Origin and Dissemination of Cultivated Rice in the Eastern Asia

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Introduction

Rice (*Oryza sativa* L.) and associated behaviors for growing rice influenced the Japanese since its introduction to the Japan archipelago. Thus, the origin, diversification and dissemination of rice and rice-growing culture have been studied by many workers.

Earlier studies considered rice to have originated from a common ancestral species (*O. rufipogon* Griff.) in the mountainous regions of the Asian mainland (Chang, 1976; Watabe, 1977). But recent findings made in archaeology, genetics and ecology disagree with this hypothesis.

The word "origin" has been used in at least two different ways. It has been used to mean evolutionary pathway or phylogenetic relationship among relative species. Another, more specific use of this term is time and the place of origin. In this paper, the phylogenesis of *Oryza* species, the geographical and ecological conditions in the homeland of cultivated rice, and the time and the route of introduction of rice and rice-growing culture to Japan are described.

Phylogenesis of wild and cultivated rice:

The *indica-japonica* differentiation:

Cultivars of Asian common rice (*Oryza sativa* L.) are genetically differentiated into *indica* and *japonica*. The classification of *indica* and *japonica* was carried out by pioneer works in 1920s, based on morphological and physiological differences (cf. Kato et al. 1928). Kato et al. (1928) discovered the occurrences of hybrid disgenesis in germ cells of F_1 plants that is caused by a set of duplicate genes. This F_1 sterility was frequently observed in *indica* x *japonica* crosses, while it was infrequent in the crosses within a single group. Later, repeated studies which focused on genetic differentiation among rice cultivars were undertaken. Oka (1958), for example, suggested a tendency of *association of characters and genes*, as represented by significant correlation between character values, or disequilibrium states, in allelic frequencies at independent loci. According to Oka (1958) and subsequent papers, *indica* cultivars are represented by positive reaction to phenol solution, susceptibility to $KClO_3$, and short hull hairs, while *japonica* showed antagonistic characters (Table 1).

Table 1 Antagonistic characters separating *indica* and *japonica* cultivars (after Oka, 1958, 1988, etc.)

Characters / Molecular markers	*indica*	*japonica*
Phenol reaction	positive	negative
$KClO_3$ susceptibility	susceptible	resistance
Hull hair length	short	long or none
Resistance to drought	weak	strong
Isozyme genes		
Pox-2	*1*	*0 (null)*
Pgi-1	*1*	*2*
Cat-1	*2*	*1*

The *indica-Japonica* differentiation in wild relatives:

Oka and his group considered that the *indica-japonica* differentiation did not occur among the strains of *O. rufipogon* (cf. Oka, 1988). However, recent work in molecular genetics supported the assumption that the *indica-japonica* differentiation arises not only among cultivars but in strains of wild progenitors as well. A 69 base-pair deletion at the ORF 100 region in chloroplast DNAs (cpDNA) is common (88%) in *indica* cultivars, while it is rare (6%) in *japonica* cultivars (Ishii et al. 1986; Chen et al. 1993). This deletion was also common in a wild progenitor, *O. nivara*, or annual type of *O. rufipogon* (Dally & Second 1991; Chen et al. 1994). These data suggest that the deletion originated before the domestication of rice and that *indica* and *japonica* belong to different maternal groups.

Restriction fragment length polymorphisms (RFLPs) separated these two types of rice. Strains of cultivated rice were grouped in two clusters that correspond to *indica* and *japonica*, based on RFLPs using more than 20 DNA loci (Wang et al. 1989; Kawase et al. 1991, see Fig. 1). Strains of *O. rufipogon* and *O. nivara* also separated into these same two groups, suggesting that the *indica -japonica* differentiation occurred in the wild progenitor (Fukuta, Y., person. communication). Two pairs of tandem repeat sequences at ribosomal DNA (rDNA) sites were found in *indica* cultivars as well as *O. nivara* populations, while a single pair tandem repeat sequences are found in *japonica* cultivars and in some *O. rufipogon* (Fukui et al. 1994). Another tandem repeat sequence in genomic DNA, *TrsA*, showed a different number of copies between *indica* and *japonica* (Ohtsubo et al. 1990). Molecular size of spacer regions at rDNA locus differed between *indica* and *japonica* cultivars (Sano & Sano 1990). These findings strengthen the assertion that differentiation of the *indica-japonica* occurred prior to domestication (Fig. 2).

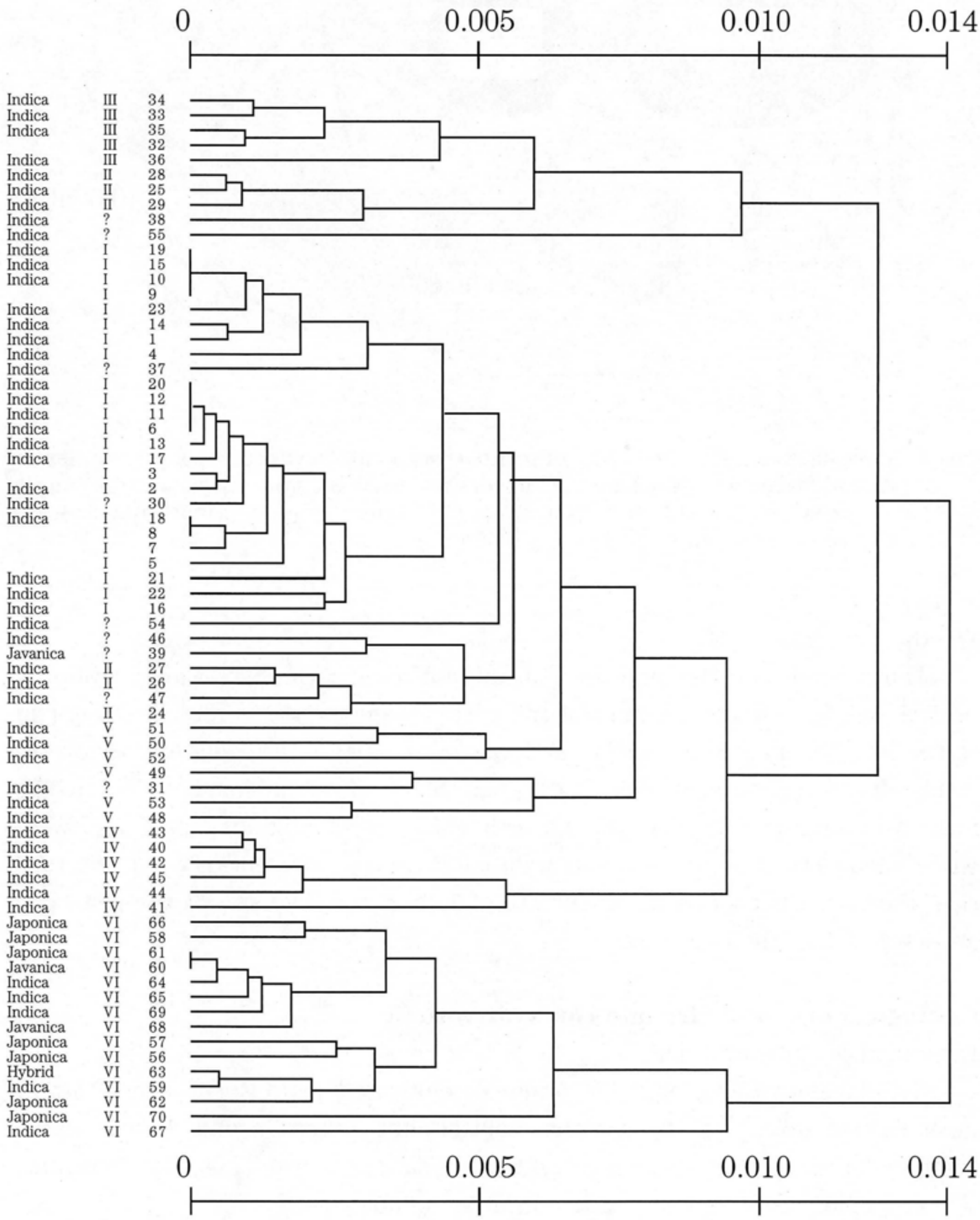

Fig. 1 Classification of rice cultivars by means of RFLP analysis. While intra-group variation is observed, two major groups are identified (Wang & Tanksley, 1989).

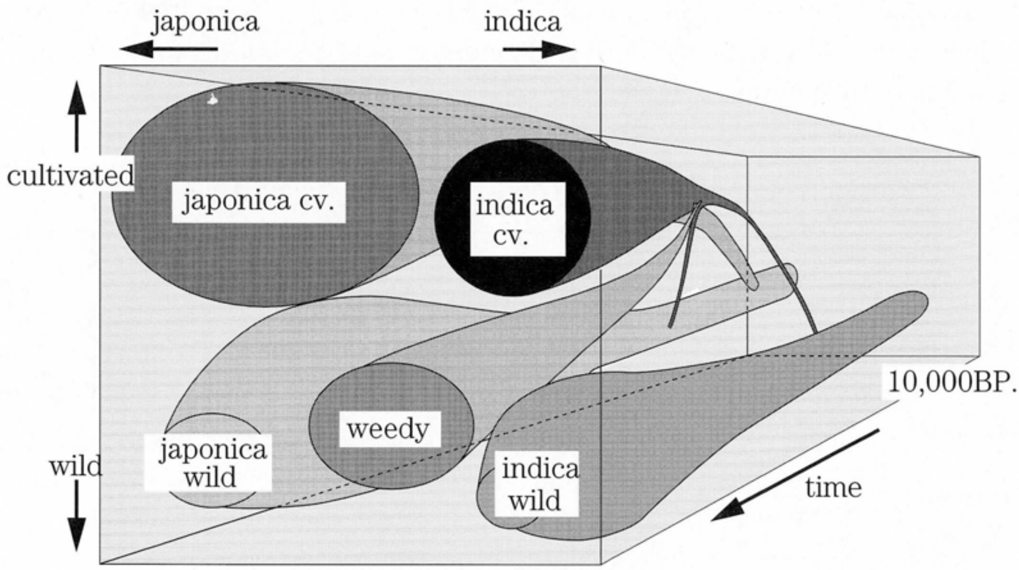

Fig. 2 Three-dimensional tree indicating the evolutionary pathways of rice. *Japonica* cultivars are depicted as having differentiated first from its wild relatives, *Oryza rufipogon*. The origin of *indica* is slightly in than the origin of *japonica*. During evolution, natural hybridization is responsible for the appearance of weedy types.

Weedy rice:

During domestication and diversification of rice, a number of inter-group hybridizations have occurred automatically. This phenomenon is responsible for intermediate types between *indica* and *japonica*. Such intermediate types are recombinant, from the viewpoint of genetics. Some of recombinant types have remained in fields as a *weedy type* since they are unfavorable for cultivation. While such weedy types are considered a problem by the present-day cultivators of rice, they have been playing an important role in the diversity of the gene pool and evolution of the rice plant.

Geological origin of rice and rice cultivation:

Homeland of cultivated rice:

To elucidate the geographic origin of cultivated plant species, analysis for plant remains excavated from archaeological sites is most useful. Domestication is an evolutionary phenomenon caused by human activities. Thus, the domestication and cultivation of plant species occur simultaneously.

According to the archaeological record, the oldest rice cultivation is believed to have originated in the middle and lower basins of Yangtze River. In the lower

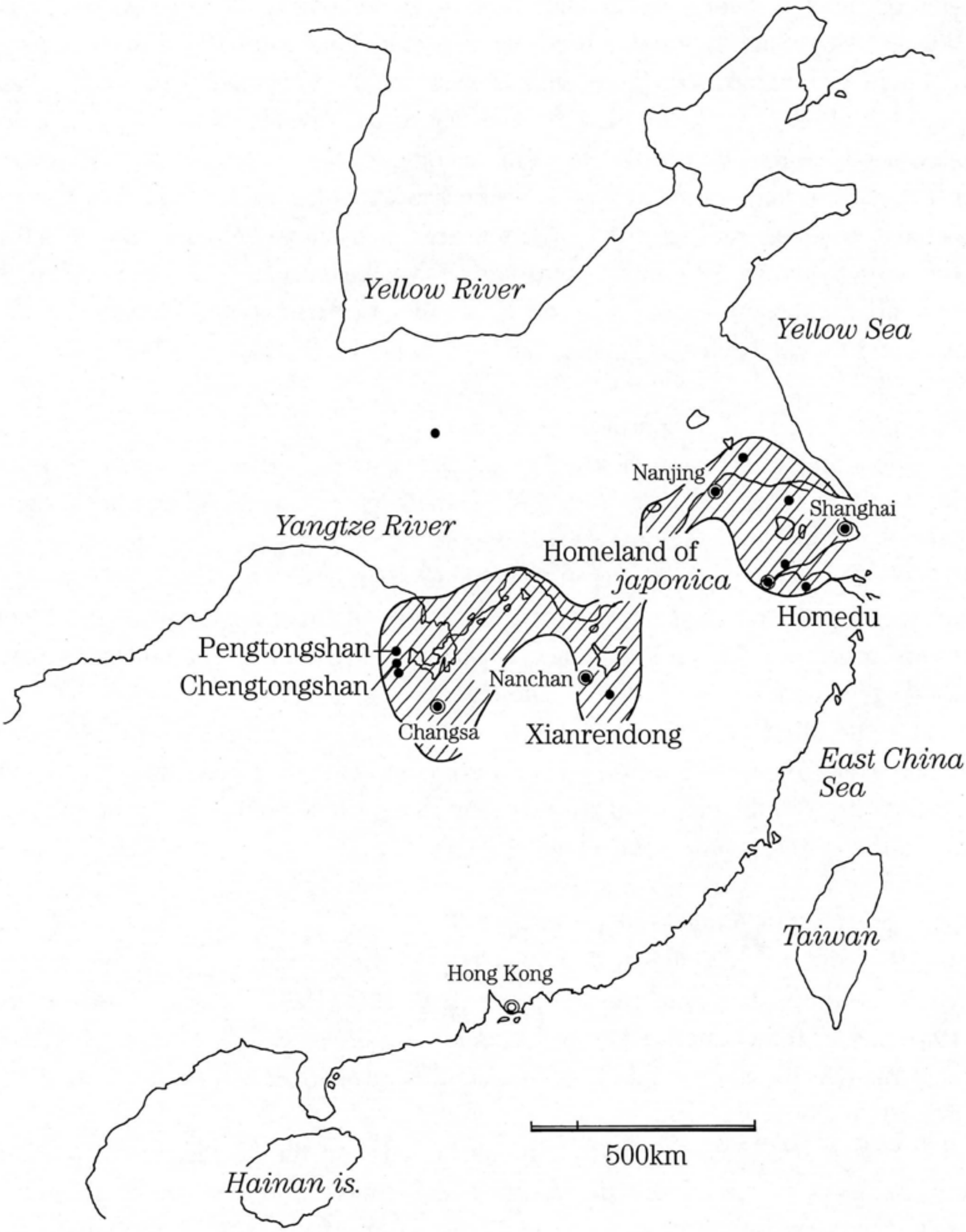

Fig. 3 A map showing the supposed homeland (shaded area) of *japonica*. Dots represent main archaeological sites at which old rice remains (older than 6,000 years BP) have been discovered.

basin of Yangtze River, rice cultivation originated about 7,000 to 8,000 years ago (Wang, 1986). Slightly older records of rice cultivated were recently discovered in Hunan and Jiangxi Provinces, middle basin of the Yangtze River (Yuan, 1992; MacNeish, 1997). At the Homedu site in Zhejiang Province, both wild and cultivated seeds were found in the same archaeological layer (Sato et al. 1991), suggesting that primitive cultivation was practiced there. MacNeish (1997) has reported the oldest rice grain to be discovered in Jiangxi Province to be 16,000 years old. Evidence for cultivation of rice, however, is lacking in these examples. Summarizing these findings, it is concluded that rice cultivation originated in the lower and middle basins of Yangtze River ca 8,000 to 11,000 yrs. BP (Fig. 3).

Beginning of rice cultivation in tropical Asia:

According to latest reviews (Wang, 1986), rice cultivation began approximately 4,000 years BP in tropical Asia, much later than it did in the Yangtze River Basin in China. People have been living in tropical Asia for more than 10,000 years ago. It is considered that domestication of plants and animals was not necessarily practiced in the tropics, because of the ready availability of rich natural resources. There is evidence to suggest that many plant resources were in a stage of semi-domestication in the tropics.

On the other hand, in the temperate zone, the amount of natural resources available as a result of hunting and gathering activities were too small to sustain populations. The limitations of plant resources as a food source undoubtedly promoted the cultivation of certain plant species.

Rice variety at the Yangtze River Basin

DNA analysis has shown that only the *japonica* variety was grown in the middle and lower basins of Yangtze River (Sato et al. 1996, Fig. 3). All rice grains (16 grains in total) analyzed from different archaeological sites (2,000 to 7,000 years BP.) in the middle and lower basins of Yangtze River had no deletion at the ORF 100 region of cpDNA.

Chinese archaeologists and agronomists insist on the coexistence of *indica* and *japonica* in the ancient times, since both round- and slender- shape grains were discovered at different sites in China (You, 1979). Sato (1991) has suggested that size and the shape polymorphisms are not good evidence for the mono-phyletic origin of *indica* and *japonica* in the ancient times. Therefore the shape of the grain is not considered a good separation of the two varieties.

Diversification and progress of rice cultivation:

In China, rice cultivation appears to have diversified throughout the whole rice-growing area (Wang, 1986; Yuang, 1981; Sato, 1996). It is further believed that the rice-growing culture is responsible for the emergence of the Yangtze River civilizations.

Some of the derivatives of rice originated in the homeland may have reached the Yellow River Basin by 6,000 BP, becoming the staple food of the civilizations of this region. Following this, however, conflict between various struggling factions led to a dramatic decline in the early civilizations of the Yantze River region in ca. 3,000 BP. During this period, it is believed that many people left this region in search of new homelands. Some of these people reached the present day southwestern provinces of China with *japonica* rice and their associated cultures. Others arrived in western Japan crossing the East China sea, or by way of the Korean peninsula.

Dissemination of rice and rice cultivation to the Japan Islands:

There are two types of *japonica*: tropical *japonica* and temperate *japonica*. *Japonica* cultivars are further divided into tropical and temperate types (Oka, 1958). Compared to temperate *japonica*, tropical *japonica* has long, thick, but fewer culms (stems), and long and broad leaves. The temperate variety further adapts to slash-and-burn cultivation in the upland fields, the tropical variety does best in paddy fields. The origin of these two types of rice is still unknown.

Introduction of rice to the Japan Islands:

Rice and rice-growing cultures promptly diversified in eastern and southeastern China during a period of a few thousand years after their first appearance. It is reasonable to assume that some of the derived strains reached Japan across the East China Sea during this period. This scenario, however, is not supported by archaeology due to the poor archaeological record during the Jomon Period. Because the oldest paddy field thus far do not have dates older than 2,400 years BP, it has led archaeologists to hypothesis that rice cultivation began no earlier than the Yayoi Period. Archaeological evidence of paddy rice cultivation include existence of dike and irrigation canal. However, in Asia, rice cultivation is practiced not only in paddy fields which require the building of dikes but also in dry upland rice fields which usually lack dikes and irrigation canals. Thus, the lack of such evidence cannot rule out rice cultivation during the Jomon Period.

On the other hand, circumstantial evidence for the existence of rice cultivation in Jomon Period has been obtained from genetic analysis of traditional rice strains (Sato, 1990). Sato (1990) has reported high frequencies of a gene responsible for F_1 weakness (*hwc*-2) in the Ryukyu Islands. In *japonica* strains, the

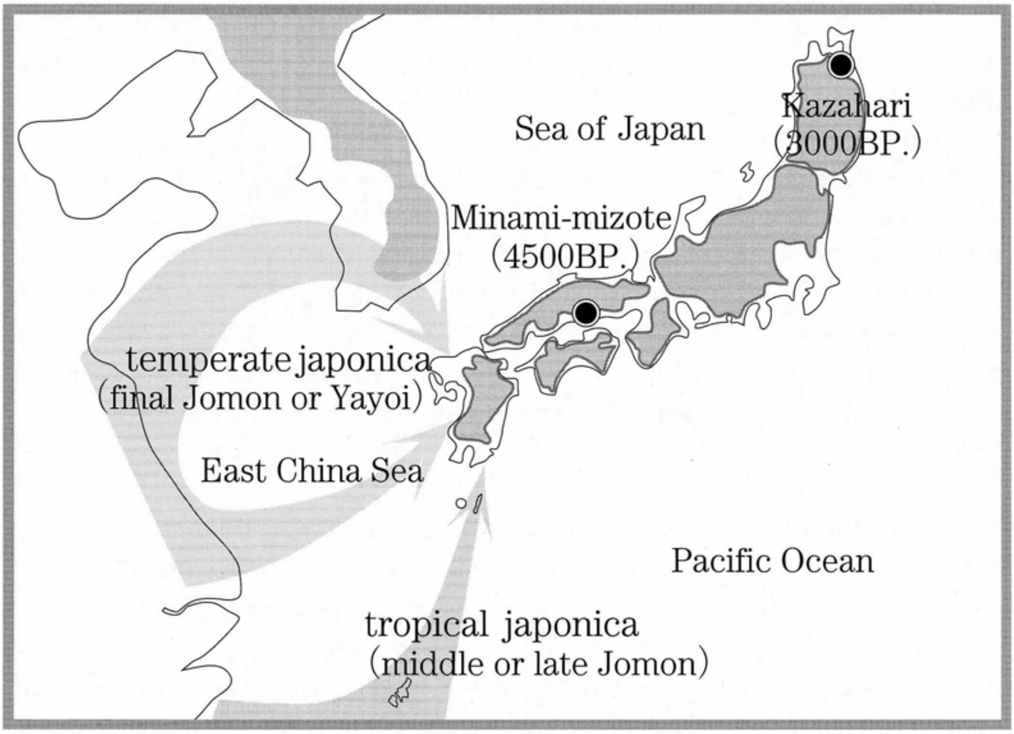

Fig. 4 Supposed migration route of rice to Japan. Tropical *japonica* is shown as having been introduced during the Jomon Period, while temperate *japonica*, which adapts to paddy rice cultivation, is shown as having arrived in late Jomon or Yayoi Periods.

hwc-2 gene is specific to strains that are adapted to upland conditions which are believed to have been transmitted to Japan Islands prior to the introduction of paddy rice cultivation (Fig. 4).

Problems left unresolved:

Where did *indica* varieties originate? In earlier hypotheses on the geographic origin, both *indica* and *japonica* were considered to have originated in the same region. Recent work suggests that only *japonica* originated in the Yangtze River Basin. Thus, for the time being, the homeland of *indica* is unknown. Based on ecological considerations, it is most probable that *indica* cultivation began in the flooded plains of the big rivers in the tropics, such as the Mekong, Chaopraya, Irawadhi, and Ganga-Bramaptra Rivers (Fig. 5).

The question of the type of *japonica* that originated in the middle and lower basins of Yangtze River is also important in identifying the features of rice-growing systems in that area and in Japan. A starch in rice seeds which is responsible for the difference between glutinous, sticky or sweet (in Japanese: *mo-*

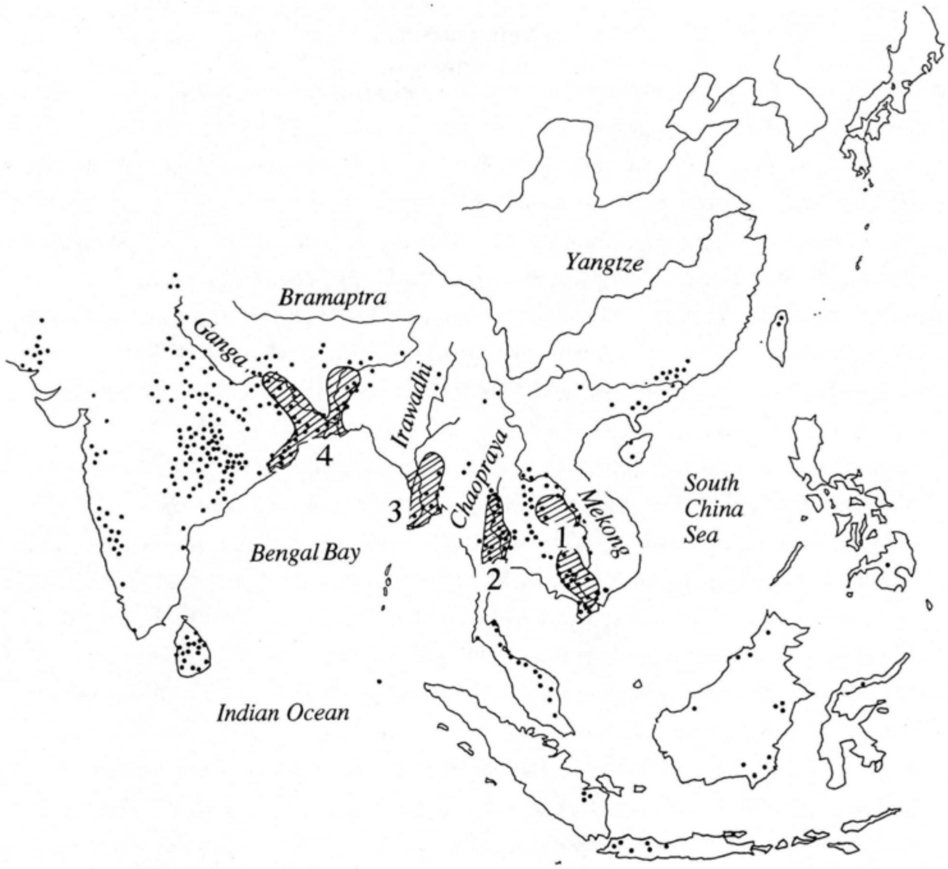

Fig. 5 Possible areas of the homeland of *indica*. 1; Mekong, 2; Chaopraya, 3; Irawadhi and 4; Ganga -Bramaptra Rivers.

chi) rice and ordinary (non-sticky) rice is an important feature in identifying the origins of rice and their respective preferences in ancient people.

Many problems require resolution in the future. An interdisciplinary approach involving biology, agronomy, anthropology and related fields of science are required for a comprehensive understanding of the origin of rice.

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