Molecular Phylogenetics and Evolution 48 (2008) 12–22

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Phylogeny, biogeography, and ecology of *Ficus* section *Malvanthera* (Moraceae)

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ARTICLE INFO

Article history:
Received 28 June 2007
Revised 2 April 2008
Accepted 5 April 2008
Available online 14 April 2008

Keywords:
Moraceae
Ficus
Malvanthera
Phylogeny
ITS
ETS
G3pdh

ABSTRACT

We conducted the first molecular phylogenetic study of *Ficus* section *Malvanthera* (Moraceae; subgenus *Urostigma*) based on 32 *Malvanthera* accessions and seven outgroups representing other sections of *Ficus* subgenus *Urostigma*. We used DNA sequences from the nuclear ribosomal internal and external transcribed spacers (ITS and ETS), and the glyceraldehyde-3-phosphate dehydrogenase (*G3pdh*) region. Phylogenetic analysis using maximum parsimony, maximum likelihood and Bayesian methods recovered a monophyletic section *Malvanthera* to the exclusion of the rubber fig, *Ficus elastica*. The results of the phylogenetic analyses do not conform to any previously proposed taxonomic subdivision of the section and characters used for previous classification are homoplasious. Geographic distribution, however, is highly conserved and Melanesian *Malvanthera* are monophyletic. A new subdivision of section *Malvanthera* reflecting phylogenetic relationships is presented. Section *Malvanthera* likely diversified during a period of isolation in Australia and subsequently colonized New Guinea. Two Australian series are consistent with a pattern of dispersal out of rainforest habitat into drier habitats accompanied by a reduction in plant height during the transition from hemi-epiphytic trees to lithophytic trees and shrubs. In contradiction with a previous study of *Pleistodontes* phylogeny suggesting multiple changes in pollination behaviour, reconstruction of changes in pollination behaviour on *Malvanthera*, suggests only one or a few gains of active pollination within the section.

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1. Introduction

Figs (*Ficus*, Moraceae) constitute one of the largest genera of angiosperms, with almost 750 species of terrestrial trees, shrubs, hemi-epiphytes, climbers and creepers occurring in the tropics and subtropics worldwide (Berg and Corner, 2005). All species of figs share the distinctive fig inflorescence (syconium), which is the site of an obligate mutualism with pollinating fig wasps of the family Agaonidae (Cook and Rasplus, 2003). Figs are important genetic resources with high economic and nutritional value. They also play an important role in generating biodiversity in the rainforest ecosystem by setting fruits throughout the year and providing an important source of food for most fruit-eating vertebrates in the tropics (Harrison, 2005). Most insects pollinate passively, but fig wasps are one of a few cases, where active pollination behaviour has evolved (Cook and Rasplus, 2003). While most genera of pollinating wasps are active pollinators, five out of 20 genera contain both passive and active pollinators (Kjellberg et al., 2001).

Recent classification divided the genus into six subgenera based primarily on morphology (Berg, 2003). The monoecious subgenus *Urostigma*, to which section *Malvanthera* belongs, is the largest with about 280 species worldwide, most of them displaying the characteristic hemi-epiphytic habit (banyans and stranglers). *Ficus* section *Malvanthera* Corner (subg. *Urostigma*) includes 23 species of hemi-epiphytes and lithophytes producing aerial, adventitious, or creeping root systems. The section has its primary centre of diversity in Australia and a second centre in New Guinea and the Bismarck Archipelago. A few species extend eastwards into Oceania (e.g. Lord Howe Island, New Caledonia, the Solomon Islands and Vanuatu). Section *Malvanthera* includes species with two very distinct ecologies: hemi-epiphytic stranglers and free-standing trees in the rainforests of Eastern Australia and New Guinea, and lithophytic shrubs and trees occurring in more arid parts of Australia (Dixon, 2003).

The section was established by Corner (1959) who recognized 19 species characterized by features including: a slit-shaped or triradiate ostiole with all bracts descending; syconia with two or three basal bracts; reniform unilocular anthers with crescentic or transverse dehiscence; ovaries attached at the base to the receptacle or imbedded in the receptacle; a red spot at the base or the apex

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1055-7903/$ - see front matter © 2008 Elsevier Inc. All rights reserved.
doi:10.1016/j.ympev.2008.04.005

of the ovary; and a stigma that is either simple or bifid. Corner (1959) and again Berg and Corner (2005) noted the similarity between subg. *Urostigma* sections *Malvanthera* and *Galoglychia* in the inflexed apical bracts of the ostiole and internal bracts. Berg and Corner (2005) also noted that similarities in venation suggest a relationship between *Malvanthera* and the *F. benjamina* group of section *Urostigma* subsection *Conosycea*. Molecular phylogenetic studies have shown sections *Conosycea* and *Malvanthera* to be sister taxa (Rønsted et al., 2005).

Corner (1965) subdivided section *Malvanthera* into two series. *Malvanthereae* is distinguished by reniform anthers dehiscing longitudinally and crescentically. The series includes 18 species in four loosely defined subseries, *Eubracteatae*, *Hesperidiiformes*, *Malvanthereae*, and *Platypodeae* based on characters of the basal bracts and whether the ovaries are partly embedded in the receptacle or not. The monotypic series *Cyclanthereae* includes *F. sterrocarpa* from New Guinea, which has depressed-subglobose anthers (Table 1).

Chew (1989) followed Corner (1965) in treating Australian *Ficus*, whereas Australian *Malvanthera* were subsequently revised by Dixon (2001a–d, 2003), who proposed a new subdivison of the section into ser. *Malvanthereae* including species with imbricate basal bracts, and ser. *Hesperidiiformes* with valvate basal bracts (Table 1).

In treating *Ficus* of the Malesian region, Berg and Corner (2005) united the monotypic section *Stilpnophyllum* (*F. elastica*, the rubber fig) and section *Malvanthera* as subsections of an expanded section *Stilpnophyllum* based on similarities between *F. elastica* and the *Malvanthera* species in the venation of the lamina, the length of the stipules and cucullate (hood-shaped) caducous basal bracts. However, *F. elastica* is distinct from the *Malvanthera* species in the shape of the ostiole and in having anthers with separate theca and connate stipules. The Indo-Chinese origin of *F. elastica*, which is widely cultivated, also has little geographical affinity to the Australian and Melanesian *Malvanthera*. A global molecular phylogenetic study (Rønsted et al., 2005) including *F. elastica*, 12 species of *Conosycea* figs and 11 species of *Malvanthera* figs strongly suggested that *F. elastica* is a member of section *Conosycea* with a derivative morphology.

Within subsection *Malvanthera*, Berg and Corner (2005) recognised 18 species in three informal groups, based on characters of the basal bracts and ostiole shape. Berg and Corner (2005) united most of Corneś species from New Guinea (*F. augusta*, *F. hesperidiiformis*, *F. heteromeka*, *F. mafuluensis*, *F. sterrocarpa* and *F. xylosycia*)

Table 1
Historical classification of *Ficus* section *Malvanthera*

Rønsted et al. (present study, Fig. 1)	Corner (1965)	Dixon (2003)	Berg (2005)[h]
Subsect. *Malvantherae*			
F. macrophylla	Subser. *Malvanthereae*	Ser. *Malvanthereae*	Subsect. *Malvanthera* C
F. pleurocarpa	Subser. *Hesperidiiformes*	Ser. *Hesperidiiformes*	Subsect. *Malvanthera* C
Subsect. *Hesperidiiformes*			
Ser. *Hesperidiiformes*			
F. hesperidiiformis[a]	Subser. *Hesperidiiformes*	Ser. *Hesperidiiformes*	Subsect. *Malvanthera* A
F. sterrocarpa	Ser. *Cyclanthereae*	Ser. *Hesperidiiformis*	*F. hesperidiiformes*[a]
Ser. *Glandiferae*[b]			
F. baola[c]	*F. obliqua*[c]	*F. obliqua*[c]	Subsect. *Malvanthera* B
F. glandifera	Subser. *Malvanthereae*	Ser. *Hesperidiiformes*	Subsect. *Malvanthera* B
F. rhizophoriphylla	Subser. *Malvanthereae*	Ser. *Malvanthereae*	Subsect. *Malvanthera* B
Ser. *Xylosyciae*			
F. augusta	Subser. *Hesperidiiformes*	Ser. *Hesperidiiformes*	*F. hesperidiiformes*[a]
F. heteromeka	Subser. *Hesperidiiformes*	Ser. *Hesperidiiformes*	*F. hesperidiiformes*[a]
F. mafuluensis	Subser. *Hesperidiiformes*	Ser. *Hesperidiiformes*	*F. hesperidiiformes*[a]
F. xylosycia	Subser. *Hesperidiiformes*	Ser. *Hesperidiiformes*	*F. hesperidiiformis*[a]
Subsect. *Platypodeae*			
Ser. *Eubracteatae*			
F. triradiata	Subser. *Eubracteatae*	Ser. *Hesperidiiformes*	Subsect. *Malvanthera* A
Ser. *Obliquae*			
F. cerasicarpa[d]	*F. leuchotricha*[d]	Ser. *Malvanthereae*	Subsect. *Malvanthera* C
F. lilliputiana[e]	*F. brachypoda*[e]	Ser. *Malvanthereae*	Subsect. *Malvanthera* C
F. obliqua	Subser. *Platypodeae*	Ser. *Malvanthereae*	Subsect. *Malvanthera* C
F. platypoda[d]	Subser. *Platypodeae*[d]	Ser. Malvanthereae	Subsect. *Malvanthera* A
F. subpuberula	Subser. *Platypodeae*	Ser. *Malvanthereae*	Subsect. *Malvanthera* C
Ser. *Crassipeae*			
F. crassipes	Subser. *Hesperidiiformes*	Ser. *Hesperidiiformes*	Subsect. *Malvanthera* A
F. destruens	Subser. *Platypodeae*	Ser. *Malvanthereae*	Subsect. *Malvanthera* B
Ser. *Rubiginosae*			
F. atricha[f]	*F. platypoda*[f]	Ser. *Malvanthereae*	Subsect. *Malvanthera* C
F. brachypoda[f]	*F. platypoda*[f]	Ser. *Malvanthereae*	Subsect. *Malvanthera* C
F. rubiginosa[g]	Subser. *Platypodeae*	Ser. *Malvanthereae*	Subsect. *Malvanthera* C
F. watkinsiana	Subser. *Malvanthereae*	Ser. *Malvanthereae*	Subsect. *Malvanthera* C

[a] *F. hesperidiiformis* includes *F. augusta*, *F. heteromeka*, *F. mafuluensis*, *F. sterrocarpa*, and *F. xylosycia* in Bergs (2005) classification.
[b] Series *Glandiferae* possibly includes *F. baola* and *F. rhizophoriphylla* based on morphological affinities such as a slit-shaped ostiole (Berg, 2002).
[c] *F. baola* C.C. Berg was raised from *F. obliqua* (Berg 2002).
[d] *F. cerasicarpa* has affinities to *F. platypoda* (Dixon 2001a). *F. cerasicarpa* and *F. platypoda* were included in *F. leuchotricha* in Corner's classification.
[e] *F. lilliputiana* is a new species with affinities to *F. brachypoda* (Dixon 2001b).
[f] *F. atricha* and *F. brachypoda* were included in *F. platypoda* in Corner's classification.
[g] *F. baileyana* was included in *F. rubiginosa* by Dixon (2001d).
[h] *F. elastica* constituted a monotypic section *Stilpnophyllum* in Corner's classification.

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