In *G. tomentosum* they are flattened in cross-section and convoluted when mature, but they are still very firmly attached to the seed, and cannot be regarded as spinnable. The seed hairs of the true cottons are of two types, long, fine, flattened and convoluted hairs that are easily detached from the seed, and an undercoat of short, coarse, firmly attached hairs called fuzz. The long, fine, easily detached hairs form the lint that is spun. The short fuzz hairs are commercially useless except as a source of cellulose. In some agricultural races the fuzz hairs are absent or much reduced, giving 'naked' or 'tufted' seeds when the lint is removed. The term cotton will be restricted to those species of *Gossypium* which have seeds bearing spinnable lint hairs.

The vast majority of the true cottons are cultivated, and most of those now found wild can be identified as escapes from cultivation. Thus, although it will be shown that there are truly wild plants that bear lint, an overwhelming proportion of the cottons depend for their existence on the fact that they are useful to man.

The earlier botanists who studied the Asiatic cottons regarded the cultivated forms as having been domesticated from wild races of the same species. Numerous representatives of both species are to be found beyond the limits of current agricultural systems, and there appeared to be no difficulty in regarding them as representative of the progenitors of the cultivated cottons, or as intermediate between wild ancestral types and modern crop plants. As they were more closely studied, however, it became evident that in most cases cotton plants now to be found growing wild were confined to ecological situations that have been created by man—hedgerows, house-yards, and abandoned cultivations—and were obviously

escapes from the crops formerly grown in the areas they now inhabit.

The evidence that wild cottons were descended from culti-vated forms was so general that the theory was put forward (Hutchinson, Silow & Stephens, 1947) that the origin of all the diploid cottons could be accounted for by evolution under domestication, followed in some cases by escape into abandoned land or even into natural vegetation. It was argued that the diploid cottons were never truly wild, and that they had all been developed under domestication from a progenitor differing from its wild relatives in perhaps no more than a single gene mutation giving a convoluted lint hair. Since it was known from historical records that the Indus civilisation that collapsed about 2000 B.C. had played an important part in the develop-ment of the cotton crop, the suggestion was made that the original domestication of *Gossypium* might have taken place there. It was believed that the group of wild species related to the cultivated Asiatic cottons was distributed not only in South-west Africa and the region south of the Sahara, but also as far east as southern Arabia. There seemed no difficulty, there-fore, in supposing that the progenitor of the cottons had been collected by travellers and introduced into the Indus Valley.

Evidence against this theory of the origin of the Asiatic cottons was soon brought forward. In the first place it was apparent that neither *G. anomalum* nor *G. triphyllum* could be regarded as representing species ancestral to the cottons since both are distinguished by advanced characters such as reduced involucral bracts and deeply divided leaves, and *G. triphyllum* also has reduced fruiting branches. The Asiatic cottons, particularly the primitive forms in both species, have the characters of the 'common type' as described above. Secondly, when *G. areysianum* was collected in the Aden Protectorate and established in culture, it turned out to be related to *G. stocksii* and *G. somalense*, and not to *G. anomalum* and *G. triphyllum* (Douwes, 1953). It thus became apparent that the species of the *G. stocksii* group (Beasley's *E* group) are to be found in the