The Gramineae of Monsoonal and Equatorial Asia. II. Western Monsoon Asia

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THE STUDY OF THE archaeology (origin, antiquity, and evolution) of a plant family calls for an analysis of the historical evolution of the types of vegetation in which the genera and species of the family could have arisen, and those in which they now are to be found. It would have been necessary for environments to have provided, during periods of geobotanical and palaeoclimatic prehistory and the early stages of man, appropriate conditions for the growth of types of vegetation, or rather biological ecosystems also incorporating resident fauna, which could have contained primitive forms of the family being studied.

The family Gramineae (other than the Bambuseae) has been chosen for study because of its (now) widespread distribution, and because of its great economic significance in providing both the progenitors of the cultivated cereals, and the major source, in a wild or a cultivated form, of grazing and cut fodder for domestic livestock. Specialists in the Bambuseae or in herbaceous plant families may consider whether and to what extent the conclusions reached apply to their material.

The region chosen for this overall study of the grasses is monsoonal and equatorial Asia, which has, with its multiplicity of diverse ecoclimates, been divided into *western monsoon Asia, Southeast Asia,* comprising monsoonal and equatorial, and *eastern monsoon Asia,* grading into temperate and continental ecoclimates. The conclusions reached in a study of Southeast Asia (Whyte 1972) indicated the significance to the Asian region as a whole of the evolution of the Gramineae of western monsoon Asia in particular.

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FOREWORD ON MALESIA

Plant geographers have used the term "Indo-Malayan" for the great assemblage of plants which covers, or formerly covered, the South Asian subcontinent, Burma, Thailand, Indo-China, southern China, "Malesia" in the terminology of the Rijksherbarium (the Malay Peninsula, Malay Archipelago, Indonesia, and the Philippines), with a probable extension into the Pacific islands to the east of the Hawaiian Islands (Balgooy 1960).

Within the Indo-Malayan floral zones of essentially tropical forest, Corner (1952) would recognize:

a. The northern monsoon forests of the south Asian subcontinent, Burma, Indo-China and Thailand, more or less deciduous

b. The southern monsoon forests of east Java, Flores, and Timor, related to the drier forests of Australia

c. The central zone of evergreen rain forest, from Sumatra and Borneo through Malesia to New Guinea and northern Queensland, in two parts: (i) Sumatra, Malaya, Java, Borneo, and (ii) the Philippines, Sulawesi, and the islands to the east

Although it may be correct for plant geographers and foresters to refer to an Indo-Malayan region, this cannot be said to be appropriate for the Gramineae. The environments and the types of vegetation in the Deccan and Malesia, for example, are too distinct to justify their inclusion in a single zone of gramineous distribution. This has been proposed by Clayton and Panigrahi (1974: map 2) and repeated by Cope (1977: map 1), on the basis of the recent collection of herbarium specimens of some 200 or more species, primarily of South Asian types, of the Gramineae in different parts of Southeast Asia (Malaya, Gilliland 1971; Java, Monod de Froideville 1968; Thailand, Bor 1961).

The species included in modern floras are those which were (and are) well adapted to spread rapidly in the Indo-Malesian environment, but only when the forest canopy had become sufficiently open or absent altogether. This happened in Malaya during the past century and in Java during the past 100 to 200 years. Throughout the area of former tropical evergreen forest, the previous close correlation between regional macroclimate and local ground microclimate has been disrupted, introducing bioclimatic conditions at the level of plant growth which are characterized by greater aridity and increased light intensity. In the undisturbed rain forest and its associated types of forest along the ecoclimatic rainfall gradients in Southeast Asia, all classifiable as "forêts denses," there were only a few ecological niches in which certain specialized species of the Gramineae (hygrophytic, shade-tolerant, or littoral) could have grown. Holttum (1954) recognizes only one genus, *Leptaspis*, as occurring in undisturbed rain forest in Malaya. Gilliland (1971) for Malaya, Monod de Froideville for Java (1968), as analyzed by Whyte (1972), as well as Bor (1961) for Thailand, mention others adapted to true forest conditions or to one of the niches on the forest fringes or along river valleys. These include the small but widely distributed tropical genus, *Centosteca* (until recently named *Centotheca* or *Ramosia*) and the small genus of tropical Asian forests, *Lophatherum*.

Soderstrom and Decker (1973) include these with their primitive Centostecoid and Bambusoid grasses, most of which are related to bamboos and are found in the shaded habitat of tropical American forests (see also Soderstrom and Calderón 1974). The former range of distribution of true forest grasses in Southeast Asia has become greatly reduced through the felling of associated trees in the original tropical forest ecosystem.

Three periods in the geobotanical history of Malesia can be recognized as significant in the evolution of the Gramineae (Whyte 1972):

i. The millennia before man, when the few genera and species adapted to persist in niches in and around the climax types of tropical and equatorial vegetation followed the course of evolution and distribution governed by geologic and climatic factors in the absence of the anthropogenic

ii. From the first appearance of man to his regional spread and increase in relatively small numbers up to quite recent times, during which period some new exotic grasses arrived with uncleaned crop seeds and livestock fodder

iii. The present, when large-scale clearance of forests created and is still providing extensive areas characterized by absence of shade and of forest humidity and by more arid soils, an environment suitable for the light-requiring, more xerophytic grasses from continents to the west of Malaysia and Sumatra.

The second and particularly the third periods have led to the meeting of grass species from many and diverse foreign ecosystems in these new Southeast Asian environments *(vacua)* from which the old indigenous forest grasses have had to retreat. The opportunity for crossing of genotypes within one or related species which have never before met must have been greatly increased. This would be the more important reason for any relatively slow revival of speciation or near-speciation which may be found in humid tropical environments, rather than the more rapid population/environment reactions to physiological stress characteristic of arid ecoclimates of western monsoon Asia.

Western Monsoon Asia

This region comprises the Makran coast of Iran, eastern Afghanistan (where monsoonal vegetation occurs on the south-facing slopes of the mountains in a catenalike alternation), Pakistan, India, Nepal, Sikkim, Bhutan, Bangladesh, Sri Lanka, and Burma.

The situation here is quite different from that in Southeast Asia (Whyte 1972) as far as the origin and evolution of the Gramineae are concerned. One has to consider in particular the evidence from studies of plate tectonics, of the orogeny of Tibet, the Karakorum, the Himalaya and their associated ranges, and of the palaeo-and more recent climates which were associated with or created by these major geological events (Whyte 1976).

Against this physical background, the rich gramineous flora of western monsoon Asia assembled and/or evolved. The grasses of the countries of South Asia have received as much attention as, if not more than, those in other parts of the tropics and

subtropics. Their systematics has been fully covered in the classic volume of Bor (1960) and by many other taxonomists; the taxonomy of this and other families is being revised by the Botanical Survey of India, and in Pakistan by the National Herbarium (Stewart Collection), Islamabad, and the Department of Botany, University of Karachi. No attempt is to be made here to discuss or revise the conclusions of these specialists. The emphasis is rather on the extent to which geological events and resultant climates may have provided the sequence and combination of factors, especially the first appearance and subsequent fluctuations in aridity combined with rising and fluctuating temperatures, which together are considered to be important in plant speciation. These conditions have been operative in those environments that had acquired aridity in relatively recent geobotanical times, and which were (and are) hot for at least part of every year, especially along the fluctuating borders between one ecoclimate and the next (Valentine 1970).

Thus it is proposed that the present grass flora of western monsoon Asia has evolved over nine major periods in palaeoclimatic and recent history (see conclusion), and that the ecologists who survey and map the present distribution and synecology of grasses in the flora and vegetation are concerned with a situation which has evolved over a period of only some 5000 years. Before that time, the vegetation of South Asia was primarily forests of various types (Champion and Seth 1968), which were totally or virtually devoid of grasses in their climax undisturbed state (S. K. Seth, personal communication, 1976).

THE EVOLUTION OF SOUTH ASIAN BIOCLIMATES

One may first recognize three different sources of influence on the bioclimates within which the biological components of the land have their being. The first are the macroclimates of the meteorologists, governed by global and regional movements in the high atmosphere. The second are the climates, sometimes macro- and sometimes micro-, arising from the effect of intrusive geomorphological or geological features on the meteorological climate. These are witnessed by rain-shadows behind mountain chains which have reached the critical altitude which prevents the passage of rain-laden winds, or by the differences between north- and south-facing slopes. The third set of influences is manmade, being caused by reduction of vegetation far below the successional level characteristic of a specific macroclimate. The microclimates within the second and third types of influence are considered in this context to be the most significant in causing stress and in initiating plant speciation in the Gramineae, which grow in the life zone up to two or three meters above ground level.

It is no longer correct to suggest an earlier connection between Southeast Asia and Gondwana and the South Asian Plate (McElhinny, Haile, and Crawford 1974; Haile 1976; Haile, McElhinny, and McDougall 1977). The history of the Gramineae in western monsoon Asia, however, does necessarily begin with the study of Gondwana, its initial location and the geological age of its progressive disruption, and the movement of one specific tectonic plate out of the southern hemisphere across the equator into the northern hemisphere. Plate tectonic theory is still not accepted in some quarters, particularly in the "greatest bastion of resistance, the

Soviet Union" (Kerr 1978), "but even here plate tectonic theory is making considerable inroads in head-to-head confrontation between mobilists and fixists." Plant historians would appear to be justified in using it in their studies (Clayton 1975).

The South Asian Plate was originally located along the eastern edge of Madagascar, which in turn lay "against the coast of East Africa rather than South Africa and Mozambique, where it has sometimes been placed. There appears to be independent geological support for a more northerly location . . . . The position of Madagascar is clearly the most enigmatic piece in the whole puzzle. Until more compelling evidence of a more southerly position comes forward than has hitherto been advanced, the Smith-Hallam reconstruction can be accepted provisionally as a reasonable approximation to the truth" (Hallam 1973: see fig. 34).

After the South Asian Plate had become separated from Madagascar in the Cretaceous, rafting was relatively rapid, the Plate moving at a rate of 10 cm per year for 50×10^6 years during the Tertiary, to reach its present position in the Miocene (McElhinny 1968), or at variable rates from the Cretaceous to the middle Eocene and from the Miocene to the Oligocene (Blow and Hamilton 1975), or at one rate up to junction with Laurasia in the Eocene, and at a slower rate thereafter (Molnar and Tapponnier 1975).

When the South Asian Plate had crossed the equator (the central part of India moved from 30°S to 20°N latitude), what is now peninsular India came into position astride the southwest winds which had hitherto blown across the Tethys Sea to bring warm rains to the southern coast of the Asian mainland (Laurasia). From this stage onward, the Western Ghats intercepted these winds. A tilting of peninsular India may also have been involved, a rise in the west and a fall in the east. From the crests of the Ghats (about 700 m asl) down to the western seaboard, rainfall became extremely heavy. Within relatively short distances from the crests to the east, however, rainfall dropped abruptly, creating a vast rainshadow of significance to the further evolution of the natural vegetation and its constituent species.

Coincident with this major bioclimatic change was the cessation of the rains hitherto received direct from the southwest along what had been the north coast of the Tethys Sea. In the north of the subcontinent after junction between Plate and mainland, the equable maritime climate of the Plate, which had already become influenced in the south by the rainshadow, now became further affected by the new monsoonal pattern which evolved as a consequence of Himalayan uplift. Gansser (1964, 1977) has presented a time scale of the phases of drift of the Indian Plate in relation to those of the Himalayan orogeny (see also Pal and Bhimasankaram 1977). This uplift introduced progressively into what was formerly a humid tropical habitat (during transit of the Plate across the equator—Frakes and Kemp 1972; Kemp 1978), the new ecological factor of aridity, of even greater intensity and variability than that produced in peninsular India by the rainshadow to the east of the Ghats. The strength of the new climate in the northern plains was such that the effects of the Pleistocene glaciations (four in all, the second being the most severe, the third and fourth the weakest) did not extend far south from the Himalayan range.

Superimposed upon this aridity came the Neothermal (see Bray 1971: 178 ff.) following the end of the Pleistocene, the change from a cool to a warm climate which took place in the Northern Hemisphere some 11,000 years ago. This com-

bination of aridity and rising temperatures is considered to be the main factor causing the physiological stress so important in plant evolution (Whyte 1977). Climatic fluctuations and trends of considerable biological and genecological significance are still occurring. Legris and Meher-Homji (1976) and Meher-Homji (1977), however, do not agree with Warren (1974) and Winstanley (1973) that aridity in the Indian arid zone has become accentuated recently. They find no indication of any substantial change either in vegetation or flora, migration of species, major shifts in landscapes, or land use to provide a phytogeographic proof of this supposed climatic trend. Krishnan (1977), however, interprets the eastward shift of the aridity index line (his fig. 5) as indicating that desertic conditions in northwest India are extending toward the east, especially in the southern region. But studies at the Central Arid Zone Research Institute, Jodhpur, have shown that desiccation and the spread of dunes have operated from the east (Aravalli range) to the west. This finding is confirmed by the aerial mapping of the four or five earlier courses of the now extinct river Saraswati.

Man has certainly greatly increased his pressure on the land and its biological resources over the past 100, even 50 years, principally through the cutting of shrubs and trees as fuel, clearing for cultivation, and the uncontrolled grazing and browsing of excessive numbers of domestic livestock. There is no doubt that this has exacerbated the aridity of the microclimates at ground level, as Meher-Homji (1976) appears to admit, and thus their effect on the physiology and the present and future genecology of the gramineous plants that grow and reproduce at that level.

EVOLUTION AND MIGRATION OF SOUTH ASIAN TAXA

It is not proposed to discuss the possible time and place(s) of origin of the Gramineae, South Asian or otherwise, within the angiosperms (Clayton 1975). Did the Gramineae as a whole arise during the Cretaceous (see geological time scale in Banks 1970: 454), when the climate over most of the earth was tropical or subtropical; from a hypothetical ancestor now extinct; or from a short, stout, solid-stemmed herbaceous "bamboo" in the early tropical forests—but where were these forests? Was there some degree of parallel or associated evolution with that of the herbivores—the ungulates?

The history of the evolution of Quaternary grassland ecosystems indicates interdependence in plant and animal evolution (Numata 1971). The radiation of the vertebrates acquired dominance in the continents of Cenozoic time (Colbert 1974), occurring in two phases, the first during the Palaeocene and Eocene, the second in the Oligocene and continuing into the Pleistocene. The herbivores of the first phase were characterized by low-crowned cheek teeth, adequate for the soft vegetation of early Cenozoic landscapes. But these animals were not adapted to cope with the fibrous herbage of the Gramineae and gave way to the modern herbivores, with cheek teeth with tall crowns, capable of withstanding the wear associated with a continuous diet of abrasive herbage. Because of the probable origin of many of the South Asian grasses in Africa, comparison might be profitable between the grass-eating faunas of South Asia and Africa (Kingdon 1971, 1974*a*, 1974*b*, 1978, 1979).

Pending a joint study between palaeontologists and graminologists, it may be proposed that the grasses, which had evolved long before the Oligocene, became dominant in the ground herbage during that period, under the influence of increasingly heavy grazing, and that there was a parallel evolution at the same time in the dental morphology of the ungulates. This would enable them to cope with this new type of fibrous herbage, the spread and dominance of which they themselves were promoting by changing the growth forms and creating grazing swards in place of the former discrete plants in miscellaneous communities.

The significance of birds in the dispersal of plants calls for careful analysis (Whyte 1972). Field evidence in the Asian tropics negates the original statement of Knud Anderson that birds migrate on empty stomachs, with clean claws, feathers, and beaks (Ridley 1930). Some dry seeds of herbs, including grasses and Cyperaceae, are dispersed by adhesion, due to viscidity, on feathers, or in and on feet and other parts, especially of waders which move between sites of one of the major ecological niches for Gramineae in Southeast Asia—the muddy coasts, estuaries, and marshes. Ridley believed that the occurrence of species of *Paspalum, Panicum,* and *Eleusine* on islands could be explained only on the basis of transport by birds.

Referring to angiosperms in general, Deodikar (1978) infers that taxa of flowering plants and their obligatory insect pollinators (grasses of the tropical forest are insect-pollinated in the still environment) may have already coexisted over undivided Gondwana much before the split and the beginning of drift.

The present consensus appears to be moving the date of origin of the angiosperms and also of the Gramineae much further back in geobotanical history (but see Hickey and Doyle 1977). West Gondwana was a primary area of evolution for many groups, possibly including birds, marsupials, snakes, and anurans, but certainly many orders of angiosperms and perhaps the earliest angiosperms themselves (Raven and Axelrod 1974). The area included vast arid to subhumid tracts in tropical latitudes; terrains and edaphic conditions were diverse, and there was ample opportunity for rapid evolution. The opening of the South Atlantic, 125–130 my B.P., which signaled the spread of more mesic climates over much of the region, seems to have triggered the main evolution, radiation, and surge of angiosperms into the mesic lowland (Raven and Axelrod 1974).

In attempting to correlate the evolution and distribution of South Asian Gramineae with that of their ancestors and relatives in the African continent, evidence from studies of fossil pollen (palynology) may be used to supplement that from the fossil material (Muller 1970).

> Authorities concur in placing the cradle of the grasses in the rainforest. Attempts to date the further development of the order founder on the paucity of the fossil records. Reliable finds go no further back than the Tertiary, and comprise a species of *Stipa* L. in the Oligocene, fossil genera doubtfully distinct from *Stipa* in the lower Miocene and species of *Panicum* and *Setaria* in the Pleiocene (Elias, 1942). (Clayton 1975)

It is unfortunate that pollen morphology in the Gramineae is so uniform that no evidence of phylogenetic differentiation can be expected from the fossil records. Grass pollen and macrospecies remains are known from the Upper Palaeocene of

the Paris basin (J. Muller, personal communication, 1977). Grass pollen has also been reported as very rare in the Maestrichtian of Japan, possibly the oldest record. Although pollen of the Gramineae is known, if sparingly, during the Eocene, it is not until the Oligocene that members of the family enter pollen assemblages in abundance (in the Caribbean region—Germeraad, Hopping, and Muller 1968). Palynological evidence for the origin of the angiosperms is still lacking, but the later development suggests a monophyletic descent, the dicotyledons probably preceding the monocotyledons (Muller 1970). The Gramineae are unanimously regarded as among the most advanced (and therefore the most recent?) of angiosperm families (Clayton 1975): they may be regarded as having evolved under conditions of ever-increasing physiological stress; Gramineae are components of vegetation communities at the lower levels of ecological succession; within the grass family itself, the more advanced genera such as *Aristida* are again in a lower place in ecological succession, in response to factors of stress.

Since Clayton concludes that the initial breakup of Gondwana in the Triassic would seem to imply an implausibly early completion of angiosperm evolution, it would appear that we have to consider some degree of parallel evolution of the bulk of the Gramineae, taxonomically and ecologically, on the African mainland through the Tertiary (Hamilton 1974) and on the South Asian Plate before and after it had collided with Laurasia. The latter group would have demonstrated a high rate of speciation which, associated with later immigration, led to the establishment in South Asia of a gramineous flora of some 250 genera and 1250 species (Bor 1960), as well as innumerable types to which Bor did not grant specific status.

One would have to review the distribution of the Aristideae and Eragrostideae, regarded by some as a classic example of biogeographical proof of continental drift (Brown and Smith 1972). These groups are thought to have evolved from some late Jurassic to mid-Cretaceous types, probably tropical, which very early acquired among their characters the Kranz syndrome incorporating the C_4 pathway. At the time of the breakup of Pangaea, these types are believed to have been in Australia, India, Africa, and South America, where they later expanded greatly (but could these groups of primarily semiarid habitats have crossed the equator into India in the rain forests of the South Asian Plate?).

A phylogeny has been proposed for 163 species in the tribe Arundinelleae, (Phipps 1968); 38 characters are stated for advanced versus primitive status, advancement indices are calculated, and trends of variation discussed (Fig. 1). Based on present distribution, one of the six lines (incorporating *Loudetia, Tristachya, Danthonia*) is probably African in origin; the Arundinelloid line may be regarded as African if the tribe is monophyletic, or Indo-Southeast Asian if the tribe is diphyletic. Present distribution might be explained in terms of continental drift, but this would require (according to Phipps) that the tribe extend back to the Jurassic if not the late Triassic or Permian, much earlier than any fossil record.

Because of the probable significance of Madagascar as a stepping stone for African species en route via Plate transport to their present location in South Asia, the present bamboo and grass flora of the island (Bosser 1969; Morat 1973) calls for an ecological/historical analysis to define the ancient species which might have existed in appropriate niches in the climax forest vegetation before it was destroyed by man.

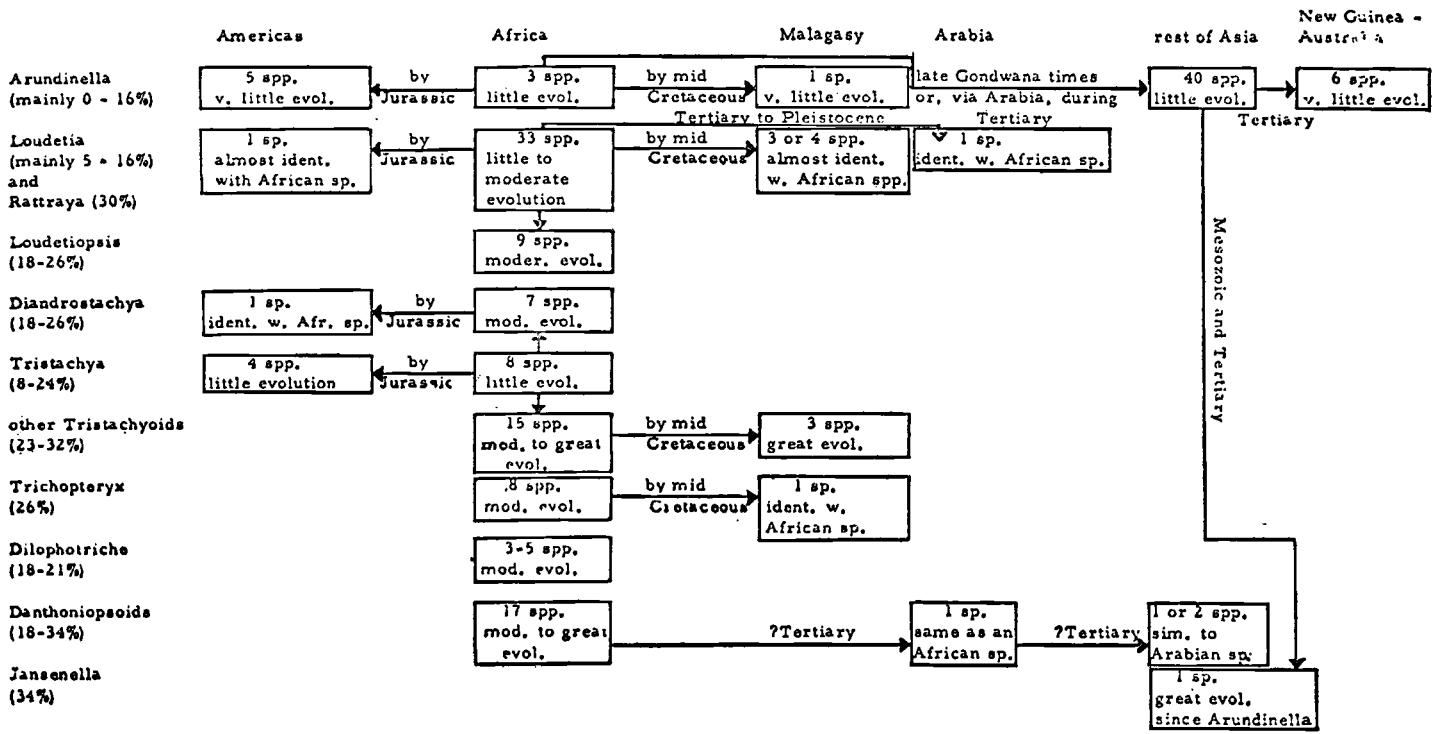

Fig. 1 Taxonomy of Arundinelleae related to continental drift (Phipps 1968).

The most "primitive" representative of the Paniceae, *Pseudolasiacus,* occurs in Madagascar, while most of the genera considered to belong to the same tribe, Microcalamineae, are also African (Butzin 1970*a, b*). Some species of *Panicum* or their ancestral precursors—Bosser (1969) notes 20 species of *Panicum* in the present degraded vegetation of Madagascar—would already have been adapted to a humid tropical environment and may possibly have evolved in time to cross the equator on the Plate in appropriate ecological niches in the tropical wet evergreen forest. When the botanical composition of the forests of the South Asian Plate later began to change and the canopies to open under the influence of aridity, any early genera and species of the Paniceae would have had to produce forms adapted to the new environment, or to retreat with the tropical wet evergreen forest to the relict areas of the present day. This mesophytic population of early origin may have been supplemented by recent recruits of more xerophytic adaptation which arrived in the northwest of monsoon Asia by natural or anthropogenic migration from east and northeast Africa, especially *P. antidotale* and *P. turgidum.*

The high-caste grasses of the early grass covers, the species of *Cenchrus, Sehima,* and *Dichanthium,* may have been Saharo-Sindian invaders, or perhaps there was a limited enclave of semiarid ecoclimate lying along the lower foothills of Baluchistan and in the adjacent plains, out of reach of the southwest monsoon even before the arrival of the Plate. Such a habitat could have supported an open type of deciduous or thorn forest, with a ground story of perennial grasses, awaiting the opportunity to advance across the subcontinent with the widespread advent of aridity. Ancient species of these grasses may have differed considerably in taxonomic characteristics and spectra of variability from their modern descendants.

So much for the problems associated with the origin and/or migration of the mesophytic and xerophytic grasses of monsoonal South Asia, a region characterized by erratic rainfall for six to nine weeks during the year, the remainder of the year being dry. The species of temperate adaptation of the high Himalaya and their associated ranges above 2000 m altitude are easier to understand (Whyte 1964; Dabadghao and Shankarnarayan 1973: 56–64). The presence of species of the nonmonsoonal genera *Agropyron, Agrostis, Calamagrostis, Dactylis, Koeleria, Phleum, Poa,* and *Stipa* again has a geological explanation, namely, the progressive orogeny of the Himalaya and the lands to the north. At one stage in this process, temperate climates would have spread from northern Asia southward through what had been up to mid- to late Tertiary the warm moist zone, which extended from the shores of the Tethys Sea up to 45°N latitude (Frakes and Kemp 1972). Temperate species advanced south over the plateaus of Tibet, through the rising Himalaya and down their southern slopes to the limits of their tolerance of a subtropical environment of about 2000 m elevation. Later this migration route was broken by the creation of the rainshadow to the north of the Himalaya and Tibet. The temperate species of the high Himalaya and their foothills may therefore have arrived from two contrasting directions. Species reported in the floras as occurring from Chitral and Gilgit to the east are of Siberian origin, relicts which were isolated by the intervention of intense aridity from their zones of origin and their relatives in northern Asia. Species reported for Baluchistan and the mountains in the northwest of South Asia would have arrived following the movements of deforesting peoples and their livestock from the Irano-Turanian and Mediterranean ecoclimatic regions to the

west. Some anomalies at high altitudes throughout the Himalaya may be taken as botanical confirmation of the Gondwanian origin of at least parts of the Himalayan landscape. Bor (1960) refers to species of the predominantly African tropical genus, *Pennisetum*, high in the Himalaya. The Gondwanian *P. flaccidum* forms a steppe from the right (southern) bank of the Brahmaputra in Tibet, on the northern slopes of the Himalaya at 3900 to 4000 m elevation, adjacent to a steppe of the Laurasian *Stipa* (King-wai Chang and Shu Chiang 1973).

Routes of Migration

To summarize, members of the gramineous flora of western monsoon Asia may have been transported into or may have migrated into the region at different periods from different directions:

a. Immigration on the South Asian Plate of primitive types (herbaceous bamboos, bambusoid, and oryzoid grasses and species evolved therefrom), which were of African origin, and which could persist in appropriate ecological niches in a tropical wet evergreen environment during the rafting of the Plate across the equator
b. Possible migration across South Asia of high-caste species adapted to semiarid ecoclimates, from a small and perhaps ancient residual enclave of ancestral types along the foothills of Baluchistan and in the adjacent plains, out of reach of the southwest monsoon even before the arrival of the Plate
c. Immigration of African types of semiarid adaptation, by natural means or more probably through the actions of man, across the Red Sea and through Arabia, within the limits of the so-called Saharo-Sindian phytogeographical zone; are the monsoonal species described by Bor (1968) for Iraq on their way through Southwest to South Asia from Africa, or did they enter Iraq from the east during the trade between Sumer and the Indus civilizations, or at other times?
d. Transfer from northeast and east Africa by the maritime trade conducted since time immemorial through the stepping stones (watering points) of the islands of the Indian Ocean (Whyte 1974*a*: 24; Renvoize 1971)
e. Possible, but less likely, immigration into the region from the east and southeast (Whyte 1972)
f. Immigration into the western Himalaya of temperate grasses of Irano-Turanian and Mediterranean adaptation to the high elevation habitats of similar ecoclimates
g. Immigration of temperate species into the Himalaya from continental Asia to the north and northeast

Interrelations of Forest Types and Grass Covers

Does the graminologist accept the conclusion of the forest ecologists that there were few if any grasses on the floors of the true climax forests before the advent of man in South Asia in effective numbers (S. K. Seth, personal communication, 1976)? Early peoples would have been few and harmless members of biological

ecosystems in a state of reasonable equilibrium. In the northwest region of South Asia, the forests were exploited by the peoples of the Indus civilization. Elsewhere, with the possible exception of the thorn forests, the tree-dominated vegetation of western monsoon Asia would have been virtually grassless until well after the arrival of the Indo-Aryans. In the initial stages, the Indo-Aryans would have destroyed the dicotyledonous ground cover of the forests. An example of this type of vegetation may be seen in the Gondwanian relict area at Mawflong, Meghalaya, where the intrusive grasses now to be found are mostly not of Gondwanian origin (S. K. Jain, personal communication, 1975).

Until long after the arrival of the Indo-Aryan speakers, the forest cover of South Asia was much more extensive than now (see Fig. 2) and the area of grass covers/

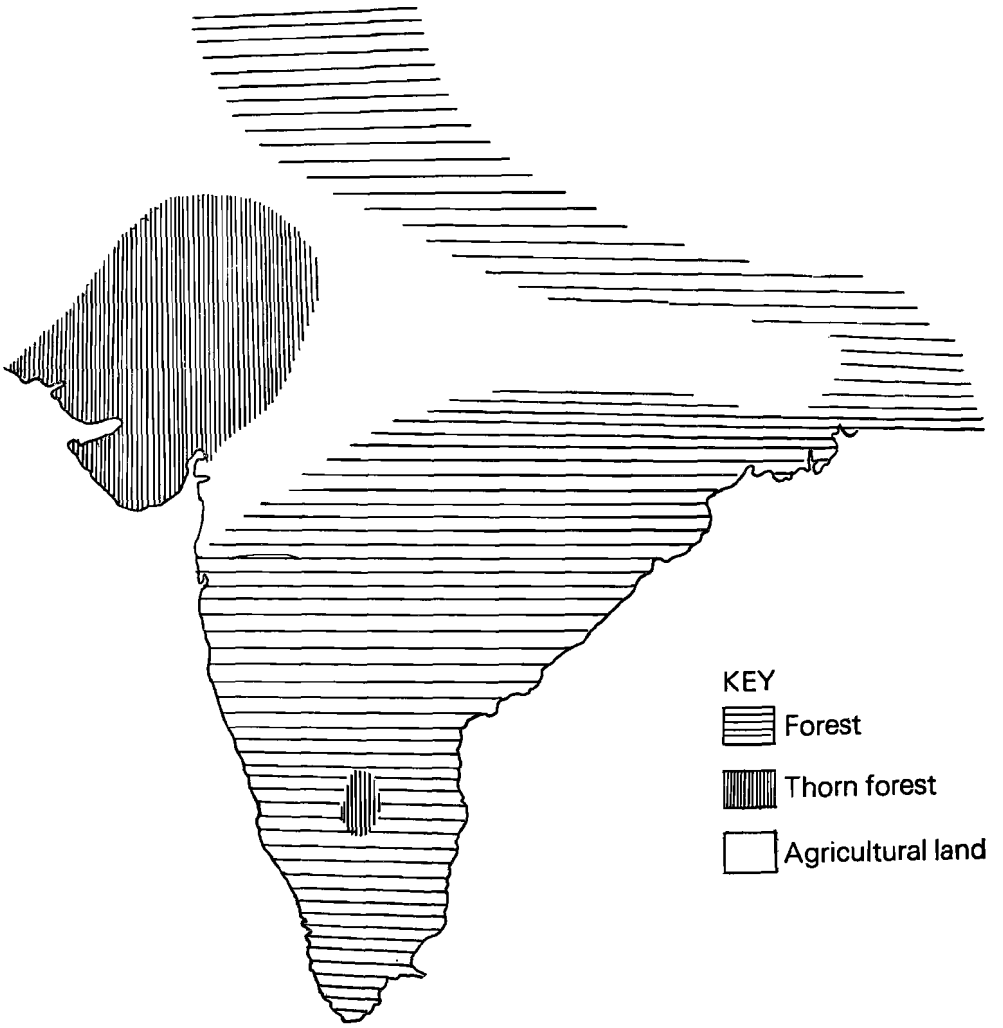

Fig. 2 Extent of forested and agricultural land in India in 629–642 A.D. (adapted from Banerjee 1966, who used a base map from Cunningham 1924).

grassland/savannahs proportionately smaller. Even now, in forests of sal *(Shorea robusta)* in the bhabar zone of northern Uttar Pradesh, a secondary stage in forest succession silviculturally managed as a subclimax, the only grass is *Eulaliopsis binata*. And again, even if taxonomic geographers insist against the evidence that the undisturbed forests of South Asia did contain grass species, these would not have been of a type which could later have withstood exposure on open sites to the intense light and heat of the South Asian sun.

Judgment must be reserved on claims for one or more "prehistoric" grassland phases in the Nilgiris indicated by pollen analyses, and on this statement of Axelrod (1974):

> Aridity increased during Miocene and later times as India moved into the permanent high pressure belt on the north edge of the tropics, as land area increased in size when India was welded to Asia, and as the general Neogene trend to aridity progressed. Increasing drought in the west confined rainforest to the moister east, savanna spread over much of central India, and thorn forest and later desert scrub spread widely over the west.

In such contexts, it is necessary carefully to disentangle geological and climatic influences from anthropogenic influences.

Within the last 200 to 300 years, and particularly during the last 50 to 100 years, anthropogenic factors have operated with ever-increasing intensity. This has led to the spread of the Gramineae in the ground story vegetation in all manner of degradation stages of forest types to which they do not truly belong, in an ecological/historical sense. It is these extensive types of grass covers and successions that are currently described for Pakistan, Nepal, Burma, and Sri Lanka (Whyte 1968, 1974*b*), and for India by the Government of India Grassland Survey (Dabadghao and Shankarnarayan 1973); this latter survey was designed to show the present composition and nature of succession within the grass flora as a basis for the practical ecological management of Indian grasslands. The combination of continuing operation of the factors of aridity and temperature with cultivation and the grazing of domestic livestock has led to the elimination over the more semiarid and arid parts of the region of the high-caste grasses, and to their replacement by inferior perennials and by annuals. The maps of the chorology of Indian grass species (Clayton and Panigrahi 1974) cannot be regarded as maps of plant distribution in a historical/ecological sense. They merely indicate the intensity of human and animal pressure on the natural vegetation, which has created conditions for the (very recent) spread of a species from an initial core area or ecological niche in a climax forest type into the widespread false ecosystems of the present day. Botanical analyses made now by grassland ecologists and taxonomic geographers show grass cover types to differ considerably in specific composition and distribution from those identified in analyses made 50 or 100 years ago, and the same will be true 50 to 100 years from now.

The taxonomic geographer learns to categorize forest types, undisturbed and disturbed, in respect of their ability to provide sufficient light and space at ground level for the persistence of members of the Gramineae. It is almost impossible for the modern vegetation ecologist and the forester to visualize what these forest types

looked like in their undisturbed state, from the periods of arrival of aridity until the introduction of the anthropogenic factor in effective intensity. There can be few relict areas which have escaped entirely from even a slight influence of man or from the side effects of the anthropogenic factor operating with greater intensity on another forest type in the vicinity.

This analytical approach based on historical ecology is now being applied to the grasses of Sri Lanka, in association with the new flora being produced by collaboration among the Smithsonian Institution, Washington, Royal Botanic Gardens, Kew, and CSIRO, Canberra. This will again involve a decision as to which species in the modern floras and descriptions of grass covers (Trimen and Hooker 1974; Holmes 1951; Senaratna 1956) may be regarded as truly indigenous and which have arrived or evolved quite recently, following clearance of the climax forest cover by man.

REASSESSMENT

It would appear that most of the grasses of South Asia must have evolved in the region itself, and that this has occurred relatively recently. It is therefore appropriate to consider how taxonomists and genecologists consider this remarkable rate of speciation might have been achieved, and whether the present degree of variability indicates that it is still continuing. Bor (1960) stated:

> In spite of the spate of papers relating to the taxonomy of the grasses, our knowledge is pitifully small in comparison with the size of the family. . . . It seems that we are at the moment witnessing a revolution in ideas concerning the taxonomy of the Gramineae. New concepts, new facts, new methods of approach all contribute to the elucidation of this most difficult family, but it seems obvious that a great deal more information must be gained before even a tentative scheme with a moderate chance of acceptance can be produced.

Taxonomists have commented frequently on the difficulties of systematic classification in species populations which show a high degree of polymorphism in morphological and cytological characters. Bor refers to particular difficulty in *Apluda mutica, Chrysopogon fulvus, Heteropogon contortus,* and *Sporobolus indicus;* he recognized 32 species as authentic in the genus *Panicum,* but noted 375 synonyms proposed for specific rank by other taxonomists.

Although studies of polymorphism, variability, and speciation are of interest to historically minded botanists, they cannot be reviewed here.

It is clear that, in the present historical/ecological context, it will be necessary to examine afresh the individual genera and species of the Gramineae in the flora of western monsoon Asia. The field material now before us for recognition and classification may represent only residual populations from different assemblages which have been depleted or changed over the millennia of geobotanical history, palaeoclimatic change, and the actions of man.

It will be desirable to locate the habitat(s) in which those members which are accepted as more primitive (according to taxonomic, morphological, and cytological criteria) are or were to be found. From this starting point, one may follow the probable history of their further spread and migration, with or without accompany-

ing speciation, but always allowing for the elimination of genera and species over geographical links. In such studies, it is essential to recognize that it is the history and evolution and the latter-day degradation of the total vegetation that are significant. It cannot be claimed that a species is truly ancient and indigenous in a vegetation which could not have provided it with a habitat, or even an ecological niche, suited to its autecology.

"While the moist, tropical forest areas [of the present day] contain the most ancient types of all, the drier subtropical areas contain many very recent forms [as a result of] reactions to increasing aridity" (Bews 1927). The evolution of the Gramineae is believed to have started on the forest borders and proceeded in two directions, one toward increased xerophytism, the other toward increased hygrophytism. In the present context, attention has to be given specifically to the ancient flora of Madagascar and adjacent parts of East Africa, as it existed when the break with the South Asian Plate became biologically effective. Could some primitive forms of the Gramineae have evolved by that time? If not, could the lowland forests have contained the herbaceous forms of the Bambuseae which some regard as ancestral to the grasses through the bambusoid, oryzoid, and centostecoid connections (Soderstrom and Calderón 1974)? There are woody forms of Bambuseae in Madagascar now at the higher altitudes. The tender lowland herbaceous forms may have been eliminated by the massive devegetation which has occurred in Madagascar in modern times. Evolution on the Plate to the primitive and then the higher forms of the Gramineae could have occurred during its rafting over the equator, as well as on the African mainland, in forms of parallel or divergent evolution.

Stebbins (1972) quotes the principle of Sewall Wright "that the most favorable population structure for rapid evolution is the division of a population into many small subpopulations which are sufficiently isolated from each other so that they can become differentiated under the influence of differential selection pressures, but between which migration can occur often enough so that adaptive gene complexes arising in one subpopulation can spread to other subpopulations." It is important to define the ecological conditions which are most likely to maintain such partly divided populations, and to permit occasional migration between them, as well as the occasional fusion of different subpopulations. This can be done by reviewing the climatic zones and ecosystems which separate the higher proportion of species complexes consisting of a mosaic of allopatric or partly allopatric and narrowly endemic species and subpopulations.

Centers of Origin, Endemism, and the Annual Habit

The concepts and terminology adapted for crop plants, namely centers or zones of origin or gene centers, do not apply to the wild genera and species of the Gramineae. Even for the cultivated members of the order, it has become preferable to use the term *zones of origin*, as Harlan (1971) has done for the cereals in the latitudinal belts in the Sahelian and other zones of Africa south of the Sahara, or as Whyte (1974*c*, 1977) proposed independently for the origin of the Asian cereal and leguminous annuals in the concentric isoxerothermic zones around the arid cores of Asia. Reconsideration is necessary of the situation described by Hartley for the Andropogoneae (1958*a*) and Paniceae (1958*b*) and for India by Arora, Mehra, and Hardas (1975) on the basis of the new data now coming forward.

The ecological historian finds it difficult to fit the concepts of the taxonomic geographer regarding endemism into the historical framework of evolution. Endemic species appear to be either (a) relict species, at high altitudes or in highly specific niches, of the vegetation of an ancient continent or an earlier geological age; (b) descendants of that relict species on the same site; (c) arrivals of species in small numbers from elsewhere which have become disjunct in distribution; or (d) species of recent origin, the young beginners of Willis (1922, 1949), and of Johnson and Raven (1973) in relation to the Galapagos.

In an ecological/historical context, it is not enough to be informed that endemic species are geographically restricted in distribution to specific and characteristic localities (Arber 1935). It is essential to know why these particular species are there, from whence they came, and whether their nearest taxonomic relatives still exist somewhere or have become extinct due to exposure to adverse environments or for other reasons. Some believe that endemic species are necessarily diploid. The endemic nature of some species of *Cymbopogon* (Gupta 1970) may be attributed to certain ecological or geographical barriers. Endemics of this genus are either diploids, being remnants of extinct ancient species, or allopolyploids of recent origin (Janaki Ammal and Gupta 1966). Bor (1960) refers to many endemic species (see also Rao 1972; Chatterjee 1939). Clayton and Panigrahi (1974) note that the Deccan region (the Western Ghats and Nilgiris in particular) and to a lesser extent the Himalaya bear largely endemic floras. There are, however, no Saharo-Sindian endemic species, "suggesting that this element is invasive." There are few if any endemics in the Indo-Gangetic Plain. Is the distinction between the high-altitude sites and the Deccan on one hand and the Indo-Gangetic Plain on the other due to the great diversity of microenvironments in high dissected country compared with complete uniformity in the Plain?

The resident and immigrant populations of the Gramineae of western monsoon Asia have during their evolution been exposed through recent geological periods to varying degrees of physiological stress caused by the major operative factors. This stress would manifest itself not so much during long intervals of stable climate as during the intermittent periods of abrupt change or crisis from one bioclimatic regime to another, particularly along ecoclimatic boundaries. These conditions may arise when the habitat changes owing not only to natural climatic fluctuations or trends, but also to factors induced by man, or when a species tries to advance, to establish itself in foreign ecological niches with a more severe bioclimate, or when seeds are sown by man in a habitat differing widely from that from which they came.

In arid and semiarid zones in particular, stress leading to reduced reproductive efficiency may be caused primarily by deficiencies in soil moisture and soil nutrients, and by excessive transpiration, with the associated damage caused to plant structures by hot, desiccating, dust-laden winds. The reproductive organs are most susceptible to the initial loss of turgor following exposure to aridity, or to a reduction in the supply up the vascular system of the precursors of the highly specialized substances which are required for the development and nutrition of the future gametes. These first reactions to stress do not become immediately visible to the naked eye, but fundamental changes are actually occurring at the microscopic level (Whyte 1975).

The ecotypes within a species persist in a particular environment to the limits of their physiological tolerance. When physiological stress caused by increasing aridity

with or without change of ambient temperature occurs, the plants may or may not respond by the production of new genotypes with minor or major changes in the chromosomal composition, ploidy, temporary or permanent apomixis, and other sequels to abnormal meiosis. If a plant responds in these ways and if the new generation is viable and has a spectrum of variability which contains types adapted to the new environment, that genus will persist in its former or a new specific form. Otherwise, it becomes rare or extinct.

These processes will be repeated with each change of effective physiological climate, or when a species in its migration comes to an ecoclimatic border between two contrasting bioclimates. In the former case, with each change of climate toward greater aridity, from labile perennial species may evolve more drought-resistant perennial types, more advanced taxonomically but lower in ecological succession. These types may be as or even more drought-resistant than annuals in the same habitat—the grass species of actual desert fringes are perennial rather than annual. In those perennials which cannot achieve this degree of drought resistance, a limit to perenniality will ultimately be reached, and the species will disappear unless it has the capacity under conditions of extreme physiological stress to produce annuals within its final spectrum of variability. These annual Gramineae may be either temporary, transient, and reversible when conditions improve, or they may become genetically and taxonomically fixed.

An understanding of the environmental and biological reasons for the origin and evolution of annual food plants may be obtained from a comparative study of the perennial and annual species and forms among the wild Gramineae. Annual plants or therophytes "are to be generally regarded as the most recent of all forms . . . they are particularly characteristic of the more adverse regions and situations [deserts and open xerophytic habitats] . . . annuals are also particularly suited to the types of habitats which have resulted from man's interference" (Bews 1927). Annual species and forms arise primarily on the semiarid and arid fringes of distribution of their perennial ancestors. It may be that many perennial forms of grasses contain an actual or latent capacity to produce a certain proportion of annual forms within their progenies, and that this proportion varies with fluctuations of climate. Species whose perennial forms do not have this capacity are eliminated by excessive drought.

Boundaries of Genecological Significance

Several such boundaries between contrasting vegetation zones may be recognized:

a. The border between contrasting climates—the monsoonal of Pakistan, the Makran coast, and eastern Afghanistan, and the Mediterranean and Irano-Turanian of Iran and Afghanistan to the west

b. The many borders, some marked, some less distinct, and in a constant state of fluctuation of physiological and genetical significance, between successive zones of progressively higher rainfall, reduced evapotranspiration and mesophytic types of vegetation and grass covers, from the Thar Desert in Pakistan across India toward those regions with higher rainfall to the east, southeast, and northeast

c. The crest of the Western Ghats, with its dramatic drop from high to low rainfall which Bor (1960) suggested would be a promising zone for the collection of "novelties," especially of annuals
d. The botanical island of Mt. Abu in Gujarat, said to be a meeting ground for north Indian and peninsular elements, where a number of endemic species have been found (Jain 1970)
e. The border zone that extends along the southern face of the Himalaya, where, at an average elevation of some 2000 to 3000 m, the monsoonal species reach the upper alititudinal limits of their tolerance of cool, temperate conditions, and the temperate species of the upper Himalaya reach the lower limits of their tolerance of a monsoonal climate, and of a Mediterranean bioclimate in the west (see studies by E. K. Janaki-Ammal and P. N. Mehra and associates, reviewed by Whyte 1975)
f. The point or points in mid-Nepal where western species of forest trees (and perhaps also of the Gramineae) give way to eastern species (Stainton 1972), the border between the heavier monsoons of the eastern Himalaya and the central and western bioclimates with more winter rain and snow, affected by moisture originating in the Mediterranean region in the western Himalaya
g. The border or borders on the east of western monsoon Asia between Burma and southern China, Thailand and Malesia, the location and significance of which have not yet been clearly defined in the present context

GEOLOGICAL SEQUENCE AND GRAMINEOUS EVOLUTION

In western monsoon Asia, speciation combined with immigration has led to the establishment of a large gramineous flora in and around the region. Some nine major periods in the geological, palaeoclimatic, and recent history of western monsoon Asia may be recognized, when the factors associated with conditions of progressively increasing aridity, later to become combined with rising temperatures, would have been effective. Progress into and out of these major periods was not smooth, however, but was characterized by abrupt changes of climate. The evolving phenotypes and genotypes were, therefore, exposed to operative factors on far more than nine or eighteen occasions:

a. The long periods of slow geological and palaeoclimatic evolution through which the vegetation of the South Asian Plate (still in the Southern Hemisphere) and that along the northern shores of the Tethys Sea passed before rafting began in the Cretaceous
b. The movement over 50 million years of the Plate across the equator into the Northern Hemisphere, and the cutting off of the southwest monsoon from the northern shores of the Tethys Sea
c. The creation of the rainshadow to the east of the Ghats and the introduction of aridity into peninsular India, after the Plate had taken up its permanent position astride the southwest monsoon
d. The uplift of the plateaus of Tibet and of the Karakorum, the Himalaya, and their associated ranges

e. The increase of aridity in the northwest and north of the subcontinent, due to the new pattern of monsoonal climate which followed the uplift of the mountain barrier, now deflecting the northerly rain-bearing winds of the Bay of Bengal to the east into China, and to the west as far as southern Iran, Pakistan, and eastern Afghanistan

f. The fluctuations of climate at lower altitudes in north India and Pakistan related to the four glaciations, and with a relatively limited geographical range

g. The beginning and extension of the Neothermal, introducing high temperatures to act in combination with the already widespread aridity as major operative factors in speciation

h. The introduction and continentwide spread of the actions of man in destroying vegetative cover or reducing it in successional status, with marked effects at least on the microclimates at ground level in which the grasses live and progress through the highly vulnerable stages of meiosis

i. The recent and modern short-term fluctuations in climate which continue to expose the grass species at irregular intervals and in varying intensities to the action of factors operative in specific variability and change

The Cultivated Cereals

The only South Asian cereals which are to be considered in the present context are rice and possibly also *Coix lacryma-jobi*. All the others (wheat, millets, maize, and ragi) have come from elsewhere; their origin from ancestral perennials has occurred outside the confines of western monsoon Asia (Whyte 1978).

Ancestral perennials of the genus *Oryza*, occupants of ecological niches in tropical wet evergreen forest, may have crossed from Africa to Asia on the Plate. If, however, evolution of the Gramineae had not proceeded that far when disruption took place, the evolution of the genus *Oryza* from herbaceous bamboos would have proceeded during the transit of the Plate itself. When aridity as a major environmental factor began to affect the original vegetation of the Plate before and after collision with Laurasia, the few component Gramineae of tropical wet evergreen forest, including species of *Oryza*, retreated with the forest to its present relict areas. One such area is along the sea face of the Western Ghats, now much degraded forest and invaded by nonindigenous grasses. That part of this vegetation type at its northern limits would have been exposed to periodic intrusions of aridity from the north, and so to the physiological stress responsible for the evolution of annuals, especially of the prototype annual forms of *Oryza* from which the people at Ahar, near Udaipur in Rajasthan, domesticated rice as a crop.

Species of *Oryza* in the other major relict area, the northeastern corner of South Asia, could have extended south from Assam and Meghalaya across the marshlands into what is now Bengal (India and Bangladesh) and Orissa. In addition, perennial species of *Oryza* crossed into the already established ecosystems of Laurasia. In due course, they spread in appropriate ecological niches in the forest climax vegetation throughout the zone now accepted by rice geneticists as the place of origin of Asian annual rices (Chang, in press), from Assam/Meghalaya in the west to the coast of the South China Sea in the east.

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