Oryza coarctata: the name that best reflects the relationships of Porteresia coarctata (Poaceae: Oryzeae)

Bao-Rong Lu and Song Ge

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Oryza coarctata is a herbaceous species that serves as an important source of germplasm for salt tolerance in rice breeding. Despite biosystematic and phylogenetic studies showing that its closest relatives are other species of Oryza, many taxonomists continue to place it in the monospecific genus Porteresia because it is morphologically and ecologically distinct from other species of Oryza. Such a treatment obscures the reality of its genetic similarities to Oryza. The authors strongly recommend returning this species to Oryza. This will have the added advantage of ensuring that all those reading about the species will immediately understand its importance to rice breeding.

B.-R. Lu, Ministry of Education Key Laboratory for Biodiversity Science and Ecological Engineering, Institute of Biodiversity Science, Fudan University, Shanghai 200433, China. E-mail: brlu@fudan.edu.cn. – S. Ge, Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China.

Introduction

The binomial system for naming plant species is a valuable tool for conveying information. question that divides many taxonomists is the nature of the information that should be conveyed. It was Linnaeus' Species plantarum (Linnaeus 1753) that lead to their universal use by botanical taxonomists. In this work Linnaeus combined the convenience of binomial system with an approach classification that made it easier for others determine where a plant belonged classification.

Linnaeus' classification relied entirely on morphological characters, so the binomials that he used conveyed information about morphological similarity. As understanding of the reasons that plants can be placed into categories increased, it became generally accepted that species in a genus were more closely related to each other than to species in other genera. "Related to" was understood to mean "genetically related" even though, in most instances, it had to be inferred from morphological and anatomical similarity. Recent years, we have seen development of molecular techniques permitting direct examination of the nucleic acids that provide the genetic blueprint for individual plants and numerical techniques for analyzing these data that reflect explicit assumptions concerning evolution.

In most instances, the new approaches reinforce or suggest minor changes to taxonomic treatments based on heuristic consideration of traditional morphological characters. There are, however, some exceptions. The perennial *Oryza coarctata* Roxb. (2n=4x=48) of the tribe Oryzeae (Poaceae) is a tufted

herbaceous species that grows in the coastal and tidal regions of India and Myanmar (Watson & Dallwitz 1988). Because of its unique ecological habitats in the mangrove locations and associated salt tolerance feature, great interest has been aroused in understanding the mechanism of its salt tolerance (Flowers et al. 1990; Farooq et al. 1996; Rangan & Swaminathan 2002). Research programs, that involve hybridization of O. coarctata with Asian cultivated rice (Oryza sativa L.), in vitro propagation of O. coarctata, and isolation of stressinduced genes that are tolerant to salt from O. coarctata, were extensively conducted as a part of the pre-breeding exploration for rice improvement (Flowers et al. 1990; Sarker et al. 1993; Latha et al. 1998). However, despite its importance as an elite genetic resource and a number of successful studies on its applied potential, the taxonomy of O. coarctata is still frequently excluded from Oryza, being placed in the monotypic genus Porteresia.

Taxonomic history of Oryza coarctata

Oryza coarctata was first described by Roxburgh in 1814. This species, and its inclusion in Oryza, was accepted by many taxonomists, including Hooker (1897),Prodoehl (1922),Roschevitz (1931),Chatterjee (1948), and Bor (1960). Griffiths (1851), however, erected the monotypic genus Sclerophyllum to accommodate O. coarctata. Tateoka (1965) subsequently discovered that this name had already been used by Gaudin in 1821 for a genus in the Compositae, therefore, Sclerophyllum coarctatum has never been a valid name for O. coarctata. He published the name Porteresia for the oryzoid

taxon, commemorating Dr Roland Portères, specialist on Oryza. Tateoka demonstrated that O. coarctata differed from other species of Oryza in its leaf anatomy and embryo morphology, two aspects of grasses that had a profound impact on taxonomic interpretation in the family during the 1950s and 1960s. Tateoka (1964) found, for example, that O. coarctata was characterized by its large caryopses, with a big embryo relative to the endosperm and with a short petiole-like attachment at the base. He later pointed out that its leaf-blades were coriaceous with prickly tuberculate margins and had a peculiar arrangement of vascular bundles that were not found in any other oryzoid grass (Tateoka 1965). On the basis of these morphological differences, he thereby proposed to remove O. coarctata from the genus Oryza and erected this species as the monotypic Porteresia coarctata (Tateoka 1965).

It is indeed evident that *O. coarctata* and other *Oryza* species differ considerably in their ecological requirements, morphology, and physiology (Table 1). Therefore, the placement of *O. coarctata* in a different genus has been widely accepted by the current taxonomists, plant breeders and geneticists, and conservationists (Chang 1985; Oka 1988; Watson & Dallwitz 1988; Tzvelev 1989; Vaughan 1994; Sarker et al. 1993; Farooq et al. 1996; Pisupati 1999; Rangan & Swaminathan 2002).

Relationships of Oryza coarctata in tribe Oryzeae

Despite the differences just discussed, studies of interspecific hybridization and molecular analyses

Table 1. A comparison of major morpho-physiological differences between Oryza coarctata and Oryza species.

Characters	O. coarctata	Oryza species
Culm	Erect	Erect to scrambling
Leaf blades	Narrowly linear	Liner or lanceolate
	Leathery	Not leathery
	Margins tuberculate	Margins not tuberculate
	Vascular bundles prominent	Main vascular bundles prominent
Caryopses	Large (>1 cm).	0.2-0.9 cm
Embryo Seed	Large relative to endosperm	Small relative to endosperm
- germination	Recalcitrant	Orthodox
- longevity	Short	Long

have demonstrated that *O. coarctata* is closely related to other species of *Oryza*. Data from interspecific hybridization have demonstrated that "Porteresia" is so far the only related genus in the tribe Oryzeae that can be successfully crossed with *Oryza* species with relative ease (Sarker et al. 1993; Farooq et al. 1996), indicating a close biosystematic relationship of "P. coarctata" with *Oryza* species. Such close affinities between "P. coarctata" and *Oryza* species were also documented in recent molecular marker (AFLP and ISSR) studies by different authors, although they did not give a proper explanation to their results in the papers (Aggarwal et al. 1999; Joshi et al. 2000).

A molecular phylogenetic study of a selected set of species in the tribe Oryzeae by sequence analysis of internal transcribed spacer (ITS) of nuclear ribosomal DNA revealed that "P. coarctata" had a close affinity to O. brachyantha and O. granulata complex of Oryza (Xie et al. 2000). A phylogenetic tree constructed based on the analysis of total chloroplast DNA restriction fragments from 20 species of Oryzeae and three species of other tribes in Poaceae (as outgroups) demonstrated evidently a three-cluster pattern of the included Oryzeae species, where all Oryza species and "P. coarctata" were included in a distinct group, and all Leersia species and species from six other related genera of the Oryzeae were separated into two independent groups (Zhang & Second 1989). In another study, the phylogeny of 23 Oryza species and one representative each from four related genera of Oryzeae (including "P. coarctata") was reconstructed by sequence analysis of two nuclear genes (Adh1 and Adh2) and one chloroplast gene (matK) (Ge et al. 1999). In the generated gene trees, "P. coarctata" was consistently embedded within the diagnosably monophyletic Oryza clade and left other related genera separated from Oryza species (Ge et al. 1999). This study further proposed that the tetraploid "P. coarctata" and O. schlechteri, another morphologically and ecologically significantly differentiated species of Oryza, shared the HHKK genomes that are closely related to the HHJJ genomes of the O. ridleyi complex. Our recent phylogenetic study based on the chloroplast gene (matK) sequences from 26 species, representing 11 genera of the tribe Oryzeae and three outgroup species, demonstrated the monophyletic origin of this tribe. It is noteworthy that the matK gene could further distinguish the Oryzeae species as two monophyletic lineages, with the first lineage consisting of species of Oryza and Leersia, where "P. coarctata" was embedded within Oryza, and another lineage including the remaining related genera of Oryzeae (Ge et al. 2002). This

finding was strongly supported by the sequence data of recent studies on the mitochondrial NAD intron (Guo & Ge 2004).

All the recent hybridization and molecular studies carried out independently by different authors have consistently confirmed a close biosystematic and phylogenetic relationship of O. coarctata with species in Oryza, although significant morphological differences are found between O. coarctata and Oryza species. The significant morphological differentiation of O. coarctata from other species in the genus Oryza provides an excellent example of divergent evolution of closely related taxa. Oryza coarctata appears to be closely related to O. brachyantha, O. granulata, and O. schlectheri, but all of these species possess substantial morphological differences. This divergent evolution can most likely be explained by the adaptive evolution of species in different ecological environments. Oryza coarctata occurs in coastal and saline areas, O. brachyantha on seasonally inundated areas of open habitats, O. granulata mainly in forests, bamboo woods, and grassy slopes of upland ecosystem, and schlectheri was found in undisturbed forests and on land slopes with sufficient moisture (Vaughan 1994). These types of ecological habitats are completely different from those occupied by other Oryza species. Species of Oryza are usually found in swampy lowlands, lagoon, and along rivers with fresh water. The adaptation to such unique environments has resulted different morphological features of e.g. O. coarctata and O. schlectheri from other Oryza species in the evolutionary process.

Taxonomic treatment

In conclusion, we strongly recommend the retention of *O. coarctata* in *Oryza*, a treatment that reflects both its phylogenetic position as revealed by cladistic analyses of molecular data and its ability to hybridize with other species of *Oryza*.

Oryza coarctata Roxb.

Hort. Beng. 87 (1814); Fl. Ind. ed. 2, II: 206 (1832).
Sclerophyllum coarctatum (Roxb.) Griff., Not. III: 8 (1851).

Porteresia coarctata Tateoka, Bull. Nat. Mus. Tokyo 8(3): 405 (1965).

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