

III.1

Phylogeny and Biogeography of the Genus *Oryza*

Duncan A. Vaughan¹(✉), Song Ge², Akito Kaga¹, and Norihiko Tomooka¹

1 Introduction

Plants with characteristics of species belonging to the tribe Oryzeae were present in India more than 60 million years ago (Ma), early in the history of grasses (Prasad et al. 2005). This tribe is now represented by 11 genera that are found in tropical and temperate regions of the world. Among genera in the tribe Oryzeae, the genus *Oryza*, with about 23 species, has been remarkably successful in evolutionary terms. Species of *Oryza* with the A and C genomes have a pan-tropical distribution. Rice has been domesticated from wild A genome wild *Oryza* several times and is the world's most important staple food. Among cereals, rice has a small genome and is considered as a model for genome studies. The genus *Oryza* is of particular interest not only because it is the genus of rice but also because of what the genus can tell us about other grasses.

The genus *Oryza* is subject to increased research attention now that the rice genome has been fully sequenced. There are now BAC libraries for species representing most of the genomes of the genus *Oryza* (Ammiraju et al. 2006). The objective of this chapter is to consider the genus *Oryza* from phylogenetic and biogeographic perspectives, with emphasis on recent research.

¹National Institute of Agrobiological Sciences, 2-1-2 Kannondai, Tsukuba, Ibaraki 305-8602, Japan
e-mail: duncan@affrc.go.jp; kaga@nias.affrc.go.jp; tomooka@affrc.go.jp

²Key State Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China
e-mail: gesong@ibcas.ac.cn

Table 1 Dates associated with the rise of angiosperms and *Oryza*

Event	Date	Basis
Origin of the angiosperms	145–208 Ma	
Origin of monocots	≈134 Ma	
Separation of Africa from other Gondwanan areas	≈105 Ma	
Origin of Poales	>100 Ma	
Origin of Poaceae	≈85 Ma	Molecular clock
Evidence of Oryzaeae	≈65 Ma	Phytolith
First grass pollen	70? 60–55 Ma	Fossil
Divergence of BEP/PACC clades	≈50 Ma?	
Northern hemisphere BEP/PACC clade evidence	≈34 Ma	Phytolith
Divergence of Oryzaeae and Pooideae	≈35 Ma	Molecular clock
Breakup of the Antarctic connection between South America and Australia	≈35 Ma	
Divergence of subtribes Oryzinae and Zizaniinae	≈20 Ma	Molecular clock
Divergence of <i>Leersia</i> and <i>Oryza</i>	≈14 Ma	Molecular clock
Divergence of <i>O. meridionalis</i> and <i>O. longistaminata</i> from other AA genome <i>Oryza</i>	≈2 Ma	Molecular clock
Divergence of <i>O. glaberrima</i> and <i>O. sativa</i>	≈0.7 or 0.64	Molecular clock
Divergence of <i>indica</i> and <i>japonica</i> subspecies	≈0.44, 0.4 or >0.2 Ma	Molecular clock

2 Phylogeny

2.1 Before Grasses

The origin of the angiosperms is believed to have been a complex process that involved various phases of rapid diversification, reflecting the interactive effects of biological traits and the environment, along different lineages (Davies et al. 2004). Fossil evidence is lacking for the time when angiosperms are thought to have diverged from other plants, but all more recent estimates based mainly on sequence data point to a time for this divergence in the Jurassic (145–208 Ma) (Table 1; Sanderson et al. 2004). Analyses of several multigene phylogenies have enabled the relationship in the angiosperms of monocots to other plant groups to be elucidated (Soltis and Soltis 2004). Within angiosperms, the monocots represent an ancient lineage and monocots are believed to have emerged before 100 Ma (Chase 2004). The herbaceous, aquatic family Ceratophyllaceae is one of the closest families to the monocots among dicots (Barkman et al. 2000; Kuzoff and Gasser 2000).

2.2 Poaceae Phylogeny

International taxonomic collaboration is being conducted in order to understand the relationships among the Poaceae using morphological, anatomical, cytological and

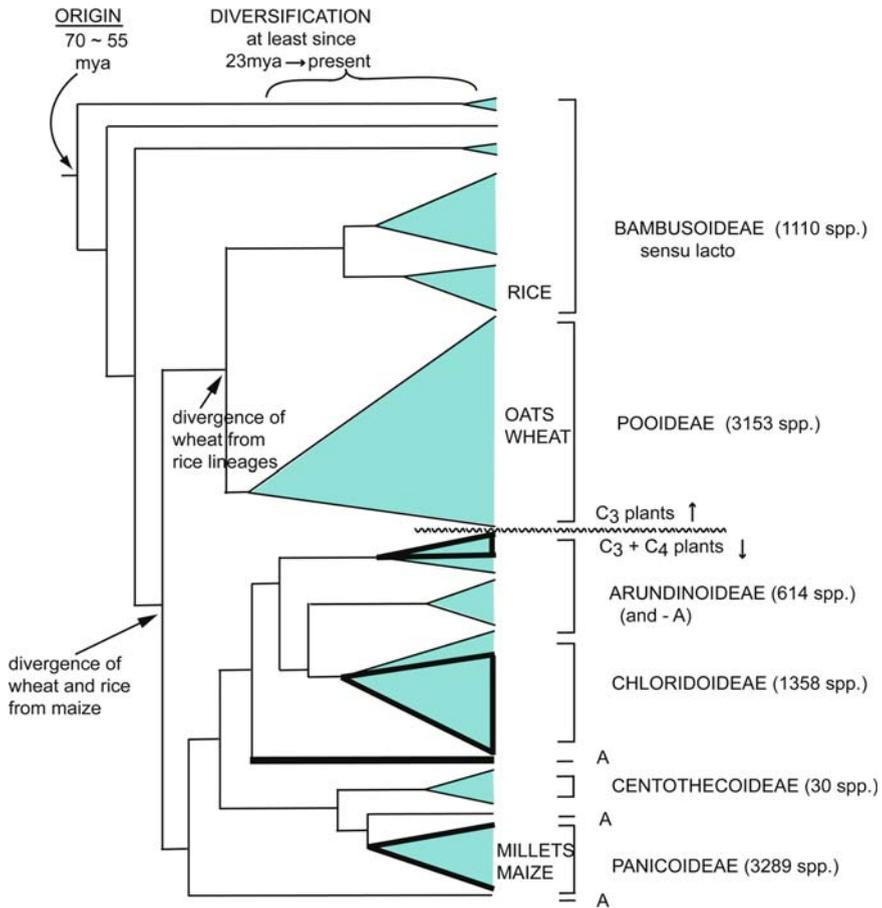


Fig. 1 Phylogeny of the Poaceae based on molecular and morphological characteristics, showing the main points of divergence. Species numbers are from Clayton and Renvoize (1986). *Thick lines* indicate C4 photosynthesis lineages. (From Vaughan et al. 2005)

genetic data (GPWG 2000, 2001). This has enabled us to determine the fundamental relationships among the major groups of grasses based on analysis of these traits (Fig. 1).

Oryza in the current grass phylogeny is in a group paraphyletic with the ‘core’ bamboos (Bambusoideae) and is placed in the subfamily Ehrhartoideae (Kellogg 1998; Zhang and Clark 2000; GPWG 2001). The Bambusoideae *sensu lato* (including *Oryza*) is a polyphyletic assemblage (Fig. 1; Zhang and Clark 2000). Among the major cereals, only rice is found in the ancient lineage of Bambusoideae (Gaut 2002).

The tribe Oryzeae is the largest tribe in the subfamily Ehrhartoideae and includes 11 genera, all but *Leersia*, *Luziola* and *Oryza* consisting of five or fewer extant species (Table 2). Molecular analysis has reinforced earlier taxonomic studies that show that the tribe Oryzeae consists of two groups of genera that have been named subtribes Oryzinae and Zizaniinae (Ge et al. 2002; Guo and Ge 2005).

Table 2 Genera of the tribe Oryzeae and their characteristics (updated from Vaughan 2003)

Subtribe Genus	Species (no.)	Distribution	Chromosome number (2n) ^a	Spikelet structure
<i>Oryzinae</i>				
<i>Oryza</i> ^b	23	Pantropical (T)	24, 48	Bisexual
<i>Leersia</i>	17	Worldwide (t+T)	24, 28, 48, 72, 96	Bisexual
<i>Zizaniinae</i>				
<i>Chikusichloa</i>	3	China, Japan (t)	24	Bisexual
<i>Hygroryza</i>	1	Asia (t+T)	24	Bisexual
<i>Zizania</i>	4	Europe, Asia and North America (t+T)	20, 30, 34	Unisexual
<i>Luziola</i>	11	North and South America (t+T)	24	Unisexual
<i>Zizaniopsis</i>	5	North and South America (t+T)	24	Unisexual
<i>Rhynchoryza</i>	1	South America (T)	24	Bisexual
<i>Maltebrunia</i>	5	Tropical and southern Africa (T)	Unknown	Bisexual
<i>Prospytochloa</i>	1	Southern Africa (t)	24	Bisexual
<i>Potomophila</i>	1	Australia (t+T)	24	Unisexual and bisexual

^aFrom the Missouri Botanical Garden's Index to Plant Chromosome Numbers database (<http://mobot.mobot.org/W3T/Search/ipcn.html>)

^bRecently the genus *Porteresia* has been merged with *Oryza* (Lu and Ge 2005)

2.3 Evolution of Grasses

Coprolites believed to be from dinosaur titanosaur sauropods have been found in India that contain diverse grass phytoliths (Prasad et al. 2005). Among the diversity of grass phytoliths found in these coprolites are bilobate and cross-shaped phytoliths characteristic of present-day genera of Oryzeae (Prasad et al. 2005). These coprolites are dated to the late Cretaceous, about 65 Ma. Other evidence of early grasses includes presumed fossil grass pollen dated to between 60 and 70 Ma and the earliest grass flower dated at approximately 55 Ma (Stromberg 2005). Molecular data suggest a date of about 83 Ma for the origin of the crown group of Poaceae (Bremer 2002). Thus early grasses, including those of the tribe Oryzeae, were present when some parts of Gondwana had not separated.

The most primitive extant grasses are found in South America (Bremer 2002). Thus Gondwana vicariance may be a factor that explains the distribution of grasses in South America and Australia, since migration between these continents via Antarctica was possible until about 38 Ma. However, the break of Africa from the rest of Gondwana was much earlier, at about 105 Ma (McLoughlin 2001).

The majority of grasses fall into two groups known by the acronyms of their constituent subfamilies: the BEP [Bambusoideae s. str., Ehrhartoideae (= Oryzoideae) and Pooideae] and PACC [Panicoideae, Arundinoideae s. str., Chloridoideae s. l., Centothecoideae] clades. Within the BEP clade are only grasses with C3 photosynthetic systems, including rice and wheat. The PACC clade includes grasses with C3 and C4 photosynthetic systems, including maize and millets (Fig. 1).

Phytolith evidence from North America indicates that both the BEP and PACC clades were present about 34 Ma (Stromberg 2005). Molecular clock data suggest a possible date of about 50 Ma for the divergence of these two clades (Bremer 2002). A much earlier date for the emergence of the PACC clade based on phytoliths (Prasad et al. 2005) is ambiguous at present (Piperno and Sues 2005).

While the origin of grasses is now considered to be the late Cretaceous and diversification occurred early in their evolution, the rise in ecosystem dominance of grasses was slow. The spread of grass-dominated ecosystems was linked with global climate change, cooling and drying, in the late Tertiary (Chapman 1996; Stromberg 2005).

2.4 An Emerging Scenario for the Origin of *Oryza*

Based on molecular clock data, an estimate of 20–22 Ma has been given for the split between the subtribes of Oryzae, Oryzinae and Zizaniinae, and 14.2 Ma for the separation of *Oryza* and *Leersia* (Guo and Ge 2005).

The genus *Oryza* has been divided into three sections: *Padia*, *Brachyantha* and *Oryza* (Lu 1999). Of these, the basal section is thought to be section *Padia* which consists of the forest-dwelling *Oryza*, *O. schlechteri*, the *O. ridleyi* complex and the *O. granulata* complex (Sharma 2003). *Oryza schlechteri* is a diminutive tetraploid species that grows on unstable forested river banks. It exhibits prolific stolon development which enables this species to spread horizontally and climb over other vegetation. It has characteristic nodal hairs that seem to be an adaptation to absorbing moisture from the air.

The species of the *O. ridleyi* complex also have stolons and are adapted to swampy forest habitats. In contrast, species of the *O. granulata* complex are adapted to non-flooded forests, often in highland areas (Table 3). The habitats of species in

Table 3 The genomes, usual habitats and life cycles of species in the four *Oryza* species complexes

Characteristic	<i>O. granulata</i> complex	<i>O. ridleyi</i> complex	<i>O. officinalis</i> complex	<i>O. sativa</i> complex
Genome(s)	GG	HHJJ	BB, CC, BBCC, CCDD, EE	AA
Usual habitat conditions:				
(a) Elevation	Tropical uplands and lowlands	Tropical lowlands	Tropical lowlands	Tropical lowlands
(b) Associated main vegetation types	Tropical deciduous forests	Tropical rain-forests	Tropical deciduous forests and grasslands	Lakes, rivers and seasonal pools
(c) Basic water requirements	Dryland	Seasonal wetlands	Seasonal wetlands	Seasonal and permanent wetlands
(d) Light requirements	Full to partial shade	Full to partial shade	Full or partial shade or full sun	Full sun
Life cycle	Perennial	Perennial	Perennial	Perennial to annual

section *Padia* are similar to the type of habitats that early grasses are thought to have evolved in (Feild et al. 2003). Recently molecular clock data have suggested that the *O. granulata* complex diverged from other *Oryza* about 8 Ma (Guo and Ge 2005). Diploid species that contributed the H, J and K genomes to the tetraploid *O. schlechteri* and *O. ridleyi* complex species are unknown. If these diploid species exist they will most likely be found in New Guinea and would reveal much about *Oryza* evolution.

Oryza brachyantha is the only species in section *Brachyantha*. This species is widely distributed across Africa, in a specific habitat of iron-pan rock pools. It is morphologically the most similar *Oryza* species to *Leersia* (Lauert 1965).

Section *Oryza* consists of two species complexes, the *O. officinalis* complex with the B, C, D and E genomes and *O. sativa* complex with the A genome. The genetically most diverged of the species of the *O. officinalis* complex is the little-studied species *O. australiensis* with the EE genome. Species with the CC genome are the most widely distributed and are adapted to a wide spectrum of environments, from semi-shade of forest clearings to open savannah (Vaughan 2003). Hybrids between different CC genome species from different areas show high sterility (Ogawa 2003). Among CC genome species, *O. eichingeri* appears to be basal (Shcherban et al. 2000, 2001).

Like the *O. officinalis* complex, the *O. sativa* complex has attained a pan-tropical distribution. However, it contrasts with the *O. officinalis* complex in that all species of this complex are diploid and have a single genome, the A genome.

There are several reports of similar dates for divergence of AA genome *Oryza* species. These suggest the first divergence was between ancestors of the Australian AA genome species, *O. meridionalis*, and other AA genome *Oryza* about 2 Ma (Zhu and Ge 2005). Divergence between African and Asian AA genome species appears to have occurred twice: the first time between ancestors of *O. longistaminata* and Asian AA genome *Oryza* and a second time between ancestors of the annual African *Oryza*, *O. barthii* and *O. glaberrima*, and Asian AA genome *Oryza*.

Dates for the first divergence of Asian–African AA genome species of 2–3 Ma have been suggested (Vitte and Panaud 2003). This would correspond to a time similar to that given for the divergence of *O. longistaminata*, the perennial African AA genome species, and *O. meridionalis* (Zhu and Ge 2005).

Based on nuclear DNA sequence data, Ma and Bennetzen (2004) estimated a date for the second divergence between Asian and African A genome species of about 0.64 Ma by looking at the divergence between ancestors of *O. glaberrima* and *O. sativa*. Zhu and Ge (2005), using intron sequence data from three nuclear genes, reported very similar dates for this divergence (approximately 0.7 Ma).

These molecular clock dates and various molecular studies do not support the hypothesis that *O. longistaminata* is the immediate perennial ancestor of *O. barthii* and *O. glaberrima* (Khush 1997). The date for divergence of *O. longistaminata* from Asian AA genome *Oryza* (2–3 Ma) and the later date for the divergence of the African-cultivated gene pool (*O. glaberrima* and *O. barthii*) (0.6–0.7 Ma) from the AA *Oryza* gene pool suggest that they represented different lineages from the Asian AA genome gene pool. If this were correct, *O. longistaminata* would not be the direct perennial ancestor of *O. glaberrima*. The studies of the catalase gene (Iwamoto et al. 1999), RFLP (Wang et al. 1992), AFLP (Aggarwal et al. 1999) and

p-SINE1 (Cheng et al. 2003) could all be interpreted to support the hypothesis that *O. longistaminata* is not the direct perennial ancestor of *O. glaberrima*. Based on a study of twin microsatellites, Akagi et al. (1998) concluded that *O. barthii* has a closer affinity with *O. rufipogon* than with *O. longistaminata*.

Several studies have reported molecular divergence dates for the two subspecies of cultivated Asian rice, *indica* and *japonica* (Ma and Bennetzen 2004; Vitte et al. 2004; Zhu and Ge 2005). These studies point to divergence of 0.2–0.44 Ma that is unequivocally before the domestication of rice. While most accumulated evidence tends to support dual or multiple domestication of rice (Fuller 2003b; Londo et al. 2006), some recent data do not support this (Lin et al. 2007). Thus the story of the evolution of cultivated rice in Asia is still unclear (Sweeney and McCouch 2007; Tao and Ge 2007).

3 *Oryza* Biogeography

Extant genera of Oryzae are found almost equally in the Americas (5 genera), Africa (4) and Asia (5). Thus it is not possible to suggest where this tribe arose. Comparison of the three Oryzae genera, *Leersia*, *Luziola* and *Oryza*, with more than 10 species shows that each has greatest species diversity in different regions of the world. *Oryza* is most diverse in Australasia (Vaughan et al. 2005), *Leersia* in Africa (Table 4), and *Luziola* is confined to the Americas. That these closely related genera have diversified in different regions is probably a reflection of the antiquity of the tribe Oryzae.

Table 4 *Leersia* species (based on Launert 1965; Pyrah 1969). (Chromosome numbers from <http://mobot.mobot.org/W3T/Search/ipcn.html>)

Species	Chromosome number (2n)	Distribution
<i>L. monandra</i>		Caribbean, Texas, Florida and Mexico
<i>L. ligularis</i>	48	Mexico to northern Argentina and Paraguay
<i>L. stipitate</i>		Thailand
<i>L. japonica</i>	96	East Africa
<i>L. hexandra</i>	48,72	Wet tropics and subtropics worldwide
<i>L. lenticularia</i>	48	Eastern USA
<i>L. oryzoides</i>	28,48	USA, Europe to Japan
<i>L. virginica</i>	48	Eastern USA and Brazil
<i>L. triandra</i>		Sierra Leone and Liberia
<i>L. nematostachya</i>		Angola and Zambia
<i>L. friesii</i>		Angola, Congo, Tanzania, Zambia
<i>L. perrieri</i>	24	Madagascar
<i>L. tisserantii</i>	24	Congo, Kenya and Zambia
<i>L. drepanothrix</i>		West Africa, Sudan and Uganda
<i>L. oncothrix</i>		Zambia
<i>L. angustifolia</i>		Congo and Sudan
<i>L. denudata</i>		Kenya and Zimbabwe

3.1 *The Distribution of Oryza Species and Species Complexes*

As discussed above, *Oryza* has been divided into three taxonomic sections. Species of section *Padia* are only found in Asia, Australia, New Caledonia and Papua New Guinea. The monospecific section *Brachyantha* is only found in Africa. Section *Oryza* has a pan-tropical distribution but is most diverse in Asia and Australia.

From ecological, genetic and morphological perspectives all but three *Oryza* species, *O. brachyantha*, *O. coarctata* and *O. schlechteri*, fall into four clearly defined species complexes. These species complexes are *O. sativa*, *O. officinalis*, *O. ridleyi* and *O. granulata* (Table 3; Tateoka 1962a). Species complexes refer to a group of species for which there are a lack of good taxonomic key characters; hence whether the taxonomic rank of species or subspecies is used is rather arbitrary. This is best illustrated with the *O. granulata* complex, for which five species names have been validly published: *O. abromeitiana*, *O. granulata*, *O. indandamanica*, *O. meyeriana* and *O. neocaledonica*. However, the main distinguishing criteria are spikelet size and shape and this has been shown to vary continuously when many samples are studied (Tateoka 1962b). Generally the two widely distributed species, *O. granulata* and *O. meyeriana*, are recognised and the other three species, represented by one or a very few known populations, are considered local variants of these two species.

The phylogenetic distribution of functional traits suggests that the ecological setting for early angiosperms was shaded, disturbed-forest understory and/or shady stream sides (Feild et al. 2003). This is precisely the habitat where *O. schlechteri* grows. The type locality of *O. schlechteri* is the Finisterre Mountains of Papua New Guinea. This young mountain range is characterised by frequent landslips (Hovius et al. 1998). *Oryza schlechteri* grows in shade along streams on unstable soil and rocks. A visit to one population of this species by the author found part of it buried beneath a natural landslide (D.A.V., pers. observ. 2005). Distribution, morphology, habit and habitat all suggest that this species is likely to be descended from an early lineage in the genus *Oryza*.

Early monocots are thought to have been aquatic (Doyle 1998) and living in forested areas or forest margins (Kellogg 2001). Among *Oryza* species complexes, the tetraploid *O. ridleyi* complex that shares the HH genome with *O. schlechteri* is found in seasonally inundated forests beside lakes and rivers. This complex is most common and diverse in New Guinea. *Oryza ridleyi* complex species share the trait of stolon formation with *O. schlechteri*. If diploid species with the genome of the *O. ridleyi* complex and *O. schlechteri* are still extant, they would be expected to be found in the vast tracks of wet forested lowlands or lower elevations in the mountains of New Guinea. Early diploid aquatic or semi-aquatic *Oryza* of wet forests may have adapted to dryer deciduous woodland habitats as climates changed in some regions, giving rise to the *O. granulata* complex species.

The *O. ridleyi* complex is distributed across Southeast Asia and New Guinea (Fig. 2). The *O. granulata* complex is also most diverse across insular Southeast

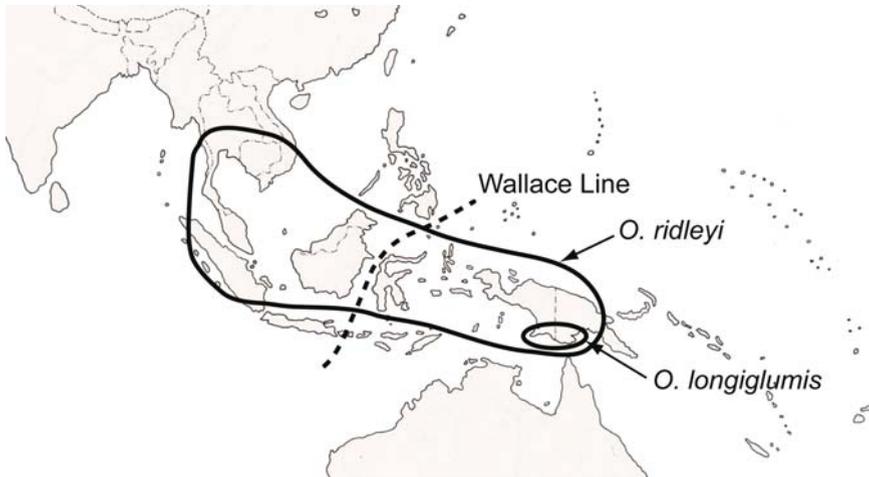


Fig. 2 Distribution of the *O. ridleyi* complex. (From Vaughan et al. 2005)

Asia, particularly Java, Indonesia, from which it likely spread to continental Asia (Fig. 3). The *O. ridleyi* and *O. granulata* complexes belong to the 'primitive' or 'ancestral' section of the genus, section *Padia* (Sharma 2003). They are distributed where many of the closest relatives of grasses (Flagellariaceae, Joinvilleaceae and Ecdeiocoleaceae) also occur, the Australasian region (Watson and Dallwitz 1992). These data suggest that this is the region where *Oryza* arose. New Guinea has greater *Oryza* genome diversity than any other geographic region (Vaughan 1991). On the basis of current *Oryza* diversity and the distribution of grass relatives, the Australasian zone appears to be the most likely region where *Oryza* first evolved and from where they spread to other tropical regions (Fig. 4). The antiquity of *Oryza* may be reflected by the fact that all four *Oryza* complexes (*O. granulata*, *O. ridleyi*, *O. sativa* and *O. officinalis*) are distributed on both sides of the biogeographical boundary called the Wallace Line. In the case of the *O. granulata* complex, one species reported east of the Wallace Line is *Oryza neocaledonica* Morat. This species grows on the island where the monotypic genus *Amborella* is found. *Amborella trichopoda* is a sister outgroup for angiosperm phylogenetic studies and testifies to New Caledonia as a special place in the evolutionary history of plants (Friedman 2006).

Section *Oryza* with the *O. officinalis* and *O. sativa* complexes appears to be the most recent lineage within *Oryza* (Sharma 2003). With regard to the *O. officinalis* complex, current centres of diversity are in East Africa and southern South Asia.

Studies of AA genome species from a wide geographic area suggest that the Australasian species *O. meridionalis* is genetically most diverged (Doi et al. 2000; Zhu and Ge 2005). Due to the domestication of rice, AA genome wild species appear most diverse in mainland Asia and West Africa. Haplotype studies of *O. rufipogon* have suggested that this species is most ancient in India and Indochina (Londo et al. 2006). However, in New Guinea, *O. rufipogon* and *O. meridionalis*

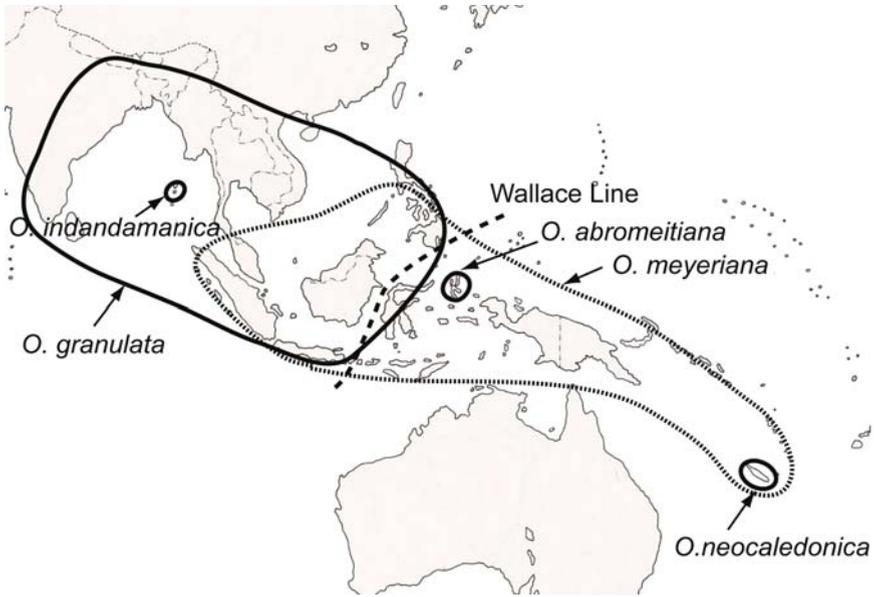


Fig. 3 Distribution of the *O. granulata* complex. (From Vaughan et al. 2005)

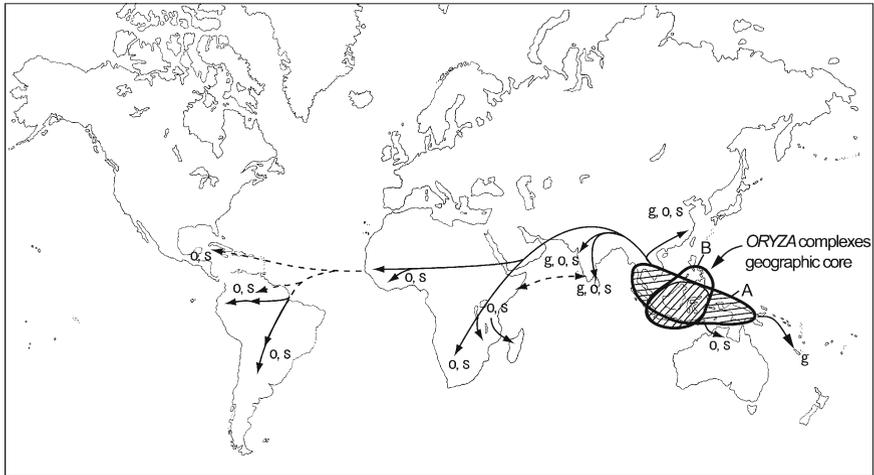


Fig. 4 The geographic center of diversity of the genus *Oryza* and possible routes of spread from this core center for the *O. sativa* (s), *O. officinalis* (o) and *O. granolata* (g) complexes. (From Vaughan et al. 2005)

lineages are found, resulting in higher genetic diversity for the A genome there than in other regions (Doi et al. 2000; D.A.V., unpublished data).

While the origin of the genus *Oryza* may have been in the Australasian region, the *O. sativa* and *O. officinalis* complex ancestors spread and diversified to other

regions. All Africa *Oryza* species can be found in East Africa. Climate change and isolation after distribution have resulted in distinct ecogeographic races within the *O. sativa* and *O. officinalis* complexes (Second 1991). The distribution of *Oryza* in the New World probably occurred later than in other areas, with introductions of the *O. sativa* complex evolving into regionally distinct Latin American forms, now usually called *O. glumaepatula* (Akimoto et al. 1997). Most studies suggest a greater affinity of *O. glumaepatula* to African members of the *O. sativa* complex than to Asian members (Vaughan and Morishima 2003).

3.2 *Animals, Humans and Birds and the Biogeography of Oryza Species*

The hypothesis that *Oryza* arose on Gondwanaland and that continental drift can explain the distribution of *Oryza* species (Khush 1997) is no longer in accordance with known facts concerning the evolution of grasses and *Oryza*. Therefore *Oryza* biogeography must be explained by long-distance dispersal. The distribution of *Oryza* species can best be explained in relation to the movement of animals, including humans and birds. Biotic dispersal is common in angiosperms, with more than 50% of species being dispersed by biotic or biotic and abiotic means (Tiffney 2004).

Many animal groups are distributed in both Asia and Africa and some of them, such as elephants and buffalo, are intimately associated with *Oryza* species. In Africa, forest elephants are believed to have adapted to savannah habitats about 2.6 Ma (Roca et al. 2005). African elephants (*Loxodontia* spp.) and Asian elephants (*Elephas maximus*) are believed to have diverged about 5–7 Ma or earlier (Debruyne 2001). Elephants eat wild rice and their role in seed dispersal has been documented (Ridley 1930).

Phylogenetic studies suggest the African buffalo (genus *Syncerus*) and Asian water buffalo (genus *Bubalus*) diverged more recently than elephants, at less than 4 Ma (Ritz et al. 2000; Buntjer et al. 2002). Buffalo and other bovine species also eat wild rice, so their role in past seed dispersal between Asia and Africa may help explain the rather recent dates (less than 1 Ma) for divergence of annual forms of African and Asian wild AA *Oryza* species (Barbier et al. 1991; Ma and Bennetzen 2004; Zhu and Ge 2005).

The phytogeographic link between Africa and Asia today looks tenuous because of the Sahara Desert and deserts of the Middle East which form a distinct barrier to plant distribution. However, these deserts were green as recently as 6000 years ago and at that time the area where the Sahara Desert is now situated had a hospitable environment for hippopotamuses, which need year-round water (Kutzbach et al. 1996; Kuper and Kröpelin 2006). In addition the archaeological record clearly shows that African plant domesticates appeared very early in South Asia (Fuller 2003a). Over the time scale that has been suggested for the divergence between Asian AA genome *Oryza* and progenitors of African rice (*O. glaberrima*) of

approximately 0.64 Ma, a hospitable environment for animals and prehistoric humans to pass between Africa and Asia existed. Isozyme analysis of wild and primitive cultivated varieties of rice from western India has suggested a link between Asian and African rice (Lolo and Second 1988). The southern movement of the African monsoon caused the Sahara region to dry up about 5000 years ago. The distribution of *O. barthii*, the presumed annual ancestor of *O. glaberrima*, is widely distributed along the entire southern fringe of the Sahara Desert from Ethiopia to Senegal (Vaughan 1994). Elephants, buffaloes and other megafauna are possible vectors involved in *Oryza* distribution. Prior to the Pleistocene extinction (50,000–10,000 years ago) there were many more large animals than there are today that could have moved plant seeds between continents (Barnosky et al. 2004). Wild *Oryza* species are important forage for cattle today in some countries (Vaughan and Sitch 1991). In addition, the role of humans in prehistoric times as a vector of *Oryza* species is also possible. *Oryza* species are likely to have been gathered as food by humans long before agriculture in a manner similar to that observed today in various parts of the world (Vaughan and Sitch 1991).

Another agent that may explain the disjunctive distribution of some *Oryza* species is migrating birds. For example, *O. eichingeri* is present in East Africa and Sri Lanka. There are birds, including many water-loving species, that migrate from Africa across the Indian Ocean to South Asia and back (Ackerman 2004). Since many aquatic birds are migratory and most *Oryza* species are found in aquatic habitats the role of birds in distributing rice seeds seems probable. Birds could have distributed *Oryza* species, particularly small-seeded forms, during their annual migration. In Sri Lanka a population of *O. eichingeri* grows at about 500 m on Ritigala Mountain as well as at the foot of the mountain (A.H.M. Jayasuriya, Plant Genetic Resources Center, Sri Lanka, pers. comm. 2004). It seems probable that birds migrating across the Indian Ocean from Africa landed on this rocky outcrop. The disjunct distribution of *Oryza minuta* in the Philippines and Papua New Guinea is also on a migratory route for birds from Australia to East Asia (Ackerman 2004). Migration of birds could also explain the introduction into Australia and the New World of species of the *O. sativa* and *O. officinalis* complexes prior to human migration.

More difficult to explain based on biotic long-distance dispersal is the apparent diversification over the last 2 Ma of the Australasian species *O. meridionalis* and Africa species *O. longistaminata* that both have the A genome. Other genera have disjunction between Africa and Australia. The wild relative of mungbean, *Vigna radiata* var. *sublobata*, is found in Africa and Australia, as are some *Sorghum* and *Gossypium* species. In the tribe Oryzeae, Duistermaat (1987) proposed that the African genera *Prospyrtochloa* and *Maltebrunia* were part of the Australian genus *Potomophila*. While this is not generally accepted, a multiple gene phylogenetic study has revealed close affinity between *Prospyrtochloa* and *Potomophila* (Guo and Ge 2005). These evidences point to the phylogeographic link between Africa and Australia. Perhaps the best explanation may be that these two basal AA genome *Oryza* species evolved from a now extinct widely distributed unknown proto AA genome *Oryza* species.

In historic times human migration has introduced not only the cultivated rices into new areas but also probably at the same time Asian wild rice as contaminants of rice. This would explain the variation found in wild AA genome germplasm in Australia and Latin America. A Cuban accession commonly used in research on 'wild' *Oryza* from Cuba (IRRI 100961, NIG 1169/70) repeatedly has shown genetic similarity to Asian rice rather than the Latin American AA genome species *O. glumaepatula* (e.g. Juliano et al. 1998). Thus this accession collected from a hybrid swarm population could be an historic introduction to Cuba from Asia. Humans may well have carried other wild *Oryza* on their voyages. The presence of *O. longistaminata* in Martinique, the Caribbean, can best be explained by an accidental human introduction (Vaughan 1994).

The hypothesis presented here that the current biogeography of *Oryza* species can be explained by the spread across contiguous land masses by animals, such as elephant and buffalo, is in accordance with dates when animals roamed between continents and when ancestors of current *Oryza* species are believed to have evolved. The disjunct distribution of *Oryza* species on land masses separated by oceans may best be explained by their introduction by birds and, in the historic past, by humans.

References

- Aggarwal RK, Brar DS, Nandi S, Huang N, Khush GS (1999) Phylogenetic relationships among *Oryza* species revealed by AFLP markers. *Theor Appl Genet* 98:1320–1328
- Akagi H, Yokozeki Y, Inagaki A, Fujimura T (1998) Origin and evolution of twin microsatellites in the genus *Oryza*. *Heredity* 81:187–197
- Ackerman J (2004) Cranes. *National Geographic*, <http://magma.nationalgeographic.com/ngm/0404/feature2/index.html>
- Akimoto M, Shimamoto Y, Morishima H (1997) Genetic differentiation in *O. glumaepatula* and its phylogenetic relationships with other AA genome species. *Rice Genet Newsl* 14:37–39
- Ammiraju JSS, Luo M, Goicoechea JL, et al. (2006) The *Oryza* bacterial artificial chromosome library resource: construction and analysis of 12 deep-coverage large insert BAC libraries that represent the 10 genome types of the genus *Oryza*. *Genome Res* 16:140–147
- Barbier P, Morishima H, Ishihama A (1991) Phylogenetic relationships of annual and perennial wild rice: probing by direct DNA sequencing. *Theor Appl Genet* 81:693–702
- Barkman, TJ, Chenery G, McNeal JR, et al. (2000) Independent and combined analyses of sequences from all three genomic compartments converge on the root of flowering plant phylogeny. *Proc Natl Acad Sci USA* 97:13166–13171
- Barnosky AD, Koch PL, Feranec RS, Wing SL (2004) Assessing the causes of late Pleistocene extinctions on the continents. *Science* 306:70–75
- Bremer K (2002) Early Cretaceous lineages of monocot flowering plants. *Proc Natl Acad Sci USA* 97:4707–4711
- Buntjer, JB, Otsen M, Nijman IJ, Kuiper MTR, Lenstra JA (2002) Phylogeny of bovine species based on AFLP finger printing. *Heredity* 88:46–51
- Chapman GP (1996) *The biology of grasses*. Cambridge University Press, Cambridge
- Chase MW (2004) Monocot relationships: an overview. *Am J Bot* 91:1645–1655
- Cheng C, Motohashi R, Tsuchimoto S, Fukata Y, Ohtsubo H, Ohtsubo E (2003) Polyphyletic origin of cultivated rice: based on the interspersed pattern of SINES. *Mol Biol Evol* 20:67–75

- Clayton WD, Renvoize SA (1986) Genera Graminum, grasses of the world. Kew Bull 13
- Davies JT, Barraclough TG, Chase MW, et al. (2004) Darwin's abominable mystery: insights from a supertree of the angiosperms. *Proc Natl Acad Sci USA* 101:1904–1909
- Debruyne R (2001) Molecular phylogeny of living elephants and discussion on infraspecific systematics of *Loxodonta africana* and *Elephas maximus*. *Proc Int Congr, The World of Elephants, Rome*, pp. 628–629
- Doi K, Nonomura M, Yoshimura A, Iwata N, Vaughan DA (2000) RFLP relationships of A-genome species in the genus *Oryza*. *J Fac Agr Kyushu Univ* 45:83–98
- Doyle JA (1998) Phylogeny of vascular plants. *Annu Rev Ecol Syst* 29:567–599
- Duistermaat H (1987) A revision of *Oryza* (Graminae) in Malesia and Australia. *Blumea* 32:157–193
- Feild, TS, Arens NC, Dawson TE (2003) The ancestral ecology of angiosperms: emerging perspectives from extant basal lineages. *Int J Plant Sci* 164 (Suppl 3):S129–S142
- Friedman WE (2006) Embryological evidence for developmental lability during early angiosperm evolution. *Nature* 441:337–340
- Fuller DQ (2003a) African crops in prehistoric South Asia: a critical review. In: Neumann K, Butler A, Kahlheber S (eds) Food, fuel and fields, progress in African archaeobotany. *Africa Praehistorica* 15, Heinrich-Barth-Institute, Cologne, pp. 239–271
- Fuller DQ (2003b) An agricultural perspective on Dravidian historical linguistics: archaeological crop packages, livestock and Dravidian crop vocabulary. In: Bellwood P, Renfrew C (eds) Examining the farming/language dispersal hypothesis. McDonalds Institute Monographs, Cambridge, pp. 191–213
- Gaut BS (2002) Evolutionary dynamics of grass genomes. *New Phytologist* 154:15–28
- Ge S, Li A, Lu BR, Zhang SZ, Hong DY (2002) A phylogeny of the rice tribe Oryzeae (Poaceae) based on *matK* sequence data. *Am J Bot* 89:1967–1972
- GPWG (Grass Phylogeny Working Group) (2000) A phylogeny of the grass family (Poaceae), as inferred from eight character sets. In: Jacobs SWL, Everett JE (eds) Grasses: systematics and evolution. Commonwealth Scientific and Industrial Research Organization, Collingwood, Victoria, pp. 3–7
- GPWG (Grass Phylogeny Working Group) (2001) Phylogeny and subfamilial classification of the grasses (Poaceae). *Ann MO Bot Gard* 88:373–457
- Guo YL, Ge S (2005) Molecular phylogeny of Oryzeae (Poaceae) based on DNA sequences from chloroplast, mitochondrial, and nuclear genomes. *Am J Bot* 92:1548–1558
- Hovius N, Stark CP, Tutton MA, Abbott LD (1998) Landslide-driven drainage network evolution in a pre-steady-state mountain belt; Finisterre Mountains, Papua New Guinea. *Geology* 26:1071–1074
- Iwamoto M, Nagashima H, Nagamine T, Higo H, Higo K (1999) A Tourist element in the 5'-flanking region of the catalase gene *CatA* reveals evolutionary relationships among *Oryza* species with various genome types. *Mol Gen Genet* 262:493–500
- Juliano AB, Naredo MEB, Jackson MT (1998) Taxonomic status of *Oryza glumaepatula* Steud. I. Comparative morphological studies of New World diploids and Asian AA genome species. *Genet Resour Crop Evol* 45:197–203
- Kellogg EA (1998) Relationships of cereal crops and other grasses. *Proc Natl Acad Sci USA* 95:2005–2010
- Kellogg EA (2001) Evolutionary history of the grasses. *Plant Physiol* 125:1198–1205
- Khush GS (1997) Origin, dispersal, cultivation and variation of rice. *Plant Mol Biol* 35:25–34
- Kuper R, Kröpelin S (2006) Climate-controlled Holocene occupation in the Sahara: motor of Africa's evolution. *Science* 313:803–807
- Kutzbach J, Bonan G, Foley J, Harrison SP (1996) Vegetation and soil feedbacks on the response of the African monsoon to orbital forcing in the early to middle Holocene. *Nature* 384:623–626
- Kuzoff RK, Gasser CS (2000) Recent progress in reconstructing angiosperm phylogeny. *Trends Plant Sci* 5:330–336
- Launert E (1965) A survey of the genus *Leersia* in Africa. *Senckenb Biol* 46:29–153

- Lin Z, Griffith ME, Li X, et al. (2007) Origin of seed shattering in rice (*Oryza sativa* L.). *Planta* 226:11–20
- Lolo OM, Second G (1988) Peculiar genetic characteristics of *O. rufipogon* from western India. *Rice Genet Newsl* 5:67–70
- Londo JP, Chiang YC, Hung KH, Chiang TY, Schaal B (2006) Phylogeography of Asian wild rice, *Oryza rufipogon*, reveals multiple independent domestications of cultivated rice, *Oryza sativa*. *Proc Natl Acad Sci* 103:9578–9583
- Lu BR (1999) Taxonomy of the genus *Oryza* (Poaceae): historical perspectives and current status. *IRRI Newsl* 24:4–8
- Lu BR, Ge S (2005) *Oryza coarctata*: the name that best reflects the relationships of *Porteresia coarctata* (Poaceae: Oryzeae). *Nord J Bot* 23:555–558
- Ma J, Bennetzen JL (2004) Rapid recent growth and divergence of rice nuclear genomes. *Proc Natl Acad Sci USA* 101:12404–12410
- McLoughlin S (2001) The breakup of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Aust J Bot* 49:271–300
- Ogawa T (2003) Genome research in genus *Oryza*. In: Nanda JS, Sharma SD (eds) *Monograph on genus Oryza*. Science Publishers, Enfield, New Hampshire, pp. 171–212
- Piperno DR, Sues HD (2005) Dinosaurs dined on grass. *Science* 310:1126–1128
- Prasad V, Stromberg CAE, Alimohammadian H, Sahni A (2005) Dinosaur coprolites and the early evolution of grasses and grazers. *Science* 310:1177–1180
- Pyrah GL (1969) Taxonomic and distributional studies in *Leersia* (Graminae). *Iowa State Univ J Sci* 44:215–258
- Ridley HN (1930) *Dispersal of plants throughout the world*. L. Reeve and Company, Kent
- Ritz LR, Glowatzki-Mullis ML, MacHugh DE, Gaillard C (2000) Phylogenetic analysis of the tribe Bovini using microsatellites. *Anim Genet* 31:178–185
- Roca AL, Georgiadis N, O'Brien SJ (2005) Cytonuclear genomic dissociation in African elephant species. *Nature Genet* 37:96–100
- Sanderson MJ, Thorne JL, Wikstrom N, Bremer K (2004) Molecular evidence on plant divergence times. *Am J Bot* 91:1656–1665
- Second G (1991) Molecular markers in rice systematics and the evaluation of genetic resources. In: Bajaj YPS (ed) *Biotechnology for Agriculture and Forestry*, 14: Rice. Springer, Berlin Heidelberg New York, pp 468–494
- Sharma SD (2003) Species of the genus *Oryza* and their interrelationships. In: Nanda JS, Sharma SD (eds) *Monograph on the genus Oryza*. Science Publishers, Enfield, New Hampshire, pp 73–111
- Scherban AB, Vaughan DA, Tomooka N (2000) Isolation of a new retrotransposon-like DNA and its use in analysis of diversity within the *Oryza officinalis* complex. *Genetica* 108:145–154
- Scherban AB, Vaughan, DA, Tomooka N, Kaga A (2001) Diversity in the integrase coding domain of a gypsy-like retrotransposon among wild relatives of rice in the *Oryza officinalis* complex. *Genetica* 110:43–53
- Soltis PS, Soltis DE (2004) The origin and diversification of angiosperms. *Am J Bot* 91:1614–1626
- Stromberg CAE (2005) Decoupling taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proc Natl Acad Sci USA* 102:11980–11984
- Sweeney M, McCouch S (2007) The complex history of the rice domestication. *Ann Bot* (in press)
- Sang T, Ge S (2007) The puzzle of rice domestication. *J Integrative Plant Biol* 49:760–768
- Tateoka T (1962a) Taxonomic studies of *Oryza* I. *O. latifolia* complex. *Bot Mag Tokyo* 75:418–427
- Tateoka T (1962b) Taxonomic studies of *Oryza* II. Several species complexes. *Bot Mag Tokyo* 76:165–173
- Tiffney BH (2004) Vertebrate dispersal of seed plants through time. *Ann Rev Ecol Evol Syst* 35:1–29
- Vaughan DA (1991) Biogeography of the genus *Oryza* across the Malay Archipelago. *Rice Genet Newsl* 8:73–75

- Vaughan DA (1994) The wild relatives of rice: a genetic resources handbook. International Rice Research Institute, Los Banos
- Vaughan DA (2003) Genepools of the genus *Oryza*. In: Nanda JS, Sharma SD (eds) Monograph on genus *Oryza*. Science Publishers, Enfield, New Hampshire, pp. 113–138
- Vaughan DA, Morishima H (2003) Biosystematics of the genus *Oryza*. In: Wayne Smith C, Dilday RH (eds) Rice: origin, history, technology, and production. Wiley, Hoboken, New Jersey, pp 27–65
- Vaughan DA, Sitch LA (1991) Gene flow from the jungle to farmers. *BioScience* 41:22–28
- Vaughan DA, Kadowaki K, Kaga A, Tomooka N (2005) On the phylogeny and biogeography of the genus *Oryza*. *Breed Sci* 55:113–122
- Vitte C, Panaud O (2003) Formation of Solo-LTRs through unequal homologous recombination counterbalances amplifications of LTR retrotransposons in rice, *Oryza sativa* L. *Mol Biol Evol* 20:528–540
- Vitte C, Ishii T, Lamy F, Brar D, Panaud O (2004) Genomic paleontology provides evidence for two distinct origins of Asian rice (*Oryza sativa* L.). *Mol Gen Genomics* 272:504–511
- Wang ZY, Second G, Tanksley SD (1992) Polymorphism and phylogenetic relationships among species in the genus *Oryza* determined by analysis of nuclear RFLPs. *Theor Appl Genet* 83:565–581
- Watson L, Dallwitz MJ (1992 onwards) The families of flowering plants: descriptions, illustrations, identification, and information retrieval. Version 2, June 2006, <http://delta-intkey.com>
- Zhang W, Clark LG (2000) Phylogeny and classification of the Bambusoideae (Poaceae). In: Jacobs SWL, Everett J (eds) Grasses: systematics and evolution. CSIRO, Melbourne, pp. 35–42
- Zhu Q, Ge S (2005) Phylogenetic relationships among A-genome species of the genus *Oryza* revealed by intron sequences of four nuclear genes. *New Phytol* 167:249–265